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History of Use, Importance and Perspectives of *Cuphea* Species

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Cuphea P. Browne (Lythraceae J.St.-Hil.) comprises approximately 240–260 species that grow wild in the warm-temperate and tropical regions of South and Central America, as well as in the southern part of North America. The economic value of these plants is broad and multifaceted, with particular interest in their ability to synthesize and store oil (ranging from 16 to 42%) in seeds rich in capric, caprylic, lauric, and myristic acids. These oils are used in the production of laundry detergents, plasticizers, perfumes, pharmaceuticals, and other industrial products. Significant efforts have been made to adapt this genus to cultivation in temperate climates for the sustainable production of specialty oils. However, *Cuphea* species retain several wild-type traits such as indeterminate growth and flowering, seed shattering, deep seed dormancy, and the presence of viscous and glandular trichomes, which limit their agricultural potential. Various breeding strategies and modern biotechnological tools have been employed to mitigate these undesirable traits. One of the earliest milestones in the domestication of *Cuphea* species was the development of the PSR23 line, characterized by partial seed retention. The chemical composition, agronomic performance, disease resistance, and productivity of this line have since been extensively evaluated. This review provides an overview of the biology, distribution, and economic importance of *Cuphea* species. It also highlights the research history of the genus, including its taxonomic classification, morphological diversity, chromosome numbers, phytochemical profile, therapeutic potential, and progress in domestication.

Keywords: *Cuphea*, fatty acids, systematic, morphology, germplasm

Introduction

The Earth's spontaneous flora represents an undeniable natural treasure. Plant species in their entirety form a huge and often unique genetic background, being characterized by valuable traits and properties not found in cultivated plants (Levenko, 2005). A crucial moment in the development of agriculture and the broadening of the genetic base of crops is the introduction of plants into cultivation. This involves exploring new germplasm sources within a country or beyond international borders and evaluating the introduced materials for their potential use in creating new crop varieties (Charitha and Rajendra 2024). It provides breeders with access to new alleles, traits, and combinations that may not be present in existing breeding materials and genetic resources. The introduction of a new genetic diversity from unadopted germplasm facilitates the development

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of varieties with higher and more stable yields, wider adaptability, and improved resistance to biotic and abiotic stress (Tanksley and Mccouch, 1996). The problem of highlighting alternative energy sources is not a novelty in recent years. Alongside solar energy, wind energy, geothermal energy, and thermal water, plants providing vegetable oils hold a special place. These compounds can be equally used in human nutrition, industry for producing a wide variety of products, and biofuel production. In nature there are many species of plants that accumulate oils in various organs. Among these are representatives of the *Cuphea* P. Browne genus (Lythraceae J.St.-Hil.) – herbaceous plants native to Central and South America. The importance of these species is highly diverse, but their ability to synthesize and store technical oils in seeds, ranging from 30–42%, is of particular interest (Thompson, 1984; El Bassam, 2010). The oil composition is determined by medium-chain fatty acids: capric, caprylic, lauric, and myristic acids. These are used in the production of soaps, detergents, plasticizers, cosmetics, and biofuels with high fuel properties. Until now, tropical species such as the African oil palm (*Elaeis guineensis* Jacq.) and coconut (*Cocos nucifera* L.) have served as sources of technical oils rich in medium-chain fatty acids. Relatively few plant species from the temperate zone are known to serve as sources of medium-chain fatty acid-rich oils. That‘s why interest in *Cuphea* species is so high. Efforts are being made in various countries to research and improve the species of the nominate genus (USA, Germany, Spain, Japan, India) (Phippen, 2004).

History of Research and the Importance of the Genus *Cuphea* P. Browne

The first descriptions of species from the *Cuphea* genus date back to 1756 and were made by Irish botanist and physician Patrick Browne in Jamaica (Graham & Knapp, 1989). Research on representatives of the genus *Cuphea* continues thanks to the efforts of the German botanist Emil Koehne, who in 1877 compiled all known *Cuphea* species, including many new species, to include them in the work "Flora Brasiliensis" (1840–1906). Koehne continued to write the monograph of the *Cuphea* genus, which was re-edited in 1903 with some modifications and additions, later becoming part of the monograph on the Lythraceae family. This work, describing 200 *Cuphea* species, remains the only comprehensive treatment of the genus to this day (Graham and Knapp, 1989, Graham et al., 2016; Sobolewska et al., 2023).

The first infrageneric classification of the *Cuphea* genus was carried out by Koehne in 1877, and later modified. Thus, Koehne divides the genus into two subgenera and 14 sections. However, at that stage, information about the representatives of the genus was very modest. Starting in 1903, the genus *Cuphea* was supplemented with over 60 new species, but there remained an acute need to conduct studies describing new species of interest due to the lipid composition of their seeds (Graham et al., 2006). A significant contribution to the accumulation of information and description of species from the *Cuphea* genus was also made by scientists Bacigalupi and Foster (Bacigalupi, 1936; Foster, 1945). A particular contribution to the description and classification of species of the genus *Cuphea* belongs to Dr. Sh. Graham of Kent State University. She has discovered several new species. In addition to traditional botanical criteria such as flower morphology, she has used pollen morphology, fatty acid chain length, and chromosome number to classify the genus (Graham, 1968a, b; Graham and Graham, 1971). He carried out thorough studies on the taxonomic revision of the genus. Since 1980, many sectional modifications of the genus have been made (Graham et al., 2006; Graham et al., 2016; Sobolewska et al., 2023). Floristic studies have been carried out evaluating the *Cuphea* species in specific geographical regions: Argentina, Brazil, Santa Catarina State (Brazil), Panama, Guatemala, Nicaragua, and the Lesser Antilles. Thanks to the studies carried out, it was found that five species of *Cuphea* are found in the South-East area of the USA: *C. viscosissima* Jacq., *C. glutinosa* Cham. & Schldtl., *C. aspera* Chapman, *C. carthagenensis* (Jacq.) J.F. Macbr., and *C. wrightii* A. Gray, which is a common member of the flora from western Mexico to southeastern Arizona. Investigations of the sections of the *Cuphea* genus, as well as pollen and seed studies, indicated the presence of new groups of species, leading to modifications in the classification of the genus *Cuphea* species (Graham et al., 1989; Graham et al., 2005; Cavalcanti and Graham, 2008; Sobolewska et al., 2023).

