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MORPHOLOGICAL DIVERSITY AND CLASSIFICATION OF FRUITS WITHIN THE LAMIIDS OF THE FLORA OF UKRAINE

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Background. The morphological diversity of fruits, including their gynoecial structure, has been investigated within the lamiid clade in the flora of Ukraine. The aim was to reveal distinct fruit features in this clade and compare them with other eudicots.

Materials and Methods. Fruit characteristics were extracted from numerous carpological sources. Gynoecial traits were also analyzed, including the number of carpels and ovules, ovary insertion, placentation, and vertical zonality. Carpological spectra were created for families, genera, and species of lamiids, and the species spectrum was compared with other eudicot clades.

Results and Discussion. Morphological features of the fruit were documented for 22 families, 163 genera, and 741 species of lamiids. With few exceptions, fruits are dimerous and superior, with synascidiate and symplicate zones in the ovary, often with intrusive placentas that divide the ovary into locules. Five basic fruit types were recognized within the lamiids: capsule, berry, multi-seeded pyrenarium, schizocarp, and one-seeded fruit. In Oleaceae, Plantaginaceae, and Rubiaceae, three fruit types were identified. The most widespread fruit types among lamiids are schizocarps (41.0 %) and capsules (41.9 %). The carpological spectrum of lamiids differs markedly from other eudicot clades (fabids, malvids, and caryophyllids), showing the highest proportion of schizocarpic fruits and the lowest proportion of one-seeded fruits (3 %). However, the overall rate of one-seeded enveloped diaspores in lamiids (fruits and fruit parts) is high (44 %).

Conclusions. These results align with previous findings on the narrow morphospace of lamiids in terms of gynoecium merosity, ovary insertion, and fruit type. Our data support the view of lamiids as a species-rich clade distinguished by the multiple origins of schizocarpic gynoecia and fruits, which split into four one-seeded semi-carpellary units. From an evolutionary perspective, lamiids of the flora of Ukraine exhibit



intermediate-advanced morphological features of the gynoecium and fruit: superior syncarpous ovaries that range from multi-seeded to oligo-seeded, and a high proportion of capsular and schizocarpic fruits.

Keywords: asterids, carpological spectrum, capsular fruit, gynoecium, schizocarp, seed

INTRODUCTION

Lamiids are one of two crown subclades of the asterids, along with the campanulids. They comprise eight orders and 41 families in the world's flora (Chase *et al.*, 2016); according to other data, they include nine orders (Zuntini *et al.*, 2024), 48 families, 2,534 genera, and 51,468 species (Stevens, 2001). Lamiids are considered a large clade, containing about 15 % of angiosperm species (Stull *et al.*, 2015; Alawfi & Alzahrani, 2023). The molecular phylogeny of lamiids is the most controversial among eudicots, specifically, numerous changes in taxonomy concerned the relationships between the orders and between families within the order Lamiales, in particular, as well as the scope of the families (Schäferhoff *et al.*, 2010; Refulio-Rodriguez & Olmstead, 2014; Stull *et al.*, 2015; 2018; 2020; Fonseca, 2021; Alawfi & Alzahrani, 2023).

It is currently recognized that four large orders, Boraginales Juss. ex Bercht. & J. Presl, Gentianales Juss. ex Bercht. & J. Presl, Lamiales Bromhead, and Solanales Juss. ex Bercht. & J. Presl, as well as a small order Vahliales Doweld, compose the core lamiids, while Cardiopteridales Takht., Icaciniales Tiegh., Garryales Mart. and Aquifoliales Senft are regarded as basal lamiids (Zhang *et al.* 2020; Zhang & Ma, 2024; Zuntini *et al.*, 2024). Most lamiid orders show the highest diversification rates among angiosperms. Currently, the relationships between the orders become more and more supported (Zhang *et al.*, 2020; Fonseca, 2021; Alawfi & Alzahrani, 2023; Zhang & Ma, 2024; Zuntini *et al.*, 2024). However, the placement of some basal orders is still unresolved, and the trends of morphological diversification are not completely elucidated (Stull *et al.*, 2018; Zhang *et al.*, 2020; López-Martínez *et al.*, 2024).

In recent years, some comprehensive analyses of the carpel and fruit evolution were conducted, where the trends of morphological diversification within main the clades of angiosperms were considered (de Souza, 2022; Liu *et al.*, 2023; López-Martínez *et al.*, 2024; Xiang *et al.*, 2024; Ahn, *et al.*, 2025). The objectives of the present study were to conduct the inventory of carpological characteristics of lamiid species in the Ukrainian flora, reveal the distinct features of the gynoecium and fruit in this, and subsequently compare them with those of other eudicots.

MATERIALS AND METHODS

For the inventory of fruit types of the lamiids of the flora of Ukraine, we analyzed literature data and compiled an annotated list of fruit types for each family, taking into account the diversity of fruits within families. Families were delimited according to POWO (2026) and presented in alphabetical order. In the flora of Ukraine, 22 families from six orders of lamiids have been referred – Aquifoliales (Aquifoliaceae Bercht. & J.Presl), Boraginales (Boraginaceae Juss.), Garryales (Eucommiaceae Engl.), Gentianales (Apocynaceae Juss., Gentianaceae Juss. and Rubiaceae Juss.), Lamiales (Lamiaceae Martinov, Bignoniaceae Juss., Lentibulariaceae Rich., Linderniaceae Borsch et al., Martyniaceae Horan., Oleaceae Hoffmanns. & Link, Mazaceae Reveal, Orobanchaceae Vent.,

Paulowniaceae Nakai, Pedaliaceae R.Br., Phrymaceae Schauer, Plantaginaceae Juss., Scrophulariaceae Juss., Verbenaceae J.St.-Hil.), and Solanales (Solanaceae Juss. and Convolvulaceae Juss.), according to currently accepted family compositions and placement in the orders (Chase *et al.*, 2016; Vynokurov *et al.*, 2024). Among them, Aquifoliaceae, Bignoniaceae, Eucommiaceae, Paulowniaceae, Pedaliaceae, and Phrymaceae are presented only in the culture.

The extent of genera and species was determined based on the Vynokurov *et al.* (2024) and updated in accordance with other taxonomic sources (Fedoronchuk, 2022; 2023; 2024; Fedoronchuk & Shyian, 2025). Family richness was estimated including cultivated species, while excluding extinct taxa, hybrids, and sub-species. For each family, we indicated the fruit names and characteristics, along with the data on gynoecium structure (the number of carpels and ovules, carpel fusion, placentation, vertical zonality of the ovary, and other features). Based on the annotated list, each fruit was assigned to one of the basic types defined in A. Odintsova (2023). These types were subsequently used for constructing carpological spectra.

