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ALEXANDER P. SUKHORUKOV

Fruit anatomy and its taxonomic significance in *Corispermum (Corispermoideae, Chenopodiaceae)*

Abstract

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Data on comparative carpology of the species of *Corispermum* are presented. Their fruits are monomorphic and characterised by similar structural peculiarities. A combination of carpological features is shown to be important in the taxonomy and systematics of *Corispermum* species. 13 groups of species are distinguished based on fruit shape and dimensions, indumentum, wing shape and width, ultrasculpture of pericarp surface, detachment patterns, thickness of the outer pericarp layer and number of macrosclereid layers in the median portion of a fruit. A diagnostic key to the species groups supplemented by further characters is provided. Differences and general trends of specialisation in the anatomic structure of *Corispermum* and the other two genera of the *Corispermoideae, Anthochlamys* and *Agriophyllum,* is shown. The delimitation of the subfamily is confirmed by the results of the fruit anatomical studies.

Key words: *Anthochlamys, Agriophyllum,* fruit, taxonomy, carpology, anatomy, systematics

1. Introduction

The genus *Corispermum* L. contains at least 65 annual psammophilic species occurring mainly in extratropical regions of Eurasia and North America. Fifty species were reported for the territory of Russia and adjacent countries alone (Czerepanov 1995). Eleven species are restricted to North America, four taxa occur in both Europe and North America (Mosyakin 2003b). Despite the presence of suitable habitats, no species are known from N Africa (Boulos 1999, Romo 2002) and the Arabian Peninsula (Miller & Cope 1996). Some species are known as introduced and naturalized in Eurasia and North America far beyond their natural ranges (e.g., *C. declinatum, C. pallasii*). Few studies of chromosome numbers of *Corispermum* species are available at present; according to them solely diploid taxa with $2n = 18$ are known (Löve & Löve 1961, Fedorov 1969, Adamkiewicz 1970, Magulaev 1976, Probatova & Sokolovskaya 1990, Lomonosova 1992, Lomonosova & al. 2005).

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Corispermum together with *Anthochlamys* Fenzl and *Agriophyllum* M. Bieb., which have their diversity centres in Asian regions with arid climate, form the subfamily *Corispermoideae.* It is characterized by: annual life form; sessile or petiole-like attenuate leaves; simple, compact partial inflorescences (sometimes almost globular) or set-apart spikes; missing bracteoles; 1-5 white, membranaceous tepals (missing in some *Corispermum* species) without vascular bundles; branched trichomes (except in *Anthochlamys*) or sometimes reduced, however, in most cases falling off readily by the end of vegetation period; seeds with vertical embryo and copious perisperm. For all species studied, non-Kranz corispermoid leaf structure and C3 photosynthesis were reported (Carolin & al. 1975, Akhani & al. 1997, Jacobs 2001). Pollen grains are either of the *Chenopodium* type *(Agriophyllum, Corispermum)* or of the recently discovered *Anthochlamys* type (*Anthochlamys* only: Mosyakin & Tsymbalyuk 2002). Fruits of all *Corispermoideae* species possess supporting tissue consisting of macrosclereids, which seems to be usually missing in the other subfamilies or to consist of brachysclereids (in some *Salsoloideae* genera). Molecular data support a common ancestry of all three genera and, consequently, the monophyly of the group (Kadereit & al. 2003).

Corispermum is known as one of the taxonomically most problematic genera in *Chenopodiaceae* and species identification is primarily based on fruit characters. The fruits, developed from the superior ovary, can be round, elliptical or oblong-elliptical in outline and are 1.5-6.5 mm long. On the adaxial side they are flat or slightly concave, on the abaxial side convex. They are glabrous or rarely covered with branched trichomes. Each fruit bears two filiform stylodia; the lower parts of the stylodia always persist on the ripe fruit, the upper parts usually fall off along with the stigmata after pollination. The pericarp is most often tightly adjoined to the spermoderm and forms a more or less developed, continuous, semi-translucent, wing-shaped projection along the margins of the fruit.

The shape and dimensions of fruits and fruit wings, presence of trichomes and/or papillae and the wing outline near the persistent part of the stylodia have been the most important carpological traits for species identification within the genus. Other commonly used diagnostic characters are leaf width, pubescence and, less often, the bract/fruit width ratio.

Different species concepts coexist in many groups of the genus due to variability of some characters, in particular, the degree of wing development and the condensed versus interrupted spike-like inflorescences.