Recent morphological and molecular analyses of specimens collected in mountains of eastern Brazil resulted in the description of a new genus of Lythraceae, Gyrosphragma T.B.Cavalc. & M.G.Facco, which is related to the genus *Cuphea* (Cavalcanti et al., 2022).

The first information regarding *Cuphea* species hybrids was found in Koehne‘s research, which described five interspecific *Cuphea* hybrids documented from herbarium samples in Europe. Unfortunately, these were lost during World War II (Rai et al., 1988). Literature indicates that Robbelen and Hirsinger also observed spontaneous crosses between species in the germplasm collection at Gottingen and initiated an interspecific hybridization program. Sterility observed in hybrids was attributed to differences in the chromosome numbers of the involved species. Following genome doubling with colchicine, fertile and vigorous amphidiploid hybrids of *C. procumbens* Orteg × *C. lanceolata* Ait. and *C. wrightii* A. Gray × *C. tolucana* Peyr. were developed (Thompson 1984).

In the early 1960s, studies established that oils from the seeds of various *Cuphea* species contain high levels of medium-chain fatty acids. Essentially, this information was overlooked for a certain period. Later, Lorey and Robbelen attempted interspecific hybridization between 18 species from five sections of the genus, as well as between four biogenetic groups characterized by different predominant fatty acids in seed oils. They were unsuccessful in obtaining hybrid combinations from species crossing different taxonomic sections or different fatty acid groups. Successful crosses were reported between *C. procumbens* Orteg × *C. lanceolata*, *C. llavea* Lex × *C. lanceolata* Ait., and *C. tolucana* Peyr. × *C. wrightii* A. Gray (Lorey and Röbbelen,1984).

In the late 1970s Princen brought *Cuphea* species to the attention of breeders as potential oil donors, and over the next two years, the industry generated strong interest and supported their research as an oilseed crop (Olejniczac, 2011). *Cuphea* species began to be investigated and evaluated as potential sources of technical oils rich in medium-chain triglycerides widely used in various industrial fields. In the work "Development of New Crops for Obtaining Industrial Materials," Princen L. H. and Rothfus J. A. described screening programs applied to various oilseed crops, including *Cuphea* representatives, and the discovery of new lipid sources and fatty acid classes (Princen, 1984). Phylogenetically, *Cuphea* species have been studied through morphological analysis of Lythraceae and later represented in a molecular phylogenetic evaluation of the family (Graham et al., 1991; Graham et al., 2005; Graham et al., 2006). Subsequent phylogenetic studies based on ITS (Internal Transcribed Spacer) sequences of nuclear DNA for 53 *Cuphea* species confirmed the monophyly of the *Cuphea* genus – a result not surprising given the large number of unique morphological characters that define the genus (Barber et al., 2009). The floristic survey, carried out by a group of researchers from Brazil in Rio Grande do Sul, resulted in the recording of 12 native species and one variety, often found in wet or dry grasslands of the Pampa biome. The new *Cuphea* species were described and illustrated: floral and vegetative morphology, pollen, cytology and habitat. The study is also accompanied by a key to identification illustrations, maps, morphological descriptions and comments on the ecology, taxonomy and geographic distribution of *Cuphea* species in the state of Rio Grande do Sul. (Facco et al., 2022).

The importance of *Cuphea* species is very varied. Among the representatives of this genus are species valued for their ornamental attributes (*C. ignea* A.DC., *C. purpurea* Lem., *C. procumbens* Orteg.). Numerous species serve as traditional medicinal remedies for various indications, including wound treatment, parasitic infections, hypertension, digestive disorders, cough, and rheumatism (*C. aequipetala* Cav., *C. carthagenensis* (Jacq.) J.F. Macbr., *C. epilobifolia* Koehne). Modern pharmacological research has revealed the exceptionally rich phytochemical profile of these plants, including bioactive compounds from the polyphenol, triterpene, alkaloid, and coumarin groups (Sobolewska et al., 2023).

Investigations have shown that most of the species in the genus *Cuphea* have seeds rich in oils with a high content of medium-chain fatty acids: caprylic (C8), capric (C10), lauric (C12) and myristic (C14) (Thompson, 1984; Graham and Knapp, 1989; El Bassam, 2010; Elgindi et al., 2011; Olejniczac, 2011). *Cuphea* oils rich in capric acid (C10:0) are valued in biodiesel production due to their suitable cetane number, low pour point, cloud point, and excellent lubricity properties. Of particular interest are the estolides synthesized by the reaction of *Cuphea* fatty acids with oleic acid (especially the 2-ethyl esters of the estolide oleic-octanoate and oleic-decanoate), which exhibit superior lubricating properties to vegetable oils. (Cermak and Isbell, 2004). The seed oils of *Cuphea* species are used in the production of cosmetic products: body lotions, emollient creams, hair care products, and decorative cosmetics (Berti and Gesch, 2015). Oil rich in decanoic acid (C10) is used in the synthesis of 2-undecanone, a compound with a characteristic odor that functions as an insect repellent (Jackson et al., 2021). In the food industry, *Cuphea* oil is used in the production of chewing gum as a substitute for saturated fats and plasticizers such as glycerol (Sobolewska et al., 2023). The oil is also employed as a solvent and release agent in candy manufacturing. The production of *Cuphea* seed oils generates significant amounts of by-products (Tisserat et al., 2012). These are being considered as potential commercial plant growth regulators. Oil cake and pressing residues can be used as organic fertilizers and soil improvers. *Cuphea* seed oil fractions are potential biodegradable 'environmentally friendly' herbicides. In addition, *Cuphea* seed oil can be used in the production of biodiesel and aviation fuel. As a jet fuel additive, it can lower the fuel's freezing point (Tao et al., 2017).

