

Original research

Taxonomic identity of *Camelina armeniaca*, a forgotten early name in *Camelina* (Brassicaceae)

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Abstract

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The long-forgotten and taxonomically problematic name *Camelina armeniaca* Desv. is one of the earliest species' names published in *Camelina* (Brassicaceae; Cruciferae). Because of that, the issue of its proper taxonomic application was important for the nomenclatural stability of taxa belonging to the *C. sativa*–*C. microcarpa* aggregate and containing the important oilseed and biofuel crop *C. sativa* and its wild relatives and progenitors. The name *Camelina armeniaca* is lectotypified here with the specimen P00652666 from the Tournefort Herbarium (Herbarium Tournefortianum No. 1634) in P, following the direct reference in the protologue. Judging from the morphological characters of the lectotype, taxonomically, it represents a morphotype of *C. sativa* sensu lato, probably most closely matching *C. caucasica* (*C. sativa* var. *caucasica*) from a morphological viewpoint. Contrary to the recent listing of *C. armeniaca* in synonymy (!) of *C. microcarpa* in several main biodiversity databases (such as GBIF, POWO, etc.), we conclude that *C. armeniaca* is definitely not conspecific with *C. microcarpa*. Because of that, nomenclatural conservation of the latter name against the earlier one is unnecessary, as well as a possible proposal to reject the name *C. armeniaca*. We prefer to treat *C. armeniaca* as a taxonomic synonym of *C. sativa*. A corrected typification (lectotypification and epitypification) of the name *C. sativa* var. *caucasica* is also provided.

Keywords: *Camelina sativa*, Cruciferae, lectotype, nomenclature, typification.

INTRODUCTION

Camelina sativa (L.) Crantz (Brassicaceae; Cruciferae) is now considered an important and promising oilseed and biofuel crop (Vollmann & Eynck, 2015; Brock et al., 2018, 2020; Blume et al., 2020a, 2022; Zanetti et al., 2021). Because of that, taxa of the genus *Camelina* Crantz are currently the focus of large-scale and diverse research projects covering various aspects of taxonomy, morphology, biogeography, phylogeog-

raphy, phylogeny, genetics, evolution, biochemistry, and biotechnology of *C. sativa* and its wild relatives and possible progenitors (Martin et al., 2017; Brock et al., 2018, 2019, 2020, 2022a, b; Žerdoner Čalasan et al., 2019; Luo et al., 2019; Mandáková et al., 2019; Chaudhary et al., 2020; Blume et al., 2020b, etc.). These projects continue the tradition of early studies of the evolution of crops and weeds using *Camelina* as a model taxon (Zinger, 1909; Tedin, 1925; Sinskaja, 1928; Sinskaja & Beztuzheva, 1931). It is evident

that for those studies to be successful and their results to be reliable, they should be based on precise and reliable taxonomy and nomenclature of the entities involved in research. Because of that, establishing the precise taxonomic identities of various scientific names applied to taxa of *Camelina*, and their proper typification (in the framework of Art. 7–10 of the *International Code of Nomenclature for algae, fungi, and plants – ICN*: Turland et al., 2018), are among the most important tasks (see Dorofeyev, 2019; Mosyakin & Brock, 2021, and references therein). During our taxonomic and nomenclatural survey, we came across the long-forgotten and taxonomically problematic name *Camelina armeniaca* Desv. Its taxonomic status and identity have remained obscure until recently. Since it is one of the earliest species names published in *Camelina*, pre-dating most of other species-rank names in the genus, we considered it necessary to clarify the application of that name and its real taxonomic identity.

MATERIALS AND METHODS

We applied traditional methods of herbarium taxonomy and used online digital resources. In particular, we checked scanned images of herbarium specimens and associated data at JSTOR Global Plants (<https://plants.jstor.org/>) and digital web resources of several herbaria, first of all, the P Herbarium (Muséum National d'Histoire Naturelle, Paris, France: <https://science.mnhn.fr/institution/mnhn/collection/p/item/search/>) and BM Herbarium (Natural History Museum, London, United Kingdom: <https://data.nhm.ac.uk/dataset/collection-specimens>). Nomenclatural considerations and decisions are based on the current edition of the *International Code of Nomenclature for algae, fungi, and plants* (from now on – *ICN*; *Shenzhen Code*: Turland et al., 2018). In addition, herbarium acronyms are cited following *Index Herbariorum* (Thiers, 2008–onward).