The first attempt of intrageneric subdivision of *Corispermum* was undertaken by Fenzl (1849), who placed all species he knew into two groups: such with glabrous and such with pubescent fruits. Morphological traits of fruits were widely used in later taxonomic treatments (Popov 1959, Klokov 1960). Klokov (1960) proposed several series for the European taxa, a system later revised, enlarged and supplemented by Mosyakin (1994, 1997), who, however, has considered his system as provisional. Mosyakin (1994, 1997) divided *Corispermum* into three sections: *C.* sect. *Corispermum,* comprising the majority of the species and divided into several subsections, *C.* sect. *Declinata* Mosyakin and *C.* sect. *Patellisperma* Mosyakin. Only two subsections in *Corispermum* sect. *Corispermum* (i.e. subsect. *Canescentia,* subsect. *Crassifolia*) seem morphologically more isolated compared to other currently recognized supraspecific taxa. Their representatives lack tepals in all or the majority of flowers. The differences between these subsections are in fact limited to the orientation of the stylodia bases: in subsect. *Canescentia* the stylodia are convergent, in subsect. *Crassifolia* they are divergent. The taxonomic position of many other taxa requires further investigation, e.g., the affinity between *C. nitidum / C. heptapotamicum* and *C. laxiflorum / C. lehmannianum* (Mosyakin 1995).

Fruit anatomy therefore seems to be of special importance. Only a few members of *Corispermum* have been anatomically studied. The general fruit structure of *Corispermum* was discussed by Butnik (1981), using *C. lehmannianum* as an example. The first comparative study was done by Kamayeva (1982) of species occurring in the Lipetsk region (central part of European Russia). She reported that anatomically the fruits of *C. declinatum, C. hyssopifolium, C. marschallii* and *C. nitidum* differ in their shape and wing width as well as in the number of cell layers in the median portion of the pericarp.

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The present research was undertaken to make a wider assessment of the diversity in the fruit structure within the genus and to study the correlation of morphological and anatomical traits. The main idea was to demonstrate the use of the totality of carpological features in the systematics of *Corispermum* and to clarify the relationships between *Corispermum* and the other two closely related genera.

2. Material and methods

The material for the present study was collected by the author in 1997-2005 in Kazakhstan and European Russia or obtained from the following herbaria (herbarium abbreviations according to Holmgren & Holmgren 1998-): H, KW, LE, MHA, MOSP, MW, TK. For the most critical or rare taxa of *Corispermum,* the material from types and other authentic specimens was used, if available. The list of the specimens investigated is given in the Appendix.

For the anatomical studies, fruits from the lower, middle and upper part of the partial inflorescences were used to detect heterocarpy or heterospermy and variations in their structure within a plant. For comparative purposes, fruits of most species of the other two, oligotypic genera *Anthochlamys* Fenzl (*A. afghanica* Podlech, *A. multinervis* Rech. f., and *A. tianschanica* Aellen) and *Agriophyllum* C. A. Mey. (*A. latifolium* Fisch. & C. A. Mey., *A. paletzkianum* Litv. and *A. squarrosum* (L.) Moq.) of the subfamily were included in the study. The material was soaked in a mixture of ethyl alcohol, water and glycerine (in equal proportions) for a few days at 37 °C. Free-hand longitudinal and transverse sections were made in different fruit parts, and were then fixed with 0.2 % neutral toluidine blue solution or processed with phloroglucinol and hydrochloric acid for revealing lignification zones. For further statistical processing of the results, always the data obtained from the sections made in the median part of the fruits were used to ensure comparability, since for some measurements (wing length, number of sclereid layers) the values are different in sections made in the upper or lower part of the fruit.

The terms “exocarp”, “mesocarp” and “endocarp” are not used in the descriptions on purpose, since no papers on fruit wall typology in the family *Chenopodiaceae* are available. The terminology of Fedorov & al. (1956) has been used for describing the fruit shape.

Pericarp surface ultrasculpture and fruit sections were studied under a scanning electron microscope HITACHI 405A at the Laboratory of Electron Microscopy of the Moscow State University. Unlike the taxa of *Chenopodiaceae* with fruits enclosed in perianth or bracteoles, the fruits of *Corispermum* and closely related *Anthochlamys* are not protected from environmental influences by leaf covers. Therefore the fruit surface was pretreated in 70 % ethyl alcohol for 4-6 hours to remove contaminants before studying the surface ultrasculpture.