Traditionally, tropical oilseed crops like coconut (*Cocos nucifera* L.) and oil palms (*Elaeis guineensis* Jacq.) provide these acids commercially. Currently, the soap and detergent industries obtain these fatty acids from the petroleum industry and imported coconut and palm oils. Coconut oil contains 45–50% lauric acid, while some undeveloped lines of *Cuphea* can produce oil that contains almost 80% of this acid. To date, there are no temperate oil plants that can supply these fatty acid. Many *Cuphea* species rich in fatty acids are summer annuals and, through crop development programs, could become domestic sources of fatty acids (Phippen, 2004).

Cuphea Seed Oil and Fatty Acids

The genus *Cuphea* is considered to be unique in the plant kingdom due to the high diversity of fatty acids produced in the seeds, with particular emphasis on medium-chain fatty acids (Graham, 1989). The composition of these oils is determined by one or more medium-chain fatty acids of high economic value, which also serve as informative markers in the interpretation of the evolutionary history of the genus. *Cuphea* species differ in terms of the predominant fatty acids in their seed oil composition. Among species native to South America, the most common dominant fatty acid is lauric acid (C12:0). In North America – a secondary center of speciation – the seed oils are more compositionally diverse: lauric acid and capric acid (C10:0) are most frequently encountered, but in some species, caprylic acid (C8:0), myristic acid (C14:0), as well as long-chain fatty acids such as linoleic acid (C18:2) and linolenic acid (C18:3) are predominant (Wolf et al., 1983). It has been found that in certain *Cuphea* species, the oil composition is predominantly made up of glycerides belonging to a single fatty acid. For example, the oil of *C. wrightii* A. Gray is rich in lauric acid (72.8%), while *C. llavea* Lex. accumulates high levels of capric acid (92%). At the same time, there are species in which the dominant oil component is linoleic acid (C18:2), such as *C. lindmaniana* Koehne ex Bacig. and *C. flavovirens* S.A. Graham, at 55% and 23%, respectively, or linolenic acid (C18:3), as in *C. spectabilis* S.A. Graham (31.0%) (Phippen et al., 2006; Crane et al., 2003).

Chemical Components of *Cuphea* Species

A large number of phytochemical studies conducted on *Cuphea* species report the presence of polyphenolic compounds and a high diversity of flavonoid structures, with content varying depending on species, variety, and plant organ. The main identified flavonoids include: quercetin glycosides, along with rhamnetin, isorhamnetin, and kaempferol; flavones such as apigenin and luteolin; the isoflavone genistein; and their respective glycosides (Krepsky et al., 2012; Sobolevska et al., 2022). In the aerial part extract of *Cuphea carthagenensis* (Jacq.) J.F.Macbr. and in the methanolic extract of *C. ingrata* Cham. & Schltdl., the rare quercetin 3-sulfate was detected (Krepsky et al 2010;) The results of several studies have shown that the phenolic content of each species tends to be organ-specific and may depend on cultivation conditions. Tannins, steroids and triterpenes have been isolated and characterized in the chemical composition of *Cuphea* species. A particular interest are the macrocyclic tannins, including dimeric ellagitannins, such as cuphiin D1, cuphiin D2, oenothein B and woodfordin, isolated from the aerial parts of *C. hyssopifolia* Kunth and which possess anticarcinogenic properties. Alongside these compounds, the presence of triterpenes (carthagenol), sterols, alkaloids, and coumarins (5,7-dihydroxy-3-methoxycoumarin 5-O-β-glucopyranoside) has also been identified (Gonzales et al., 1994; Mousa et al., 2019).

Genus *Cuphea* – Plants with High Therapeutic Values

Thanks to phytochemical studies, numerous compounds have been identified in the chemical composition of *Cuphea* species representatives, conferring them undeniable value as medicinal plants. *Cuphea* species are of great interest due to their therapeutic value and are widely used in traditional South American and Mexican medicine. Plant extracts and their natural compounds have been employed in various treatments as anti-inflammatory, diuretic, antipyretic, antimicrobial, astringent, and antihypertensive agents Elgindi et al., 2011; Sobolewska et al., 2023; Santos et al., 2024).

Scientific research has demonstrated that *Cuphea* species contain active compounds capable of treating various diseases, including cancer. From the aerial parts of *Cuphea hyssopifolia* Kunth., have been extracted four macrocyclic hydrolyzable tannin dimers, cuphiin D1, cuphiin D2, oenothein B and woodfordin C, which possesses an antitumor effect on human promyelocytic leukemia (HL-60) cells and human cervical carcinoma (Wang et al., 2000). Plant extracts of *Cuphea aequipetala* Cav. exhibit antiproliferative and apoptotic activities on melanoma cancer cell lines in mice (Avila et al., 2004).

Representatives of the *Cuphea* genus can be used as natural antivirals. The hydroethanolic extract of *C. carthagenensis* has proven to be highly effective against Herpes simplex virus type 1 (HSV-1). *Cuphea* species are sources of new antimicrobial agents. For example, *C. aequipetala* Cav. – a plant with anti-inflammatory and gastroprotective properties has shown strong activity against *Helicobacter pylori*, while *C. carthagenensis* (Jacq.) J.F. Macbr exhibits a destructive effect on *Staphylococcus aureus*, *Micrococcus luteus*, *Bacillus subtilis*, *Escherichia coli*, *Pseudomonas aeruginosa*, and *Salmonella typhimurium* (Andrighetti-Fröhner et al., 2005; Palacios-Espinosa et al., 2014).