RESULTS AND DISCUSSION

The protologue of *Camelina armeniaca*: a brief analysis

The name *Camelina armeniaca* Desv. (J. Bot. Agric. 3: 182. 1815) was validated by a short description in Latin (“*CAMELINA armeniaca*, annua: caule

erecto, foliis linearis lanceolatis acutis, villosis; siliculis elongatis, basi longè attenuatis. *Habitat* in Armeniâ”) and in French. Desvaux (1815) also indicated the main morphological differences between his new species and the cultivated *C. sativa* (L.) Crantz and mentioned that his species in the Tournefort Herbarium was named as “*Alyssoides armenia annua myagrofolio*” (“Elle est désignée dans l’herbier de Tour-fort [Tournefort], sous le nom d’*Alyssoides armenia annua myagrofolio* [*myagrifolio*]”).

Desvaux (1815) mentioned in the original description: “Cette Cameline se distingue par sa silicule beaucoup plus allongée et plus longuement amincie à sa base que la Cameline cultivée (*C. sativa*)”, meaning that *C. armeniaca* could be distinguished by its elongated silicle, which is significantly thinner at the base if compared to that of *C. sativa* sensu stricto.

Morphological characters reported in the protologue do not allow establishing the precise taxonomic identity of *C. armeniaca* clearly; however, they generally match the characters of at least some morphotypes of species currently known as *C. sativa* (L.) Crantz (sensu lato) or *C. microcarpa* Andr. ex DC. (Syst. Nat. 2: 517. 1821) (sensu lato), or some forms of other related taxa of *Camelina* L.

Camelina armeniaca in taxonomic literature and databases: controversial evidence

The name *Camelina armeniaca* was not in use for a long time. A search (11 August 2022) for the species name “*Camelina armeniaca*” in the Biodiversity Heritage Library (<https://www.biodiversitylibrary.org/>, here and below, all online sources were accessed on 11 August 2022 and double-checked on 26 September 2022, if not noted otherwise) resulted in just four matches, of which one was the protologue, one Steudel’s *Nomenclator Botanicus* (Steudel, 1821), in which the combination *Myagrum armeniacum* (Desv.) Steud. (Nomencl. Bot.: 541. 1821) was validated, and two were seed catalogues of botanical gardens (Bordeaux and St. Petersburg). Also, *C. armeniaca* was accepted as a separate species by Candolle (in Syst. Nat. 2: 514–515. 1821); in that treatment, he also recognised *C. sativa*, *C. dentata* (Willd.) Pers., and *C. microcarpa*. Two other species listed by Candolle in *Camelina* sect. *Pseudolinum* DC. are now placed in *Rorippa* Scop.

The application of the name *Camelina armeniaca* caused confusion already in the 19th century. For example, Herder (1869: 98), in the seed catalogue of the St. Petersburg Botanical Garden (Index Seminum Petropolitani), provided a list of misapplied names and misidentified plant material received from various botanical gardens and (or) cultivated in St. Petersburg (“Nomina emendata plantarum sub nominibus falsis vel ex hortis variis acceptarum vel in horto nostro antea cultarum”), in which he indicated that “*C. armeniaca*” received from Berlin in 1865 was in fact *C. dentata* (Willd.) Pers. (that name is now usually treated as a synonym of *C. alyssum* (Mill.) Thell.: “*Camelina armeniaca* h. Berol. 1865 = *C. dentata* Pers.”).

The name *C. armeniaca* is not mentioned in main floras and manuals covering the territory of the Caucasus and adjacent regions of Turkey and Iran (Vassilczenko, 1939; Hedge, 1965, 1968; Avetisyan, 1966; Dorofeyev, 2012). Furthermore, this name is also absent in BrassiBase (<https://brassibase.cos.uni-heidelberg.de/>; checked on 29 September 2022).

In his recent taxonomic and nomenclatural overview of *Camelina*, Dorofeyev (2019) has mentioned *C. armeniaca* as a synonym (!) of *C. pilosa* (DC.) N.W. Zinger (in Trav. Mus. Bot. Acad. Sci. St. Petersburg. 6: 22. 1909) (Zinger, 1909). Therefore, if these two names are considered conspecific, the name *C. armeniaca* is of priority and should be, in that case, used as the correct name for the taxon known as *C. pilosa*, if the latter is recognised as a separate species and not as a synonym of *C. sativa* or *C. microcarpa*. Moreover, *C. pilosa* (\equiv *C. sativa* (L.) Crantz subsp. *pilosa* (DC.) N.W. Zinger, nom. altern.) is an ambiguous taxon itself, with rather variable diagnostic characters (Mirek, 1980); however, its lectotype (G00203713, see Dorofeyev, 2019; image available at <https://www.ville-ge.ch/musinfo/bd/cjb/chg/ade-tail.php?id=177978&lang>) is still morphologically different from *C. armeniaca*.