RESULTS

The morphological features of the fruit have been referred to 22 families, 163 genera, and 741 species of lamiids (**Table 1**). The ovary is superior in most lamiids, except Rubiaceae and, probably, *Hippuris vulgaris*. For some families (e.g., Boraginaceae, Lamiaceae, Solanaceae, etc.), the structure of the gynoecium and fruit has been widely used in taxonomy at infrafamilial levels (see **Annotations**). Characters of the fruit in the former Scrophulariaceae s.l. are widely applied for the taxonomy of currently recognized families Scrophulariaceae s.str., Orobanchaceae, and Plantaginaceae (Hartl, 1956; Juan *et al.*, 1997a; 2000; Fischer, 2004b; Mourad *et al.*, 2015).

Annotations to families' carpological characteristics

Apocynaceae Juss. Splitting fruit is composed of two dehiscent follicles (bi-follicle, double-follicle); carpels are connected postgenitally at anthesis and detach at post-anthesis (Endress *et al.*, 2018). Ovules are attached to the linear ventral placenta (Schumann, 1897a,b). In *Asclepias syriaca* L., carpels decline during the development from upright to horizontal position (**Fig. 1A, B**).

Aquifoliaceae Bercht. & J. Presl (*Ilex aquifolium* L.). Fruit is a pyrenarium with four to six stones, red colored, with a terminal style. Ovary is isomerous to the corolla, ovules are apically-axile (Loizeau *et al.*, 2016).

Bignoniaceae Juss. (*Campsis* Lour. and *Catalpa* Scop.). Capsule dehisces with dorsal and septifragal slits onto two deciduous valves; the thin septum bearing seeds is persistent (Schumann, 1895; Fischer *et al.*, 2004a).

Boraginaceae Juss. Two types of fruit are revealed: schizocarp (A) and capsule (B). The ovary is bulged during early pre-anthesis, the style is gynobasic, except *Heliotropium* L., *Heliotropium sibiricum* (L.) J.I.M. Melo and *Phacelia tanacetifolia* Benth. The inner gynoecium structure is strongly deformed during development due to apical septa in the symplicate zone, imitating the synascidiate zone; placentas are parietal (Hartl, 1962; Hilger, 1992).

A. The fruit is a microbasarium – a schizocarp, split into four semi-carpellary mericarps (nutlets, mericarpids, or eremocarps) or “coenobium of four erems” (Brisseau-Mirbel, 1815). Locules are biovulate, divided longitudinally by false basal and apical

septa into two halves each (in *German*, die Klausen) (Eichler, 1875). Eremis attach to the conical **gynobasis**, which is considered a central part of the gynoecium or receptacle. The lower part of the gynobasis forms a nectary disc; the middle part of the gynobasis between erems is a **columella**. After erem falling, on the gynobasis remains the scar named **areole**, while the scar on erem is named **cicatrix** (Hilger, 2014; Weigend *et al.*, 2016). In *Anchusa* L., the base of erem forms elaiosoma (Roth, 1977).

Table 1. The main morphological characteristics of fruits within lamiids of the flora of Ukraine

No	Family	Genera/ species number	Ovule number per carpel	Basic fruit types according to A. Odintsova (2023)
1.	Apocynaceae	7/23	many	schizocarp
2.	Aquifoliaceae	1/1	1	multi-seeded pyrenarium
3.	Bignoniaceae	2/6	many	capsule
4.	Boraginaceae	32/100	2	capsule; schizocarp
5.	Convolvulaceae	4/27	2	capsule
6.	Eucommiaceae	1/1	2	one-seeded fruit
7.	Gentianaceae	6/23	many	capsule
8.	Lamiaceae	37/147	2	schizocarp; one-seeded fruit
9.	Lentibulariaceae	2/8	many	capsule
10.	Linderniaceae	1/1	many	capsule
11.	Martyniaceae	1/1	many	capsule
12.	Mazaceae	1/1	many	capsule
13.	Oleaceae	10/35	2	capsule; berry; one-seeded fruit
14.	Orobanchaceae	14/106	many, 2	capsule; one-seeded fruit
15.	Paulowniaceae	1/1	many	capsule
16.	Pedaliaceae	1/1	many	capsule
17.	Phrymaceae	1/1	many	capsule
18.	Plantaginaceae	13/119	many, 2, 1	capsule; schizocarp; one-seeded fruit
19.	Rubiaceae	9/65	1	berry; schizocarp; one-seeded fruit
20.	Scrophulariaceae	4/36	many	capsule
21.	Solanaceae	13/32	many	capsule, berry
22.	Verbenaceae	2/6	2	schizocarp

A1. Schizocarp is tetraeremous, covered with a calyx – most species; sometimes it is heterocarpic (Weigend *et al.*, 2016). In some *Heliotropium* species, the ovary is entire, erems detach by septicial slits (Hilger, 1992; Diane *et al.*, 2016; Jeiter *et al.*, 2018).

A2. Schizocarp is dieremous with two persistent two-seeded dierems (whole carpels, two carpids, double nutlets) – *Cerintho minor* L. (Hilger, 1992; Weigend *et al.*, 2016). Sometimes, two heterocarpic dierems develop simultaneously, forming so-called “syn-mericarpids” (Hilger, 1992).

A3. Schizocarp is pseudomonomerous, with 1–2 persistent erems, composed of a single abaxial carpel (Hilger, 1984; Weigend *et al.*, 2016). – *Rochelia retorta* (Pall.) Lipsky.

A4. Schisocarp is split into two mericarps – *Heliotropium sibiricum* (L.) J.I.M. Melo.

B. Loculicidal capsule with 1–4 seeds – *Phacelia tanacetifolia* Benth. (Hofmann *et al.*, 2016). The ovary is unilocular with intrusive parietal placentas (Hofmann, 1999; Vasile *et al.*, 2021; 2022).

Convolvulaceae Juss. The ovary is usually bilocular. However, in *Ipomoea* L. the ovary is 3–5-locular, while in *Calystegia* R. Br., it is unilocular or incompletely bilocular (Eichler, 1875). Capsule in *Calystegia* is covered by calyx or bracteoles (Peter, 1891). Fruit with four seeds, dehisces by two or four valves. In *Calystegia*, the fruit opens by a hippocrepiform slit from the top to the bottom. In *Cuscuta* L., placentas are parietal, fused in the center, and stylodia are free. Four types of fruit were found in *Cuscuta* (Ho, Costea, 2018): (1) with circumscissile dehiscence through a lid; (2) indehiscent; (3a) rupturing due to undeveloped endocarp, and (3b) rupturing by longitudinal basal slits due to compression. In indehiscent fruits, the interstylar aperture develops, a perforate thickening around the stylodia.