Some species of *Cuphea* are used to control parasitic infections, which are a serious problem in tropical and subtropical regions (Sobolewska et al., 2023). Extracts from the roots of *C. pinetorum* Benth. have been shown to be effective against protozoa Entamoeba histolytica and Giardia lamblia. The action of extracts from *C. carthagenensis* (Jacq.) J.F. Macbr., *C. glutinosa* Cham. & Schldtl. and *C. ingrata* Cham. & Schldtl. has also been tested on the epimastigote form of Trypanosoma cruzi. The results of the study that elucidated the high level of hepatoprotective activity of *C. hyssopifolia* methanol leaf extract of *C. hyssopifolia* Kunth in preventing liver injury on paracetamol-induced hepatotoxicity in experimental rats are reported. *C. carthagenensis* (Jacq.) J.F. Macbr extracts were found to exhibit a vasorelaxant effect on aortic ring segments in experiments with rats. The antidiuretic effect of *Cuphea* mesostemon Chodat leaf extract on the frog bladder was also studied and confirmed *in vitro*. Thanks to their high polyphenol content, *Cuphea* species exhibit strong antioxidant activity. Research has demonstrated their high capacity to scavenge free radicals, as well as to inhibit the production of reactive oxygen species (*C. aequipetala* Cav., *C. carthagenensis* (Jacq.) J.F.Macbr., *C. calophylla* Cham. & Schldtl., and *C. hyssopifolia*). The species of the genus *Cuphea* are used in the treatment of gastric diseases, diarrhea (*C. aequipetala* Cav.); arterial hypertension (*C. aperta* Koehne); rheumatism (*C. epilobifolia* Koehne) (Elgindi et al., 2011).

The infusion of *C. glutinosa* Cham. & Schldtl is used in the treatment of nervous system disorders, while its leaves and shoots serve as diuretic, blood-purifying, antihypertensive, and antimalarial remedies. Additionally, a decoction of the plant is used as an emmenagogue (Elgindi et al., 2011; Sobolewska et al., 2023).

One of the most valued and extensively studied species in traditional medicine is *C. carthagenensis* (Jacq.) J.F. Macbr, also known as Colombian waxweed. It is recognized as an anti-nociceptive, antiviral, antimicrobial, anti-inflammatory, and weight-reducing agent. In addition, its cardioprotective, hypolipidemic, and antioxidant properties have also been demonstrated (Das et al., 2018).

Phytochemical studies confirm the therapeutic value of the genus. There is a need for clinical studies to evaluate the pharmacological actions of the genus, bioactive mechanisms, structure-activity relationships and their safety under *in vivo* conditions (Elgindi et al., 2011; Sobolewska et al., 2023; Santos et al., 2024).

Systematic Position and Distribution

The Lythraceae J. St.-Hill. family comprises 27 genera and about 620 species of dicotyledonous plants widely distributed in subtropical and tropical regions of both hemispheres, less so in temperate regions (Graham, 1991; Graham, 2005; Graham, 2007; Christenhusz and Byng 2016). Representatives of this family include herbaceous plants, shrubs, and trees of high ecological and economic value. Many species within the family are cultivated as ornamental plants (genus *Lagerstroemia* – the brightly colored flowers and bark that exfoliates, exposing shades of brown to gray), medicinal (genus *Lythrum*) and as a source of natural dyes (genus *Lawsonia*). Some species have also been studied for their phytoremediation potential due to their ability to absorb soil and water pollutants (Zhenghao and Meihua, 2017). Of particular interest are species from the *Cuphea* genus, the most numerous in this family, comprising, according to various authors, 250–260 species native to Central and South America (Graham, 1989; Olejniczak, 2011).

Taxonomically, the *Cuphea* genus is divided into two subgenera and 13 sections: Subgenus *Cuphea* Koehne (Lythrocuphea Koehne); Sections: *Archocuphea* Koehne, *Cuphea*. Subgenus Bracteolatae S.A. Graham (Eucuphea Koehne); Sections: Amazoniana Lourteig, Brachyandra Koehne, *Diploptychia* Koehne, Euandra Koehne, *Heteranthus* Koehne, *Heterodon* Koehne, *Leptocalyx* Koehne, Melicyathium Koehne, *Melvilla* Koehne, Pseudocircaea Koehne, *Trispermum* Koehne (Graham and Knapp, 1989).

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Two major centers of *Cuphea* species diversification are known:

1. the eastern region of Brazil;
2. the mountainous area of southeastern Mexico.

A single species is native to the Central and Eastern United States. An exceptionally high diversity and abundance of *Cuphea* species have been noted in the Brazilian savannas of Bahia, Goiás, and Minas Gerais. They grow at an altitude of up to 3,000 m above sea level, usually at the edge of roads, in open, wet areas, and grasslands (Graham, 1988, 2019; Graham and Knapp, 1989; El Bassam, 2010; Graham et al., 2006; Facco et al., 2022).

Successes Obtained in Domesticating Species of the Genus *Cuphea* P. Browne

With the discovery of the lipid composition of *Cuphea* seeds, the domestication of the genus has made progress. As with develop any new crop, the time required to domesticate and develop new varieties utilizing traditional methods is extremely slow (Byrd, 1987). *Cuphea* species have characteristics typical of wild plants, namely: indeterminate growth and flowering; seed shattering from mature fruits; seed dormancy; the presence of glandular, sticky trichomes on stems, leaves, and flowers, which create difficulties in the harvesting process (Knapp and Crane, 2000; Phippen, 2004; El Bassam, 2010). These are major barriers to introducing *Cuphea* species into cultivation and achieving high seed yields. However, the genus has some promising properties that make it possible to obtain large quantities of seeds: most species are vigorous and productive; *Cuphea* plants reproduce easily both generatively and vegetatively; the great variation in fatty acid chain length could be exploited to meet specific oil needs; the high variability of agronomic characteristics is a favorable factor for successful plant breeding (Byrd, 1987).