In the *Plants of the World Online* database (POWO, 2022), the names *Camelina armeniaca* and *Myagrum armeniacum* are listed as synonyms (!) of *C. microcarpa*. The same taxonomy is currently accepted by the *Global Biodiversity Information Facility* (GBIF, 2022). Of course, the name *C. armeniaca* (1815) has priority over *C. microcarpa* (1821). Therefore, if we accept the above taxonomic concept,

the well-known and universally recognised species currently accepted as *C. microcarpa* should be called *C. armeniaca*.

Likely, such confusion was initially caused by the taxonomic decision of Boissier (1867: 311–312), who in his *Flora Orientalis* listed *C. armeniaca* as a synonym of *Camelina sylvestris* Wallr. α [var.] *sylvestris*. Moreover, Boissier indicated that he had seen the type specimen of *C. armeniaca* in Tournefort’s Herbarium (“*Alyssoides Armena* Tournef. Cor. et herb! *C. Armeniaca* Desv. Journ. III, p. 182!”). Such conclusions of Boissier (1867: 311–312) are quite surprising since *C. armeniaca* and *C. sylvestris* ($=C. microcarpa$, which he also listed as a synonym of *C. sylvestris* α [var.] *sylvestris*) are rather different by several traits. Probably Boissier has not seen any reliable type material of *C. sylvestris* or *C. microcarpa*. We think that the incorrect listing of *C. armeniaca* as a “synonym” of *C. microcarpa* (POWO, 2022) was probably caused by the confusion rooted in Boissier’s concept of *C. sylvestris*. This name is now usually considered to be a synonym of *C. microcarpa*. The reason why Dorofeyev (2019) has listed *C. armeniaca* as a “synonym” of *C. pilosa* (DC.) N.W. Zinger ($= C. sativa$ α [var.] *pilosa* DC.) could be similar: Boissier (1867: 311–312) has listed the name *C. sativa* α [var.] *pilosa* DC. (together with *C. armeniaca*) as a synonym of the mentioned *C. sylvestris* α [var.] *sylvestris*, which may have caused further confusion.

In addition to its wide acceptance in floras, manuals and numerous other publications, *C. microcarpa* was, and still is in, the focus of recent molecular phylogenetic, phylogeographic, and genetic studies aimed at a better understanding of the origin and evolution of an important crop species, *C. sativa*, and its improvement as a significant oilseed and biofuel crop (Brock et al., 2018, 2019, 2020; Mandáková et al., 2019; Žerdoner Čalasan et al., 2019; Mandáková & Lysak, 2022).

As currently understood, plants morphologically corresponding to *C. microcarpa* (sensu lato) are genetically non-uniform through their vast native and introduced geographical range; in particular, they are represented chiefly by hexaploid cytotypes with $2n = 38$, which are distinct from the main crop lineage with $2n = 40$. It has been demonstrated that the original material of *C. microcarpa* sensu

stricto was collected by Andrzejowski “in the eastern part of present-day Moldova or adjacent parts of Ukraine (probably Odesa Region)”, and its type (G00203789; Geneva, De Candolle’s Prodrum Herbarium – G-DC) and isotypes (KW001003103, KW001003104, KW001003105; National Herbarium of Ukraine, Besser Collection – KW-BESS) are identified correctly (Mosyakin & Brock, 2021). It has also been recently revealed that “populations of *C. microcarpa* from Transcaucasia (South Caucasus) are most closely related to *C. sativa* based on cytotype and population structure” (Brock et al., 2022b). Thus, plants from the Caucasus (probably Armenia and/or adjacent areas) collectively known under the name *C. microcarpa* (sensu lato) are among the direct wild progenitors of the crop species *C. sativa*. Caucasian (and Armenian, in particular) origin and domestication of the *Camelina* crop have also been supported by archaeological findings (Hovsepian & Willcox, 2008; Hovsepian, 2010), which is consistent with the results of molecular genetics analyses (Brock et al., 2022b). Therefore, it would be reasonable to assume that a higher level of genetic and phenotypic variance might be observed within hexaploid *Camelina* species and morphotypes native to that region.