Eucommiaceae Engl. (*Eucommia ulmoides* Oliv.). The family is represented by a single species, having the dry samara fruit (Zhang, 2016). The gynoecium is bicarpellate, pseudomonomerous; the ovary is unilocular, with two pendulous ovules (placentation is apical), one of which is aborted (Guo *et al.*, 2025). The ovary insertion (superior/inferior) is not applicable due to the lack of a perianth (Endress, 2010).

Gentianaceae Juss. The capsule is unilocular, composed of postgenitally fused carpels, septicidally dehiscent into two valves. Placentas are parietal, intrusive (Struwe, Pringle, 2018).

Lamiaceae Martinov (incl. *Vitex agnus-castus* L. and *Clerodendrum bungei* Steud., which were formerly placed in Verbenaceae). The fruit is a coenobium composed of four erems (A); a pseudotetralocular fruit covered with a calyx (Harley *et al.*, 2004), or a pyrenarium (B). In the anatomical structure of the fruit wall, mucilaginous cells in the exocarp, a cristalliferous layer, and a lignified inner layer in the mesocarp, as well as an unlignified endocarp, are evident (Roth, 1977).

A. Coenobium with gynobasic style and nectary discus – most species of Lamiaceae (Briquet, 1897b; Wojciechowska, 1966). Placentation is parietal (Hartl, 1962) or treated as intermediate between parietal and axile (Sharman, Singh, 1982). In *Clerodendrum*, the ovary is slightly lobed, the style is almost terminal; the fruit is drupaceous with four stones (Bocquillon, 1861–1862; Briquet, 1897a). No information on dispersal unit in this species (the whole fruit or separated eremes) was found.

B. Pyrenarium with one tetralocular stone, with a single seed per locule. Such a type of fruit is represented in *Vitex agnus-castus* L. The ovary is entire; the style is terminal (Bocquillon, 1861–1862; Briquet, 1897a; Harley *et al.*, 2004). Fruits are often one-seeded (Godley, 1971), which is why I classify this fruit as one-seeded, although the ovule and carpel number correspond to the gynoecium structure of *Lamiaceae* and *Verbenaceae*, to which the genus *Vitex* L. formerly belonged.

Lentibulariaceae Rich. The capsule is unilocular, lysicarpous (Fischer *et al.*, 2004b); the placenta is free-central, fleshy (Eichler, 1875; Kamienski, 1895); the calyx and style are persistent. In *Utricularia* L., the capsule is valvate, with septicidal dehiscence, sometimes rupturing or indehiscent (Kamienski, 1895; Taylor, 1977).

Linderniaceae Borsch, Kai Müll. & Eb. Fisch. (*Lindernia procumbens* (Krock.) Borbás). In this species, the capsule is hemi-lysicarpous, septicidal (Fischer, 2004).

Martyniaceae Horan. (*Proboscidae louisianica* (Mill.) Thell.). In this family, fruit is a paracarpous, dorsally dehiscent capsule with T-shaped placentas (Ihlenfeld, 2004a). Fruit structure is unique – the apical part of the ovary forms a long, enrolled beak, which divides into two halves (“horns” or “claws”).

Mazaceae Reveal. (*Dodartia orientalis* L.). The species is characterized by a syncarpous, loculicidal or subindehiscent capsule (Fischer, 2004).

Oleaceae Hoffmanns. & Link. The ovary is bilocular, the placenta is axile, located in the middle height of the ovary; only one of the two ovules often develops a seed (Eichler, 1875). Three fruit types are revealed.

A. Capsule dorsiventral, few-seeded occurs in *Syringa* L., *Forsythia* Vahl (Knoblauch, 1895). In *S. vulgaris* L., the capsule dehisces by two T-shaped valves (**Fig. 1C**).

B. Berry with 1–4 seeds occurs in *Ligustrum vulgare* L. (**Fig. 1D,E**) and species of *Jasminum* L. In *Jasminum*, the fruit is divided into two “mericarps” (didymous berry), only one of which develops to ripening (Green, 2004).

C. One-seeded fruit with a pendent seed occurs in the rest of the genera. In *Chionanthus* L., *Olea* L., *Osmanthus* Lour. and *Phillyrea* L., the fruit is a one-seeded pyrenarium with a hard stone. In *Fontanesia phillyraeoides* Labill and *Fraxinus* Tourn ex L., the fruit is a samara.

Orobanchaceae Vent. In the family, the ovary with synascidiate and symplicate zones with massive bilobate placentas is typical (Fischer, 2004). In *Melampyrum* L. (15 species) and *Tozzia* L., only two ovules occur per carpel (Wettstein, 1895). Most species have capsular fruits (A), except *Tozzia* with a one-seeded fruit (B).

A. Capsule is covered with a calyx, dorsi-ventrally dehiscent, in most of Orobanchaceae species (Fischer, 2004). In *Lathraea squamaria* L. and *Orobanche* L., the capsule is unilocular, fleshy, dorsally dehiscent, with parietal placentas (Beck von Mannagetta, 1895; Heinricher, 1892). Dorsal grooves of *Lathraea squamaria* fruit are evident in the pre-anthetic stage (**Fig. 1F–H**). Most species have numerous (100+) dust-like seeds.

B. One-seeded drupaceous fruit, enveloped in a calyx – *Tozzia alpina* subsp. *carpathica* (Wof.) Pawl. Three of four ovules degenerate during development (Fischer, 2004).

Paulowniaceae Nakai. (*Paulownia tomentosa* (Thunb.) Steud.). The fruit is a syncarpous loculicidal capsule (Fischer, 2004). According to the present concept, the dehiscence is dorsiventral, with two deciduous valves.

Pedaliaceae R. Br. This family in Ukraine is represented by cultivated *Sesamum indicum* L. The capsule is syncarpous, with additional septa and a beak; incompletely loculicidally dehiscent (Ihlenfeld, 2004b).

Phrymaceae Schauer. (*Erythranthe guttata* (DC.) G.L.Nesom). The capsule is syncarpous, loculicidal, with an enlarged calyx (Fischer, 2004).

Plantaginaceae Juss. Various fruits appearing in this family can be classified into three types, which are described below.

A. Bilocular capsule with axile placentation and various modes of dehiscence:

A1. Circumscissile capsule with additional septifragal slits – *Plantago* L. (Schwarzbach, 2004); fruit is a few-seeded pyxidium, with a very deep lid and deciduous seeds (Harms, Reiche, 1895) (**Fig. 2A**).

A2. Capsule with dorsal dehiscence – *Veronica* L. (Fischer, 2004).

A3. Capsule with 2–3 subapical pores having irregular, valvate framing. Such a kind of fruit is present in the former Antirrhinaceae Pers. family, also considered as a tribe

Antirrhineae Dumort. of Plantaginaceae (*Anarrhinum* Desf., *Antirrhinum* L., *Chaenorhinum* (DC.) Rchb., *Cymbalaria* Hill., *Kickxia* Dumort., *Linaria* Mill., and *Misopates* Raf.) (Juan *et al.*, 1996; 1997b; 1999; Jachula *et al.*, 2018). In *Linaria vulgaris* Mill., in each locule, two openings are formed by several longitudinal apical slits (**Fig. 2B**).