According to literature data, the first research programs on *Cuphea* species as a temperate source of technical oils began in the 1970s by a consortium of agronomists and chemists (Thompson, 1984). By the late 1980s, successful hybridization work was reported by a group of scientists in the USA (University of Arizona) – Thompson, Gathman, Ray. They obtained 18 interspecific hybrids, confirmed morphologically and cytologically. The report presented by Thompson and colleagues mentions the possibility of reproducing sterile hybrids vegetatively – through cuttings. Following the segregation of fertile hybrid populations, new flower color combinations were recorded. The resulting hybrids were evaluated as potential plants for flowerbeds and pot plants (Ray et al., 1988).

During the same period, domestication programs for *Cuphea* species were initiated in Germany. At Oregon State University, under the guidance of scientist Steven Knapp, an intensive breeding and domestication program for *C. viscosissima* (native to the United States) and *C. lanceolata* (native to Mexico) was launched (Graham, 1988; Roath et al., 1992).

By the mid and late 1990s, significant progress was made in eliminating seed shattering and dormancy by exploiting the interspecific diversity of the hybrid population *C. viscosissima* × *C. lanceolata* f. *silenoides* and a cultivar *C. viscosissima* × *C. lanceolata* f. *silenoides*. Knapp also succeeded in developing elite *Cuphea* lines that do not shatter, are self-fertile, and have reduced levels of glandular trichomes (sticky hairs) (Knapp and Crane, 2000a, b, c.). Research initiated in the early 1980s focused on studying the fatty acid profile of *Cuphea* species collected from nature. In 1988, scientists Thompson and Kleiman presented the results of a breeding program for the species *C. wrightii* A. Gray, characterized by a high level of lauric acid in seed oil. Unfortunately, the domestication of this species has proven to be extremely difficult due to seed shattering, cross-pollination, and poor agronomic characteristics (Ray et al., 1988). Breeding programs utilizing mutations aimed at increasing fatty acid accumulation in seeds had limited success (Phippen, 2004).

The *Cuphea* species breeding programme, maintained by Knapp, also included the creation of the basis for genetic analysis and selection using markers. A huge progress in this regard is represented by the development of over 200 STS markers (sequence-tagged-site); elaboration of the genetic map of *Cuphea* species that allows to determine the quantitative loci for the seed rest period, seed shattering, self-pollination and other economically important features (Webb et al., 1992). Several successful attempts have been made to develop commercial *Cuphea* lines. For this purpose, scientists Knapp and Crane launched the PSR 23 ("Partial Shatter Reduction") line, obtained by interspecific hybridization of *Cuphea viscosissima* Jacq. and *C. lanceolata*, f. *silenoides* W.T.Aiton (Knapp and Crane, 2000a). PSR23 was the first line to possess the trait of partial seed-shattering reduction. It inhibits the rotation of the placenta in the capsule, leading to increased seed retention and reducing seed loss by 20–30%. The seeds of the PSR 23 line are characterized by a relatively high oil content of 295 $g.kg^{-1}$, a high level of capric acid – 72%, are self-fertile, and have no deep dormancy (Knapp and Crane, 2000 b,c,d). Numerous research projects have followed, focusing on improving cultivation practices for the *Cuphea* PSR23 line, namely: seed germination response to temperature, row spacing, sowing dates, temperature sensitivity, nutrient requirements, irrigation studies, seed physiological maturity, seed drying and harvesting methods (Gesch et al., 2002; Gesch et al., 2003, 2004; Cermak et al., 2005; Olness et al., 2005; Berti et al., 2007; Gesch and Forcella, 2007; Forcella et al., 2007; Berti and Johnson, 2008; Berti, and Gesch, 2015).

The basic knowledge acquired through the above-mentioned experiments represented the greatest progress in the improvement and, eventually, the commercializing of the PSR 23 line. Several successful attempts have been made to develop commercial *Cuphea* lines (Knapp, 1993). Evaluation of the lipid composition of the seeds revealed that the PSR 23 line contains 4–5% more oil than the parental forms (*C. lanceolata* Ait. and *C. viscosissima* Jacq.) (Table 1). In addition, oil production at PSR23 can increase with increasing latitude.

On the fields of cultivation of PSR 23 (in the states of Illinois and Minnesota), special descendants were observed after pigments: plants with completely white flowers and variations with pink flowers. The white-flowered variety was named "Snowflake" in IL and "Blizzard" in MN; these are lines exhibiting inbreeding depression, are less vigorous, produce a lower number of seeds, but have a higher seed retention capacity. The stable character of the Snowflake genotype is reported even after 5 years of self-pollinated generations in a growth chamber. After each crossing the hybrid vigor decreases. Under field conditions Snowflake shows good growth and development potential only at the beginning of the season, gradually the plants decline, being affected by environmental stress factors. Since anthocyanin pigments provide resistance to plants by acting as powerful antioxidants, the objective was proposed to perform backcrosses between PSR23 and Snowflake in order to obtain offspring with white flowers, while limiting anthocyanin synthesis to vegetative tissues. The white-flowered offspring are not only ornamental, but also have better seed retention capacity, and the lack of pigments in the seed coat would reduce oil production costs (Phippen, 2004).