Fine-scale taxonomy of the *C. sativa*–*C. microcarpa* polyploid aggregate remains largely unresolved. There are still problematic names of taxa described from or reported in the Caucasus, Turkey and (or) Iran (*C. longistyla* Bordz. in Trudy Bot. Sada Imp. Yur’evsk. Univ. 13: 20. 1912; *C. paphlagonica* Bornm. in Repert. Spec. Nov. Regni Veg. Beih. 89: 66. 1936; *C. caucasica* (Sinskaya) Vassilez. in Komarov, Fl. URSS 8: 652. 1939; *C. bornmuelleriana* Hub.-Mor. & Reese in Feddes Repert. Spec. Nov. Regni Veg. 52: 41. 1943, etc.). It is not clear yet which of those names are correctly applicable in a narrow sense to specific morphotypes and (or) genotypes of wild relatives and possible progenitors of *C. sativa* known from the Caucasus and Eastern Europe.

Under these circumstances, we initially assumed that the possible taxonomic resurrection of the long-ignored and almost forgotten, taxonomically obscure name *C. armeniaca* might result in synonymisation of some well-known and widely accepted name (probably *C. microcarpa* sensu lato?).

On the other hand, it may as well obscure the proper usage of some names applicable to “narrow” taxa of *Camelina* in the Caucasus and adjacent areas, which are hotspots of genetic diversity of wild relatives of the crop species *C. sativa*. Also, the current listing of the priority name *C. armeniaca* as a “synonym” of *C. microcarpa* in main online biodiversity databases (see above) is not acceptable from a taxonomic and nomenclatural viewpoint.

Based on the arguments presented above, we initially considered submitting a formal proposal to reject the taxonomically obscure and firmly forgotten name *C. armeniaca* under Art. 56 of the ICN (Turland et al., 2018) as a solution for maintaining nomenclatural stability in the group containing an increasingly important oilseed and biofuel crop (*C. sativa*) and its wild relatives and progenitors. However, before finalising such a proposal, it was necessary to clarify (if possible) the proper taxonomic application of the name *C. armeniaca*.

Lectotypification of the name *Camelina armeniaca* Desv.

Initially, we were unable to find online data on images of any original specimens of *C. armeniaca*. However, following our request, Germinal Rouhan (Herbier National – P; Muséum National d’Histoire Naturelle, Paris, France) kindly provided information and a link to the high-resolution image of a specimen from the Tournefort Herbarium at P. The label information of P00652666 closely matches the protologue, in which a direct reference to a specimen in the Tournefort Herbarium has been made (see above). Thus, there is no doubt that the specimen P00652666 is part of the original material of *C. armeniaca*. Since it is the only known original element, it could probably be treated as a holotype; however, it is possible that Desvaux also used some other original material. Because of that, following the recommendations of McNeill (2014) and Mosyakin et al. (2019), we designate the specimen from the Tournefort Herbarium as a lectotype.

Camelina armeniaca Desv., J. Bot. Agric. 3(4): 182. 1815.

Lectotypus (here designated; or perhaps holotype):

P00652666, Herbarium Tournefortianum No. 1634, “*Camelina armeniaca* Desv. | Alyssoideis armenia, annua, Myagri | sativi folio”; Fig. 1; image available at: <https://science.mnhn.fr/institution/mnhn/collection/p/item/p00652666>

The taxonomic identity of the type specimen of *Camelina armeniaca*

The specimen P00652666 (designated here as the lectotype of *C. armeniaca*, see above) contains two plants, one (right-hand plant) with rather well-developed fruits, which are shown in Fig. 1. Judging from the size and morphology of fruits, that plant may belong to some morphotype of the *C. sativa* aggregate. In particular, the shape of fruits is very similar to that of *C. caucasica* (Sinskaya) Vassilcz. (in Komarov, Fl. URSS 8: 601, 652. 1939). Also, morphotypes similar to the left-hand plant at P00652666 may occur in other morphologically outlined groups of *C. sativa* sensu lato, as it was discussed above.