3. Results

3.1. Fruit anatomy of *Corispermum*

The fruits of all studied species of *Corispermum* were found to be homomorphic, with the same anatomical structure (Fig. 1A+B). No differences were revealed in the pericarp and seed coat structure on the adaxial and abaxial fruit sides in cross sections.

Pericarp. – Cross sections show that the pericarp consists of two zones, standing in marked contrast to one another. Zone 1 consists of either one or two layers, usually with colourless contents. Some cells, however, may contain brown pigments (turning blue when processed with toluidine); clusters of such cells are common in fruits of many species and can be seen with an unaided eye as dark brown spots at the fruit surface. The cells of the outer zone 1 layer are round or rectangular in cross section and (12-)20-50(-90) µm thick. Some species *(C. papillosum, C. tylocarpum)* have papillae (Fig. 2A) in addition to the isodiametric cells of the outer layer and/or branched trichomes (Fig. 2B), which easily fall off and are therefore often not observed in sections. The outer zone 1 layer is continuous and always well discernible along the periphery of the fruit. The

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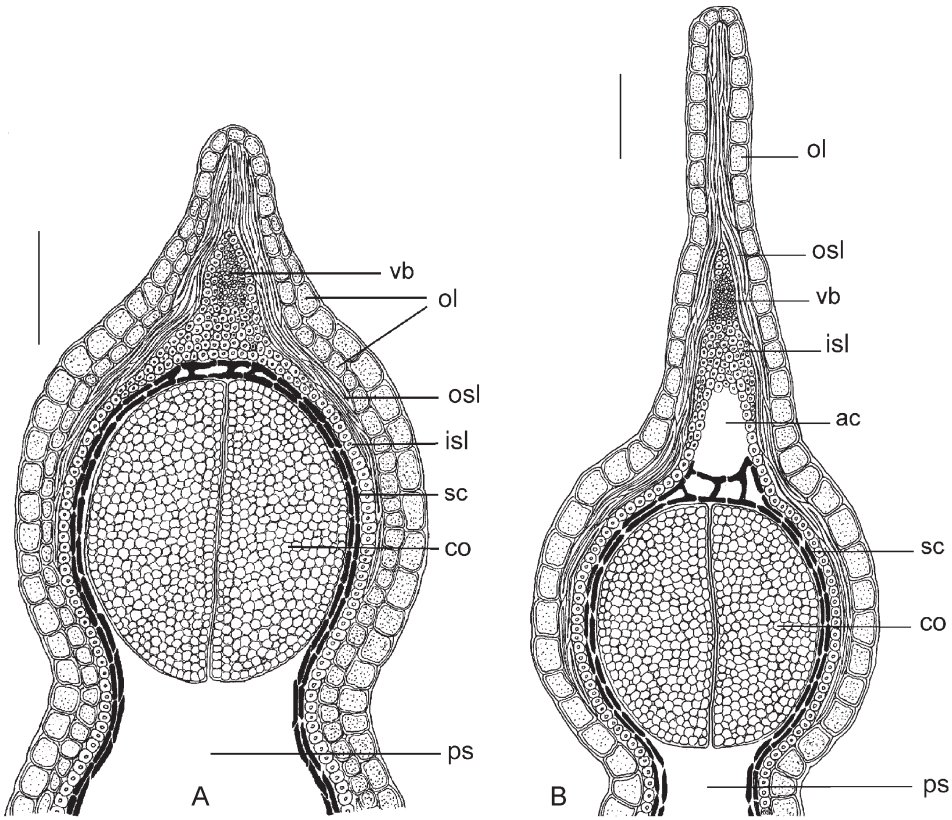


Fig. 1. Cross sections of the median part of the fruit of *Corispermum heptapotamicum* (A) and *C. macrocarpum* (B). – Abbreviations: ac = air cavity, co = cotyledons, isl = inner sclereids layer(s), ol = outer pericarp layer(s) (Zone I), osl = outer sclereids layer(s), ps = perisperm, sc = seed coat, vb = vascular bundles. – Scale bars: 100 µm.