Research programs have been conducted to regenerate *in vitro* germplasm of *Cuphea* species. Early work focused on explant propagation methodologies for *C. wrightii* A. Gray and *C. tolucana* Peyr (Janick and Whipkey, 1986; Przybecki et al., 2001). Other studies began screening a wider variety of species for the potential of utilizing engineering techniques (Millam et al., 1997). Species of the genus *Cuphea* serve as a rich source of genes encoding enzymes specialized for, seed – specific, synthesis of short- and medium-chain fatty acids. Rowland et al. (2003) obtained transgenic flax plants with significant alterations in the fatty acid thioesterase gene, BFAT2, from *Cuphea wrightii* A. Gray. Transgenic plants with significant changes in the fatty acid profile were obtained. Total saturated were greatly elevated in some of the seed and there was the appearance of both myristate (C14:0) and lauric (C12:0) fatty acids (Rowland et al., 2003). A group of American researchers obtained oleaginous vegetative sorghum by introducing the diacylglycerol acyltransferase *Cuphea viscosissima* Jacq. and two combinations of specialized acyltransferases of *Cuphea lysophosphatidic* acid and thioesterases of medium-chain acyl-acyl carrier proteins (Park et al., 2024).

In India, research is being conducted to acclimate the species *C. procumbens* for seed oil production (Pandey et al., 2000). In South America, evaluations of *C. carthagenesis* (Jacq.) J.F. Macbr. and *C. glutinosa* Chain. & Schltdl species have been conducted for their potential use as medicinal plants (Das et al., 2018).

Table 1 Medium-chain fatty acid content in seeds of *Cuphea* species

***Cuphea* species**	**Oil (%)**	**C8:0 (%)**	**C10:0 (%)**	**C12:0 (%)**	**C14:0 (%)**
C. lanceolata	20–33	1–2	78–91	1–4	1–5
C. calophylla	26–34	0.4–4	19–33	58–72	2–7
C. tolucana	30–38	0.4–0.7	21–42	46–65	1–5
C. procumbens	19–35	1	81–89	1–2	1–2
C. viscosissima	30	17	72	3	1
C. hookeriana	16	65	24	0.1	0.2
PSR23	27–33	1	77–84	2–3	2–4

Notes: Data by McKeon et al., 2016

Japanese researchers have studied the possibility of including *C. leptopoda* in human nutrition (Saikusa et al., 2001).

Remarkable progress has been made in the improvement and development of new *Cuphea* hybrids and cultivars. Research has been directed toward the domestication of *Cuphea* species and the development of genotypes with valuable traits as a source of medium-chain fatty acids. As previously mentioned, many species of the genus *Cuphea* are of interest as ornamental plants – *C. ignea* A DC., *C. llavea* Koehne, *C. micropetala* Kunth, *C. ramosissima* Pohl ex Koehne, *C. angustifolia* Jacq. ex Koehne etc. Through interspecific hybridization between various decorative species, hybrids and varieties have been developed that are suitable for interior decoration and are ideal for growing in containers, pots, and flower beds, showing high value in landscape design. There are over 100 known varieties of *Cuphea* that are suitable for decorating rooms, but with the same success they can also be useful for beautifying borders, gardens, flowerbeds.

The ornamental species *Cuphea glutinosa* Chain. & Schltdl., native to Brazil, holds particular horticultural interest. Three notable cultivars of this species have been identified: 'Lavender Lady', 'Lavender Lei', and 'Purple Passion'. These varieties were selected from among 25 individuals out of a total of 220 *C. glutinosa* plants that successfully survived the winter conditions in Tifton, Georgia. These cultivars are ornamental, perennial landscape plants with high cold tolerance. They overwinter successfully, and after the first growing season reach heights of approximately 12 cm (cv. Lavender Lady), 14 cm (cv. Lavender Lei), and 20 cm (cv. Purple Passion). They reproduce by rooting of stoloniferous shoots, by underground stolons, and by seeds. Within 100 days of planting, the plants form a superior ground cover 50-cm-diam circle (cv. Lavender Lady), 42 cm (cv. Lavender Lei), and 51 cm (cv. Purple Passion). They produce small flowers with six petals, which vary in color depending on the cultivar. 'Lavender Lady' displays ventral petals colored purple-violet (81C), dorsal petals in a deeper purple-violet shade (80A), with petal veins highlighted in purple (77A). The plant produces approximately 27 flowers per 100 cm^2. 'Lavender Lei' exhibits ventral petals in purple-violet (81C), dorsal petals in a slightly deeper shade (80A), the flower petal veins are purple (77A), and forms up to 20 flowers per 100 cm^2. The flowering period begins in April and continues until the first frost. The leaves are small and possess an attractive green coloration. Stems and foliage located more than 5 cm above the soil surface are susceptible to damage from cold winter temperatures, whereas those near the ground, which form a complete ground-covering mat, remain visually appealing and green throughout the cold season. The shoot tips and the undersides of young leaves of 'Purple Passion' and 'Lavender Lei' exhibit a purplish hue – an attribute not observed in 'Lavender Lady'. Plants of these varieties grow, expand and proliferate into a dense mat of rooted shoots that completely cover the ground, and this – characteristic may add value for erosion control and beautification along highways and as potted plants (Jaworski and Phatak, 1991, 1992).

In 1995, researchers Thompson, Roath, and Widrlechner (USA) reported the development of the hybrid 'Starfire', resulting from the interspecific cross between *Cuphea ignea* A. DC. and *C. angustifolia* Jacq. ex Koehne. This hybrid was introduced as a container plant suitable for greenhouse or indoor cultivation. 'Starfire' exhibits unique floral and foliar characteristics. The plant displays an intermediate growth habit compared to its parental forms, with a height range of approximately 50–75 cm. Leaves are dark green (green 137A) on the adaxial surface and light green (green 138C) on the abaxial side. The calyx tubes are striped pink (pink 63B) on a white background, with a white dorsal tip featuring a pronounced spur. The dorsal petals are white with a purple vein (purple 75A), while the ventral petals range from deep purple ton (purple 75A) early white (purple 75D). This hybrid is sterile, but it can be propagated vegetatively through cuttings. Once rooted, the plants flower profusely (Thompson et al., 1995).