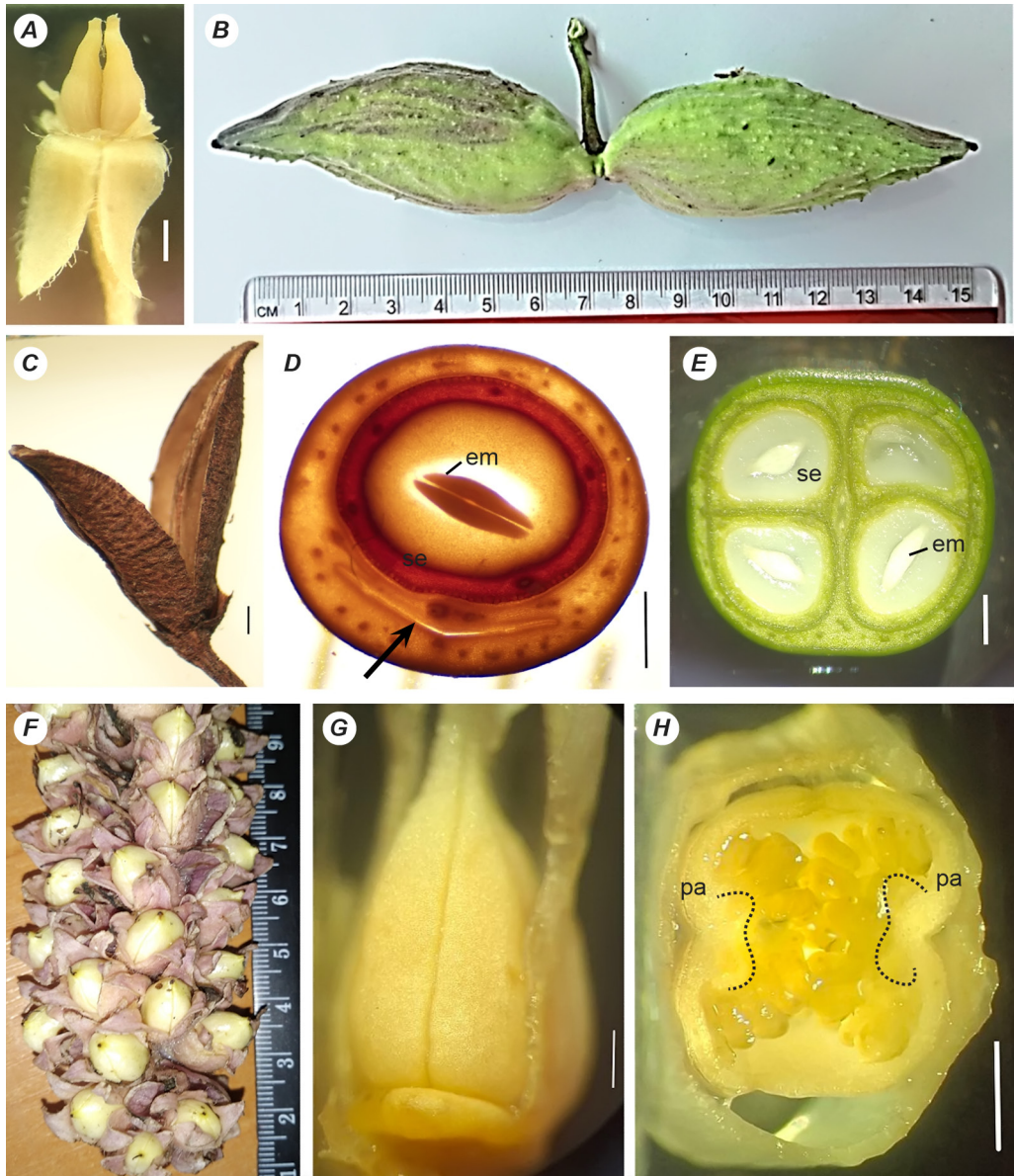


Fig. 1. Gynoecium and fruit structure in lamiid families Apocynaceae, Oleaceae, Orobanchaceae: *Asclepias syriaca* pre-anthetic gynoecium (**A**) and fruit (**B**), *Syringa vulgaris*, dorsally dehiscent fruit (**C**), *Ligustrum vulgare* transversal section of one-seeded (**D**) and four-seeded berry (**E**), in **D** sterile locule is marked with an arrow; *Lathraea squamaria* L., fruiting inflorescence (**F**), anthetic ovary with dorsal groove (**G**) and transversal section of unilocular ovary with parietale placentas (pa) (**H**); em – embryo, se – seed. Scale bar 1 mm