However, plants of *C. armeniaca* are sparsely villose or almost glabrous and have a few branches, while plants of *C. caucasica* were reported as pubescent and much-branched. Branching pattern could probably be considered a species-defining trait, but only in well-developed plants. It has been reported that *Camelina* plants that emerge during late summer may be significantly shorter than normally developed ones (Zinger, 1909). This particular feature has also been observed by one of the authors (RB) during *C. sativa* cultivation experiments in 2020–2021 (unpublished data). Moreover, it has recently been reported that *C. sativa* demonstrates four distinct types of branching within different genotypes of *C. sativa* deposited at the USDA genebank (Hotton et al., 2020), even though all these genotypes have previously been found to be highly genetically uniform (Luo et al., 2019). In addition, the description of *C. alpkoyensis* Yild. as a separate species (Yildirimli, 2011), based on the absence of stem branching, has been criticised. That character is considered an ecotype-specific feature (German & Özüdođru, 2020), and thus *C. alpkoyensis* is placed in the synonymy of *C. laxa* C.A. Mey.

A comparison of the lectotype of *C. armeniaca* with the lectotype of *C. sativa* (BM000646251)

suggests that Desvaux’s observation regarding the fruit shape of his species (see above) is rather precise (Fig. 2). It is visible that the fruits of the type of *C. sativa* are more globose, rather abruptly narrowing into the pedicel, while silicles of the type of *C. armeniaca* are significantly elongated, pyriform, and gradually becoming narrower down to the pedicel. Semi-mature fruits of the type specimens of both species keep the main traits of ripe fruits. However, the young fruits of the type of *C. armeniaca* may have a globose or elongated-globose shape and seem similar to those of *C. sativa*. Thus, the shape of the observed fruits of *C. armeniaca* is consistent with the description provided by Desvaux (1815: 182) in the protologue.

The differences in fruit morphology (one of the most important characteristics for *Camelina* species differentiation) reported by Desvaux (1815: 182) and observed in the lectotype are not sufficient for considering *C. armeniaca* a separate species or even an infraspecific entity of *C. sativa*. An early comprehensive study of *C. sativa* genetics (Tedin, 1925) has demonstrated that the length, width and thickness of fruits are inherited separately and could be combined in different ways. Consequently, almost any possible combination of fruit traits can be obtained: long, broad and thick; long, narrow and thick; short, broad and thin, etc., and the different shapes of the fruit, considered by some taxonomists to be typical for certain “species” or “subspecies”, do not genetically behave as lump units; thus a great many intermediate forms between these narrowly circumscribed “species” can be obtained. Therefore, it would be reasonable to assume that *C. armeniaca*, indeed, represents a morphotype, or form, of *C. sativa*, probably native to the region of collection or a local landrace, but not a stable taxonomic unit, since its main traits fall well within the range of variation of fruit shapes observed for *C. sativa* by Tedin (1925) and other authors.

Judging from the size and shape of silicles, as well as other observable characters of the specimen P00652666, *C. armeniaca* is definitely not conspecific with *C. microcarpa*, but in fact, represents a morphotype of *C. sativa* sensu lato. Because of that, we abandoned our initial idea to submit a proposal to reject the name *C. armeniaca* as an earlier name, possibly threatening *C. microcarpa*, and thus a rejection proposal is no longer necessary.



Fig. 1. Specimen P00652666, designated here as the lectotype of *Camelina armeniaca* (possibly holotype), deposited at Herbarium National (P), Muséum National d'Histoire Naturelle (MNHN)

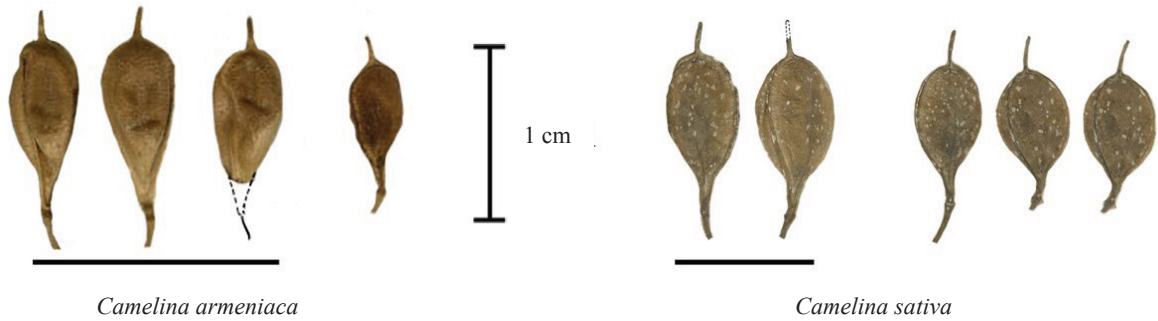


Fig. 2. Fruits of the lectotype of *Camelina armeniaca* (left, mature fruits are underlined) and the lectotype of *Camelina sativa* (right, pre-mature fruits are underlined). Damaged or non-visible parts of the fruit are drawn with dashed lines