Ornamental hybrids of the *Cuphea* species have gained high popularity thanks to their indispensable qualities: the ability to tolerate heat and the specific flowering period that starts once the plant is planted and continues until the fall frost. The brightly colored, tubular flowers are an epicenter for attracting pollinators: bumblebees, butterflies and hummingbirds. Although they prefer moisture once established, the plants can tolerate drought to some extent without negative effects (Jaworski and Phatak, 1991, 1992; Thompson et al., 1995).

Biology of *Cuphea* Species

Representatives of the *Cuphea* genus are annual or perennial herbaceous plants, widespread in temperate, subtropical, and tropical regions of the American continent. The species vary from low-growing annual and perennial herbaceous plants to subshrub up to 2 meters tall. However, for most *Cuphea* species, the plant‘s height is up to 1.5 m (Graham 1989; 1991; 2007).

The genus name *Cuphea* is derived from the Greek κυφός, meaning bent, leaning forward, or hunched over backward (Elgindi et al., 2011; Sobolewska et al., 2023). The term probably refers to the shape of the fruit capsule. In the Spanish-speaking world, *Cuphea* plants are also known by the generic name of sete-sangrias (seven-bleeding) (Sobolewska et al., 2023).

The plants develop a taproot system, with erect, decumbent, and procumbent stems, monopodially branched, where primary, secondary, and tertiary shoots are arranged (Graham 1989; Cavalcanty and Graham, 2008).

The leaves are usually simple, elongated, ovate-lanceolate, with entire margins, arranged oppositely or in whorls. In most species, the leaf size gradually decreases towards the top of the plant (Graham 1989; Facco et al., 2022).

The flowers are solitary or grouped in inflorescences – leaf raceme that are not well separated from the vegetative parts of the plant, occupying one-third of the length of the stem and branch. Some species are distinguished by terminal racemes or floriferous panicles – (sect. *Heteranthus*) (Graham and Knapp, 1989). Solitary flowers develop at branch nodes (Graham 1989; 2007).

The flowers are small, zygomorphic with a bilaterally elongated cylindrical floral tube. The corolla consists of six petals unequal in shape and size and the calyx includes six concentric sepals. The floral tube is ribbed on the outside and is most often colored in shades of violet or red (Figure 1). The sepals form the terminal edge of the tube. The androecium includes 9–11 stamens, borne on filaments of unequal lengths, the ovary is superior, and elliptical, with a dorsal or cupuliform nectariferous gland at the base. The predominant color of the flowers varies from violet (*C. lanceolata* W.T. Aiton) to red (*C. nudicostata* Hemsl.), though some rare specimens have yellow flowers (*C. nudicostata* S.A. Graham & T.B. Cavalc.) or bicolored floral tubes, such as *C. annulata* Koehne, *C. cyanea* Moc. & Sessé ex DC., and *C. spectabilis* S.A. Graham. The leaves, stems, and flowers are covered with sticky or glandular hairs and excrete a resinous and sticky exudate (Graham, 1988, 2019).

Another specific feature of the representatives of the *Cuphea* genus is the high diversity of trichomes covering the stems, leaves and flowers. This characteristic is taxonomically important, but only

Figure 1 *Cuphea lanceolata* Ait. – a species of annual plant native to Mexico
A – flower, floral tube in lateral view; B – seed capsules
Photo by Mihaila and Brinzan, 2015

glandular trichomes are valuable for agriculture (Graham and Knapp, 1989). The fruit is a capsule with thin walls of various shapes, with longitudinal-dorsal dehiscence through which the placenta erupts, allowing the release of seeds (Figure 1).

The seeds are orbicular, obovate, elliptic, with sharp or obtuse margins, have either a smooth or wrinkled surface, with inverted, spiral, mucilaginous trichomes. They are attached through coordinated slits in the dorsal wall of the capsule and the floral tube. The majority of species produce between 6 and 20 seeds per flower, the number depending of the species. The seed embryo includes two cotyledons and germination is hypogeal (Graham and Knapp, 1989; Graham, 1988; Barber et al., 2010; Facco et al., 2022; Sobolewska et al., 2023).

Several characteristics distinguish the genus from other members of the Lythraceae family: the interpetiolar position of flowers; the "disc" – an independent nectariferous organ located at the base of the ovary; 11 stamens (rarely fewer), with two dorsal stamens positioned lower than the other nine; oblique pollen; a unique seed dispersal mechanism; flattened, biconvex seeds with mucilaginous, inverted trichomes in a spiral arrangement; and seed fixation through coordinated slits in the dorsal capsule wall and floral tube. At maturity the placenta typically arches upward, rupturing the placental membrane and calyx tube longitudinally, leaving the seed exposed for dispersion. (Byrd, 1987; Graham, 1988; Graham and Knapp, 1989; Barber et al., 2010; Facco et al., 2022; Sobolewska et al., 2023).

The pollen morphology of *Cuphea* species is highly variable, and its characteristics are used in describing the evolutionary lines within the genus as well as in identifying related species. The most commonly found pollen in the genus is flattened, oval-triangular in shape, with three slightly prominent pores and three furrows extending to the poles (Figure 2).

Essential differences are observed in diporate pollen grains (sect. Pseudocircaea), grains with walls thickened between the pores (Sect. *Trispermum*), and very small grains lacking any sculpture pattern the exine and without extendet furrows (sect. *Archocuphea*) (Graham, 1989, 2019; Facco et al., 2020).

The species in the *Cuphea* genus are also varied by the number of chromosomes. This has also been confirmed by research conducted by Feitoza (Feitoza et al., 2024). The haploid number of chromosomes in *Cuphea* species ranges from $n = 6$ to $n = 86$ (Pozzobon et al., 2022). The most commonly recorded sets include 8, 10, and 12 chromosomes. The basic genus number is $n = 8$. The most chromosomally diverse species belong to the Euandra section, centered in eastern Brazil, with haploid chromosome numbers of 8 and 12. Exclusively for genotypes found in Mexico, haploid chromosome numbers of 10 or 12 are characteristic (sect. *Heterodon* and *Leptocalyx*). Within the genus are species of polyploid origin they have the number of chromosomes $n = 14$ and more. The *Melvilla* and *Diploptychia* sections, which include many species growing at higher altitudes, are characterized by high polyploidy, with a haploid chromosome set of 30 or more.