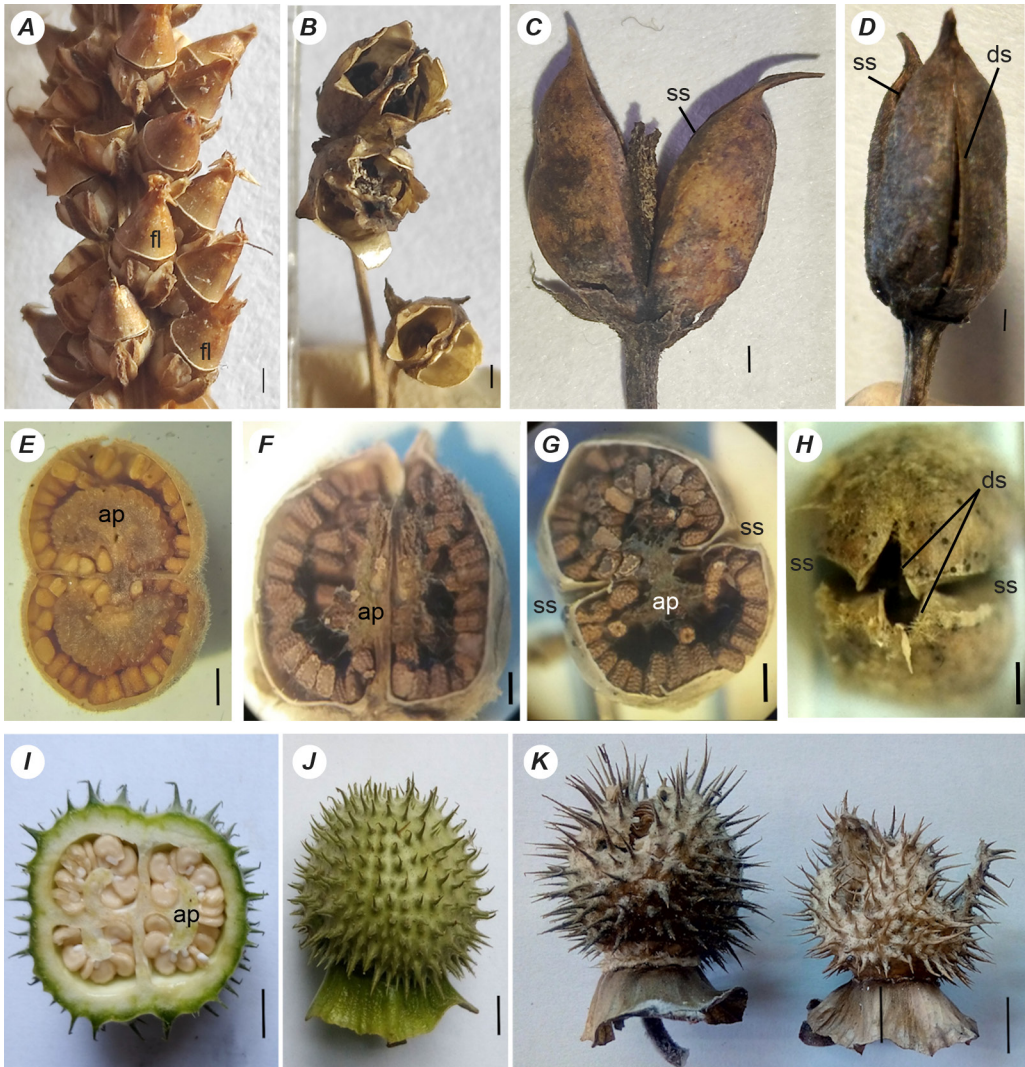


Fig. 2. Gynoecium and fruit structure in lamiid families Plantaginaceae, Scrophulariaceae, Solanaceae: *Plantago major* L., fruiting inflorescence at the dehiscence stage, fruit lids (fl) are visible (**A**), *Linaria vulgaris* Mill., opened fruits (**B**), *Digitalis grandiflora* Mill., bivalvate opened fruit with placental region between valves (**C**), dorsal slits form after fruit drying (**D**), transversal section of the fruit (**E**); *Verbascum phlomoides* L., dehiscing fruit in radial section (**F**), transversal section (**G**), viewed from above (**H**); *Datura innoxia* Mill., transversal section of the fruit (**I**), unripe fruit at final size (**J**), opened fruits (**K**); ap – axile placenta, ds – dorsal slit, ss – septicidal slit. Scale bar 1 mm (**A–H**), 1 cm (**I–K**)

A4. Septicidal capsule – *Digitalis* L. (Wettstein, 1895; Juan *et al.*, 1998). In *Digitalis grandiflora* Mill., fruit opens with septicidal and dorsal slits, then (**Fig. 2C,D**), a central column with placentas detach from the valves by septifragal slits (**Fig. 2E**).

B. Schizocarp splitting into four drupaceous erems (Hegelmaier, 1864; Erbar, Leins, 2004) – *Callitriche* L. The gynoecium structure is similar to that in Lamiaceae, with pendulous ovules (Eichler, 1878).

C. One-seeded fruit, derived from the pseudomonomerous (dimerous) uni-ovulate gynoecium with a pendulous ovule, occurs in *Globularia trichosantha* Fisch. et C.A. Mey. and *Hippuris vulgaris* L. In *Globularia trichosantha* the ovary is superior; the fruit is a thin-walled nut, covered with a calyx, with two unequal stigmatic lobes (Eichler, 1875: Fig. 124B). In *Hippuris vulgaris*, only the anterior carpel developed (Eichler, 1878: Fig. 193, p. 466); the ovary is considered to be inferior, but the perigonium is lacking; the fruit is drupaceous (Leins, Erbar, 2004).

Rubiaceae Juss. Fruits are various, classified into three types; all representatives possess one-seeded undehiscent carpels.

A. Dry schizocarp, di-achene or achenarium occurs in most of the genera. The fruit wall is thin, unligified (Salazar-Duque *et al.*, 2021). Ovary is inferior, bilocular (Eichler, 1875).

B. One-seeded pyrenarium with thickened pedicel, serving as an elaiosoma, is found in *Theligonum cynocrambe* L. In this species, a unique pseudomonomerous gynoecium with a gynobasic style is formed by shifting the style from apical to lateral position during the flower development (Eichler, 1878; Wunderlich, 1971). The seed is basal (Eichler, 1878).

C. Berry-like fruit with a seed coat adnated to the fruit wall occurs in *Rubia tatarica* (Trevir.) F. Schmidt and *R. tinctorum* L. (Schumann, 1897c).

Scrophulariaceae Juss. The fruit is a valvate capsule (Fischer, 2004). The ovary is bilocular, the placenta is axile (Eichler, 1875), persistent after valve detachment (Wettstein, 1895). In the ovary, synascidiate and symplicates zones occur at various rates (Hartl, 1956; Fischer, 2004), sometimes with apical septa (Hartl, 1962). In *Verbascum* L., the capsule is dorso-septifragal dehiscent (Juan *et al.*, 1997a). In *V. phlomoides* L., dorsal slit appear at the top of the capsule along with septicidal and septifragal slits (**Fig. 2F–H**). In *Scrophularia* Tourn. ex L., the capsule is hemi-lysicarpous (septa present only in the base of the ovary), dehiscent septicidally (septicidally-septifragal according to Fischer, 2004). In *Limosella* L., the capsule is incompletely septicidally dehiscent or indehiscent (Wettstein, 1895), while in *Buddleja* L., it is septicidally dehiscent (Oxelman *et al.*, 2004).

Solanaceae Juss. Fruits are multilocular, capsules (A) or berries (B); placentation is axile (Eichler, 1875; Knapp, 2002; Pabón-Mora & Litt, 2011; Barboza *et al.*, 2016).

A. Bilocular capsule with intrusive placentas is characteristic of most species. Capsule dehisces with septicidal-dorsal (*Datura* L.), septicidal-septifragal (*Nicotiana* L.), or circumscissile slits (*Hyoscyamus* Tourn. ex L., *Scopolia* Jacq.). In *Datura innoxia* Mill., the ovary is partly tetralocular due to the presence of false septa (**Fig. 2I**); the calyx is drying and falling out along a circular slit, leaving a short collar surrounding the ovary (**Fig. 2J**) (Barboza *et al.*, 2016). In fact, in *D. innoxia*, the dehiscence is incomplete, resulting in the formation of four lobes; it also tends to be irregular (**Fig. 2K**). The capsule is initially fleshy and becomes dry later during development (Pabón-Mora & Litt, 2011), thus the fruit is supposed to be intermediate between a capsule and a berry, a semicapsule (Roth, 1977).