A corrected typification of the name *C. sativa* var. *caucasica* ≡ *C. caucasica*

Dorofeyev (2019), who has recognised *C. caucasica* as a separate species, has commented on his search for any original material of *C. sativa* var. *caucasica* in the collections of the N.I. Vavilov All-Russian Institute of Plant Genetic Resources (VIR) as unsuccessful. Because of that, he decided to designate the specimen LE01053073 (see the original label citation below) as the “neotype” (with two “isoneotypes”: LE01053074 and LE01053076); that specimen was supposedly seen by Vassilchenko (Vasilchenko), who apparently discussed that taxon with Sinskaya (also transliterated as Sinskaja in some of her publications), the author of the basionym.

However, while proposing that neotype designation, Dorofeyev overlooked that, according to Art. 9.13 of the *ICN*, a neotype may be selected only if no original material is extant or as long as it is missing. Also, a lectotype always takes precedence over a neotype. The protologue of *C. sativa* var. *caucasica* (Sinskaja, 1928) contains Figure 105 on page 543. That illustration is part of the original material of the name (see Art. 9.4(b) of the *ICN*: “any illustrations published as part of the protologue”). Thus, the original material of *C. sativa* var. *caucasica* is not missing. Because of that, we designate here the illustration in the protologue as the lectotype. However, that illustration is not sufficiently diagnostic, being just a general habit photograph of a plant; moreover, the technical quality of that illustration is also insufficient for diagnostic purposes. Because of that, we designate here the specimen LE01053073 as the epitype (Art. 9.9 of the *ICN*) (see below).

Camelina sativa (L.) Crantz var. *caucasica* Sinskaya in Trudy Prikl. Bot. [Труды по прикладной ботанике, генетике и селекции] 19(3): 544. 1928. ≡ *C. caucasica* (Sinskaya) Vassilcz. in Komarov, Fl. URSS [Флора СССР] 8: 601, 652. 1939.

Lectotypus (here designated): Fig. 105 in Sinskaya (Sinskaja, 1928: 543).

Epitypus (here designated): LE01053073: “Princeps W. Massalsky: Plantae Armeniae 1886. Есмак (гур.) культив. в Хорасанском участке Кагызманского округа, для масла употр. в пищу”, the specimen proposed by Dorofeyev (2019) as the “neotype”; see Fig. 11 in Dorofeyev (2019).

The provided description of *C. sativa* var. *caucasica* by Sinskaya (Sinskaja, 1928) states that this taxon has relatively small pyriform-elongated thin fruits, 0.9–1.0 cm long (“siliculis oblongo-pyriformibus, valvis plerumque concavis 0.9–1.0 cm longis”), which is also clearly observed on the epitype specimen, the image of which has been provided by Dorofeyev (2019). However, such diagnostic features of *C. sativa* var. *caucasica* suggest that this taxon may be conspecific with *C. armeniaca*, since all of these fruit morphology characteristics could be found in its type (lectotype) specimen (Fig. 1).

CONCLUSIONS

The long-forgotten and taxonomically problematic name *Camelina armeniaca* is one of the earliest species-rank names published in *Camelina*. Thus, the proper taxonomic application of that name is important for the nomenclature of taxa belonging to the *C. sativa*–*C. microcarpa* aggregate that contains the major oilseed and biofuel crop *C. sativa* and its wild

relatives and progenitors. The name *C. armeniaca* is lectotypified here with the specimen P00652666 from the Tournefort Herbarium in Paris (P). Morphological characters of the lectotype (a high-resolution digital image is available from the P Herbarium website) indicate that taxonomically it represents one of the Caucasian morphotypes of *C. sativa* sensu lato, probably similar or related to *C. caucasica* (*C. sativa* var. *caucasica*). *Camelina armeniaca* is not conspecific with *C. microcarpa* (contrary to what has been suggested recently in some online biodiversity resources). At present, we treat *C. armeniaca* as a synonym of *C. sativa*; however, further studies may result in its recognition as one of the infraspecific entities (most probably a variety or form) of *C. sativa*. A corrected typification (lectotypification and epitypification) of the name *C. sativa* var. *caucasica* is also provided.

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