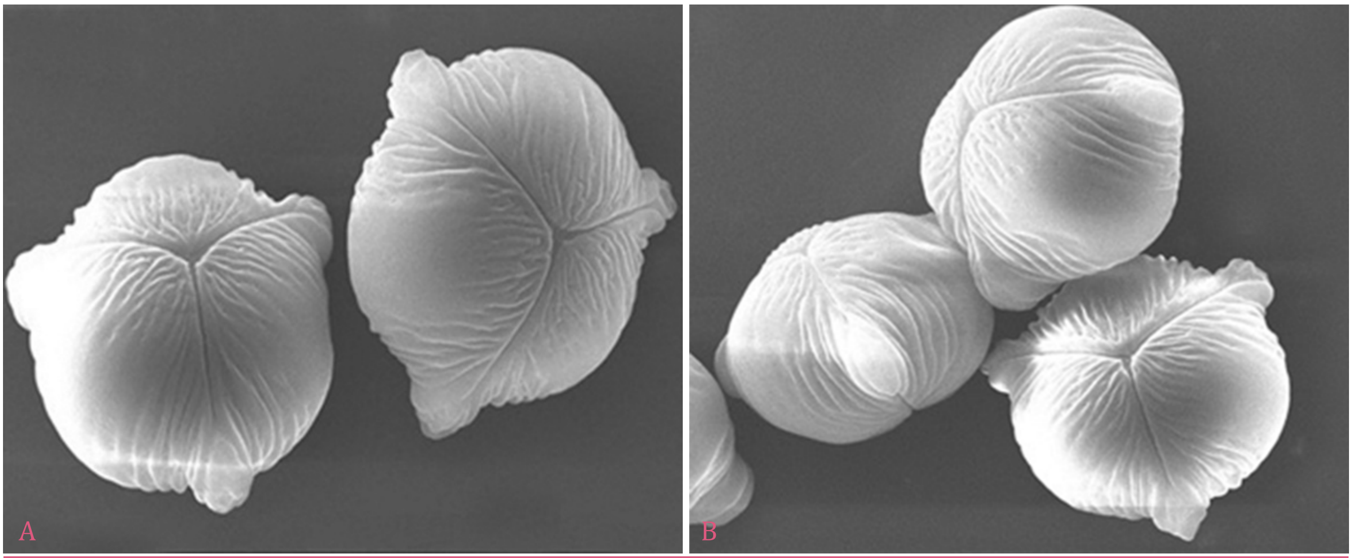

Figure 2 Morphology of *Cuphea lanceolata* Ait. pollen
A – general aspect, polar view; B – polar and equatorial view
Photo by Mihaila and Brinzan, 2015

A positive correlation was established between the number of chromosomes and the total size of the selected morphological features, with the polyploid species showing longer floral tubes. Moreover, a possible association between polyploidy and adaptive radiation of *Cuphea* species has been revealed during the expansion of its distribution in North America (Graham, 1989).

At the Institute of Genetics, Physiology, and Plant Protection, Moldova State University (Chisinau, Republic of Moldova), research was initiated to determine the productivity potential and resistance of three *Cuphea* species: *C. lanceolata* Ait., *C. viscosissima* Jacq., and *C. lutea* Rose. The study included the description of morpho-botanical particularities of *Cuphea* species; evaluation of quantitative parameters and resistance of species to the action of unfavorable factors of the environment (Mihaila et al., 2015; 2022). Samples showing high productivity levels and strong resistance to abiotic stress factors under introduction conditions were identified. *Cuphea* species are heliophilous, demanding specific soil types, requiring additional irrigation, and responding well to soil nutrient solutions. The central region of the Republic of Moldova, from a pedoclimatic perspective, is favorable for cultivating *Cuphea* species, although optimal development is limited by high summer temperatures.

Conclusions

The *Cuphea* genus is a monophyletic taxon that includes herbaceous plants and shrubs spread across warm temperate and tropical regions of the American continent. Species of the genus *Cuphea* are of interest as decorative plants (*C. ignea* A. DC., *C. purpurea* Lem., *C. procumbens* Orteg.), medicinal plants (*C. aequipetala* Cav., *C. carthagenensis* (Jacq.) J.F. Macbr., *C. epilobifolia* Koehne) but also as plants that have seeds rich in technical oils used in the production of biofuel and other industrial products. The oil composition is determined by the presence of medium-chain fatty acids: capric, caprylic, lauric, and myristic acids, used in the production of laundry powders, plasticizers, and also in perfumery, medicine and other sectors. In order to domesticate *Cuphea* species, research and breeding programs have been carried out, and as a result, elite lines have been obtained that combine desirable traits that ensure high seed productivity. The lipid composition of *Cuphea* seeds is very diverse (30– 42%), and the dominant fatty acid in the seeds is determined by the genotype and remains constant throughout the range of the species. Based on the knowledge of the varied lipid composition of the seeds of *Cuphea* species and the contrasting ecological distribution, it would be possible to adapt crops to produce certain fatty acids on demand under a variety of growing conditions. The creation of the genetic analysis base, selection using markers, and the genetic map of *Cuphea* species have helped to identify quantitative loci for various economically valuable characters. *Cuphea* species can be a diversified source of seed-specific genes for modifying the fatty acid content of other oil crops. *Cuphea* species can be a diversified source of genes for seed-specific fatty acid content modification in other oilseed crops.

Conflicts of Interest

The authors have no competing interests to declare.

Ethical Statement

This article does not include any studies that would require an ethical statement

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