B. Berry is multi-seeded or few-seeded, red or black colored, sometimes with an inflated calyx (*Alkekengi* Mill., *Nicandra* Adans., *Physalis* L.), with enlarged placentas; it appears in most of the Solanoideae species, including the *Atropa* L., *Capsicum* L., *Solanum* L., *Lycium barbarum* L. In *Nicandra*, the ovary is 4–5-locular, sometimes designated as an irregularly dehiscent capsule (Roth, 1977).

Verbenaceae J. St.-Hil. Fruit is a dry schizocarp with four one-seeded fruitlets, entitled as a coenobium of four erems (Sanders, 2001; Atkin, 2004). The style is terminal, the ovary is not bulged, the placentation is subapical, derived from axile. In *Aloysia citrodora* Paláu, only the abaxial carpel developed, split into two erems (Atkin, 2004).

DISCUSSION

Gynoecium morphological structure within lamiids. According to present data, the number of carpels within lamiids is constantly two, with few exceptions (*Ilex aquifolium*, *Ipomoea*, and *Nicandra physalodes*). Gynoecium is syncarpous, multi-locular (most families) or lysicarpous (hemilyscarpous) in Lentibulariaceae, Linderniaceae, some Scrophulariaceae; sometimes it is typically paracarpous (unilocular with parietal placentation) – in Gentianaceae, *Phacelia tanacetifolia* (Boraginaceae), *Proboscidea louisianica* (Martyniaceae), *Orobanche* and *Lathraea squamaria* (Orobanchaceae). In most syncarpous ovaries, both vertical zones occur: synascidiate and symplicate. The latter is often with intrusive placentas, which secondarily divide the ovary into locules. Carpels are multi-ovulate in 481 species (65 %); in other species, the ovule number per carpel is two or one. The pseudomonomerous gynoecium was referred in four species, *Eucommia ulmoides*, *Globularia trichosantha*, *Hippuris vulgaris*, and *Theligonum cynocrambe*. The other one-seeded fruits develop from the bilocular syncarpous ovaries with bi-ovulate locules (*Olea*, *Fraxinus*, *Tozzia*, *Vitex*, etc.).

Basic fruit types within lamiids. According to our previously approved approach (Odintsova, 2023; 2025), five basic fruit types have been found within lamiids of the flora of Ukraine (**Table 2**): capsule, berry, multi-seeded pyrenarium, schizocarp, and one-seeded fruit. Within most families, a single fruit type has been revealed. There are also families with one dominant fruit type and a few taxa with another fruit type: Boraginaceae, Lamiaceae, Orobanchaceae, and Solanaceae. The most diverse families by fruit type were Oleaceae (capsule, berry, and one-seeded fruit), Plantaginaceae (capsule, schizocarp, and one-seeded fruit), and Rubiaceae (berry, schizocarp, and one-seeded fruit). The capsular fruits are found in early branching lamiids and within Boraginales (Weigend *et al.*, 2013) and could be synapomorphic for Lamianae clade ([Lamiales + Solanales] + Vahliales), while drupaceous fruit (pyrenarium) is considered to be the ancestral state for lamiids as a clade (Stull *et al.*, 2015, 2018).

Table 2. Distribution of the basic fruit types in families of lamiids of the flora of Ukraine

Basic fruit type	Families
Capsule	Bignoniaceae, Boraginaceae (<i>Phacelia</i>), Convolvulaceae, Gentianaceae, Lentibulariaceae, Linderniaceae, Martyniaceae, Mazaceae, Oleaceae (<i>Forsythia</i> , <i>Syringa</i>), Orobanchaceae p.m.p., Paulowniaceae, Pedaliaceae, Phrymaceae, Plantaginaceae p.m.p., Scrophulariaceae, Solanaceae p.p.
Berry	Oleaceae (<i>Jasminum</i> , <i>Ligustrum</i>), Solanaceae p.p., Rubiaceae (<i>Rubia</i>)
Multi-seeded pyrenarium	Aquifoliaceae
Schizocarp	Apocynaceae, Boraginaceae p.m.p., Lamiaceae p.m.p., Plantaginaceae (<i>Callitriche</i>), Rubiaceae p.m.p., Verbenaceae
One-seeded fruit	Eucommiaceae, Lamiaceae (<i>Vitex</i>), Oleaceae p.p., Orobanchaceae (<i>Tozzia</i>), Plantaginaceae (<i>Hippuris</i> , <i>Globularia</i>), Rubiaceae (<i>Theligonum</i>)

Capsules of lamiids were found in 16 families; they are syncarpous or paracarpous, multi-seeded or oligo-seeded, superior, and differently dehiscent. The dehiscence of fruit in most cases is combined with two or three kinds of slits. Most often, dorsal slits are formed (Bignoniaceae, Boraginaceae (*Phacelia tanacetifolia*), Martyniaceae, Mazaceae, Oleaceae, Orobanchaceae, Paulowniaceae, Pedaliaceae, Phrymaceae, and Plantaginaceae (*Veronica*). Septicidal slits are formed in Gentianaceae, Lentibulariaceae, Linderniaceae, *Digitalis* (Plantaginaceae), *Datura* (Solanaceae), Scrophulariaceae. Septifragal slits are always formed in addition to other slits (Bignoniaceae, *Plantago*, *Digitalis*, and Scrophulariaceae). Valvate pores in the fruit wall are formed in *Calystegia* and in the tribe Antirrhineae of Plantaginaceae. Circumscissile dehiscence through a lid (the fruit is a true pyxidium) is characteristic for *Plantago*, *Hyoscyamus*, *Scopolia*, and some *Cuscuta* species.

Berry within lamiids is a syncarpous fruit with low (Oleaceae, Rubiaceae) or high (Solanaceae) seed number. It is found in a few taxa of three families only, in which the other fruit types dominate. **Multi-seeded pyrenarium** is an exceptional fruit type in lamiids studied. It is found only in *Ilex aquifolium*.

Schizocarps within lamiids are found in six families; they are usually dry and vary in structure. Three kinds of schizocarps have been revealed: 1) dehiscent and multi-seeded bi-follicle (Apocynaceae); 2) coenobium of four erems (Lamiaceae, Boraginaceae, some Plantaginaceae, Verbenaceae); 3) inferior bi-achene (Rubiaceae). Dehiscent schizocarp in Apocynaceae is regarded as a secondary apocarpous fruit, related to the postgenital connection of carpels at the flowering stage (Endress, 2018). It is not a typical case of schizocarpy and resembles the capsular fruit as the dispersal unit in both cases is a naked seed.

Dimerous superior coenobium in four families of lamiids has a convergent or parallel origin that is supported by anatomical, micromorphological, and molecular evidence (Wagstaff & Olmstead, 1997). The precondition for the formation of such fruit is a low carpel and ovule number, as well as similar needs of herbaceous plants for dispersion by various vectors. Coenobium is characterized by the common specific pre-anthetic ovary structure – locules divided into one-seeded halves by false septa, gynobasic style (except for Verbenaceae), nectary discus beneath locules. This structure provides the absence of septicidal splitting of the fruitlets (erems are formed as distinct units *ab initio*). Anatomically, the schizocarpic coenobium is most similar to tetra-seeded pyrenarium. Schizocarp in Rubiaceae has quite a different structure: there is a single ovule in a locule, the fruit wall is not drupaceous, the ovary is inferior, the fruit is split through septicidal slits between locules.

One-seeded fruits are found in six families of lamiids (**Table 2**). They can be one-seeded pyrenaria (*Olea*, *Tozzia*, *Theligonum*, *Hippuris*, and *Vitex*), samaras (*Eucommia* and *Fraxinus*) or thin-walled nutlets (*Globularia*). True drupaceous, endozoochorous fruits are found only in *Olea* and *Vitex*. In *Vitex agnus-castus*, the fruit is intermediate between one-seeded and multi-seeded pyrenarium with a single tetralocular pyrene (stone), having 1–4 seeds inside. Here, the fruit type is recognized as a one-seeded fruit because all seeds are kept in a common container and cannot be dispersed independently.

Carpological spectra of lamiids and other eudicots. According to fruit types detected for all genera and species of 22 families of lamiids in the flora of Ukraine (Tables 1, 2), the quantitative estimation of fruit rates has been conducted. The most species-rich families (with more than 100 species) of lamiids in the flora of Ukraine are Boraginaceae, Lamiaceae, Orobanchaceae, and Plantaginaceae. Two of them have the dominant fruit-type capsules, while the other two have schizocarps. Such a taxonomic composition of lamiids in the flora of Ukraine determines the carpological spectra. The most widespread fruit type across lamiid families is the capsule (Fig. 3A). However, at the genus taxonomic level, schizocarps are most widespread; at the species level, capsular and schizocarpic fruits are almost equally represented, capsular fruits 41.9 % and schizocarps 41.0 % (Fig. 3 B,C). The other fruit types have minute spreading, less than 5 % of the general species diversity each (Table 3).

Table 3. Distribution of the basic fruit types in four clades of eudicots of the flora of Ukraine

Fruit type	Clade		Fabids		Malvids		Caryophyllids		Lamiids	
	species	%	species	%	species	%	species	%	species	%
Aggregate fruit	220	19.7	0	0	0	0	0	0	0	0
Multi-seeded monocarp	342	30.6	0	0	0	0	0	0	0	0
Capsule	240	21.5	359	71.7	247	47.5	349	41.9		
Berry	28	2.5	7	1.4	4	0.8	26	3.1		
Schizocarp	0	0.0	54	10.8	0	0.0	341	41.0		
Multi-seeded pyrenarium	69	6.2	3	0.6	0	0.0	1	0.1		
One-seeded fruit	217	19.4	78	15.6	269	51.7	24	2.9		
Total	1116	100	501	100	520	100	741	100		

Note: data for subclades fabids and malvids obtained from A. Odintsova (2023); for caryophyllids – from A. Odintsova (2025), for lamiids – first published in this article

The species' carpological spectrum of lamiids was compared with the spectra for the other investigated eudicot clades within the flora of Ukraine, rosids, and caryophyllids (Odintsova, 2023; 2025). For more comparable scope of the clades, rosids were divided into two sub-clades, fabids and malvids, with 1116 and 501 species correspondingly. For the first time, a different composition and rates of fruit types were quantitatively detected between four clades (Fig. 3D). For fabids, six fruit types were found, for malvids and lamiids – five fruit types, and three fruit types were revealed within caryophyllids. About 50 % of fabid species possess apocarpous fruits (aggregate and multi-seeded monocarps), while in the other clades, no apocarpous fruits were found (except a few cases of secondary apocarpy).

According to the generally recognized evolutionary trend from multi-carpellar and multi-seeded fruits to one-seeded fruits in angiosperms (Roth, 1977; Xiang *et al.*, 2024), the proportion of one-seeded fruits was chosen as a marker for the clade's evolutionary advancement. The rate of one-seeded fruits is intermediate in fabids (19.4 %) and malvids (15.6 %), high in caryophyllids (51.7 %), and very low in lamiids (2.9 %) in the

flora of Ukraine (**Table 3**). The schizocarps are not found in fabids and caryophyllids; they occur in 10.8 % of malvids and in 41.0 % of lamiids. Together, the rate of one-seeded enveloped diaspores (one-seeded fruits and one-seeded fruitlet of schizocarps) in lamiids is almost 44 %; it is comparable to caryophyllids, and strongly higher than in fabids and malvids (less than 30 %, considering one-seeded apocarpous fruits).

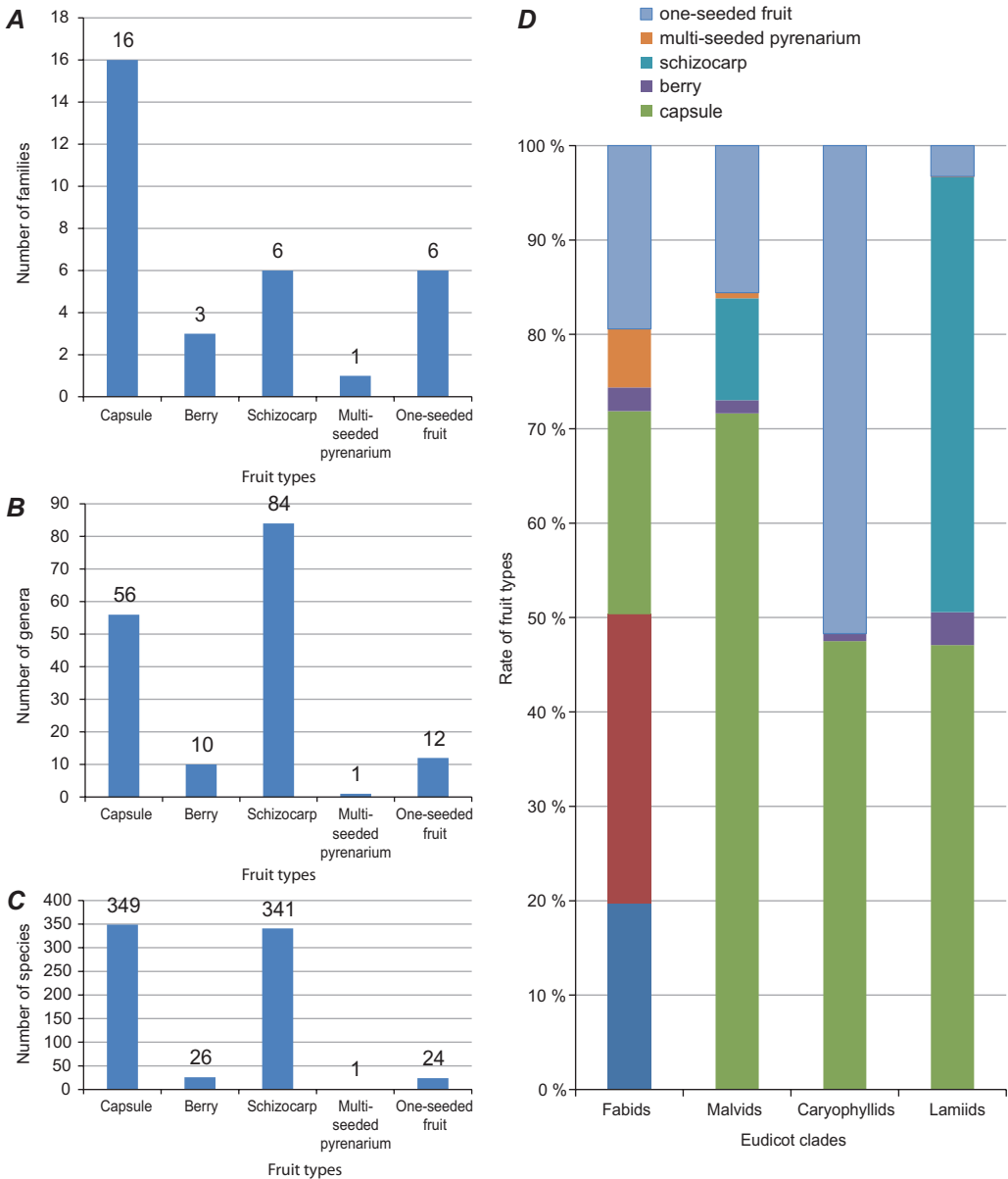


Fig. 3. Rates of fruit types within eudicot clades of the flora of Ukraine. Number of taxa of lamiids, representing basic fruit types, occurring at the families (**A**), genera (**B**), and species (**C**) levels. Carpological spectra of fabids, malvids, caryophyllids, and lamiids (**D**). Fabids and malvids proportion of fruit types were estimated from A. Odintsova (2023), caryophyllids – from A. Odintsova (2025)

Some definitions of fruit types within lamiids are ambiguous; these are bi-follicle in Apocynaceae (schizocarp or secondary dimerous apocarpous fruit, or capsular fruit with naked seeds as dispersal unit); *Vitex agnus-castus* (tetra-seeded pyrenarium with a single pyrene); *Clerodendrum bungei* (schizocarp or tetra-seeded pyrenarium with four pyrenes). These examples represent continuous morphological diversity of fruits, which does not always fit into discrete types.

Compared to the other clades of eudicots, the diversity of fruits within lamiids is not enormous. Some flower and fruit features are strongly canalized in this clade (López-Martínez *et al.*, 2024). Among them are the number of carpels, ovary insertion, and vertical zonality of the ovary. Previous research revealed the narrow morphospace and a trend to high stabilization of floral structure in lamiids. The unique feature for lamiids is a multiple convergent origin of schizocarpic gynoecium and fruit, split into four one-seeded semi-carpellary units, and high general occurrence of schizocarpic fruits of various structures.

CONCLUSIONS

In our research, five fruit types and the main features of the gynoecium within lamiids in the flora of Ukraine were revealed. The morphological diversity of fruits can be effectively categorized into five fruit types: capsule, berry, multi-seeded pyrenarium, schizocarp, and one-seeded fruit, with only a limited number of cases remaining ambiguous. The narrow morphospace of lamiids in terms of the gynoecium merosity, ovary insertion, and fruit type was supported through numerous sources. The lamiids were evaluated as a highly rich clade in the occurrence of schizocarpic fruits of diverse structure. Evolutionary-morphological approach allows us to recognize the lamiids as a moderately advanced clade, characterized by a superior and multi-seeded to oligo-seeded syncarpous ovary and by a high frequency of one-seeded enveloped diaspores in the form of fruitlets of schizocarpic fruits, as well as diaspores in the form of naked seeds released from capsular fruits.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of Interest: the authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Animal Rights: this article does not contain any studies with animal subjects performed by any of the authors.

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МОРФОЛОГІЧНА РІЗНОМАНІТНІСТЬ І КЛАСИФІКАЦІЯ ПЛОДІВ ЛАМІЇД ФЛОРИ УКРАЇНИ

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Вступ. Морфологічну різноманітність плодів у представників кладу ламіїди, включно з будовою гінецею, досліджено на прикладі флори України. Метою було виявити характерні риси плодів у цій кладі та порівняти їх з іншими еудикотами.

Матеріали та методи. Характеристики плодів отримано з численних карпологічних джерел. Проаналізовано також ознаки гінецею: кількість плодолистків і насінних зачатків, положення зав'язі, тип плацентації та вертикальну зональність. Створено карпологічні спектри для родин, родів і видів ламіїд, а видовий спектр порівняно з іншимикладами еудикотів.

Результати й обговорення. Морфологічні особливості плоду наведено для 22 родин, 163 родів і 741 видів ламіїд. За небагатьма винятками, плоди є димерними та верхніми, зі синасцидіатною та симплікатною зоною у зав'язі, часто з інтрузивними плацентами, що поділяють зав'язь на гнізда. У межах кладу ламіїд виявлено п'ять основних типів плодів: коробочка, ягода, багатонасінний піренарій, схізокарп і однонасінний плід. У родинях Oleaceae, Plantaginaceae та Rubiaceae знайдено по три типи плодів. Найпоширенішими серед ламіїд є схізокарпії (41,0 %) та коробочки (41,9 %). Карпологічний спектр ламіїд істотно відрізняється від інших клад еудикотів (фабід, мальвід і каріофілід), демонструючи найвищу частку схізокарпних плодів та найнижчу частку однонасінних плодів (3 %). Водночас загальна частка діаспор типу насінина в оплодні у ламіїд (плоди та їхні частини) є високою (44 %).

Висновки. Отримані результати узгоджуються з попередніми даними про вузький морфопростір ламіїд щодо кількості плодолистків, положення зав'язі й типів плодів. Наші дані підтверджують уявлення про ламіїди як багату на види кладу, що вирізняється багаторазовим виникненням специфічного схізокарпного гінецею та плоду, який розпадається на чотири однонасінні напівплодолисткові одиниці. З еволюційної точки зору, ламіїди флори України демонструють морфологічні риси середнього рівня просунутості гінецею та плоду: верхню, синкарпну, багатонасінну або малонасінну зав'язь та високу частку коробчастих і схізокарпних плодів.

Ключові слова: астериди, карпологічний спектр, коробчастий плід, гінецей, схізокарпій, насінина