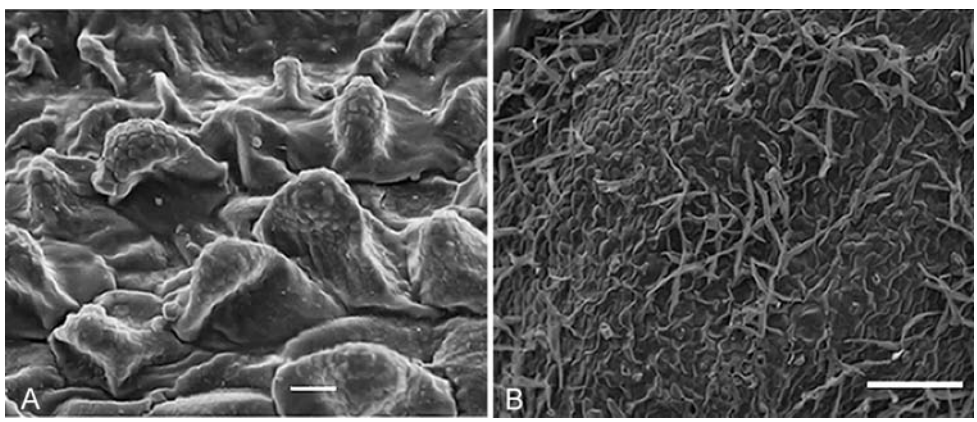


Fig. 2. Pericarp surface of *Corispermum papillosum* (A) and *C. gelidum* (B). – Scale bars: A = 30 µm, B = 300 µm.

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cells of the inner layer are usually thinner, compressed, or entirely absent. *C. filifolium, C. heptapotamicum, C. korovinii, C. lehmannianum, C. papillosum, C. krylovii,* and often *C. gallicum* and *C. nitidum* aggr., appeared to possess a pronounced two-layered zone 1 with cells developed to about the same extent except for the wing area.

The pericarp layers of deeper location (zone 2) consist of supporting tissue of macrosclereids. The cell thickness in different species varies from 3 to 7(-12) μm and the number of layers markedly increases from the middle of the fruit toward its periphery (i.e., toward the wing). The way of how these layers are oriented in different directions, always noticeable in the wing area, is peculiar for the subfamily: in the outer layers, facing zone 1, the longish cells are oriented perpendicular to the long axis of the fruit, while the inner ones, adjoining the spermoderm, are oriented along its long axis. In cross section the sclereids of the outer layers are thus of ribbon-like outlines, whereas the ones of the inner layers are round. The wing is composed of both pericarp zones, the cells of zone 2 (supporting tissue) making the major contribution to its formation. Despite the fact that some species (*Corispermum orientale, C. heptapotamicum,* etc.) are often described as lacking a wing, it is noteworthy that the wing always exists but can be minute (0.08-0.1 mm long). In the median part of the fruit, the number of supporting tissue cell layers is 1-5(-6) but the outer layers of sclereids are lacking in many species, and in such cases the supporting tissue is represented by 1-4 inner layer only. In other species *(C. laxifolium, C. aralocaspicum, C. caucasicum, C. hookeri)* no supporting tissue is found in the median part of the fruit, or is represented by a single (the innermost), interrupted layer. Thus, in these species the pericarp in the median part is made of only 1-2 zone 1 cell layer(s). The supporting tissue sclereids located on both sides of the wing meet at the wing edge and the number of layers grows significantly towards the edge from 4 up to 15. It is believed that sclereids contribute to the seed-protective function (Netolitzky 1926, Kamayeva 1982). Nevertheless, when supporting tissue is missing in the medium part of the fruit, the protective function is transferred, to a certain extent, to the spermoderm.

Air cavities are often found between the spermoderm and the inner sclereid layer in the wing; in many taxa it is especially pronounced in the upper and lower part of the fruit. In a few species *(C. heptopotamicum, C. mongolicum, C. pamiricum, C. patelliforme, C. piliferum)* this cavity is not developed; on the contrary, in *C. ulopterum* or *C. puberulum* is it large (up to 100 μm in diameter), going through end-to-end. Derivatives of vascular elements can only be found in the wing part between the outer and the inner sclereid layers.

Zone 1 cells most often adhere to zone 2 (or to the seed coat in *Corispermum laxiflorum, C. aralocaspicum, C. caucasicum,* and *C. hookeri*), but in many taxa the zone 1 layer can be detached from the zone 2 layers, forming cavities, usually small (up to 70 μm). Occurring only in the non-wing part of the fruit, these cell detachments are optional in the majority of species. They can be visualized as whitish warts at the fruit surface. Only in *C. ulopterum* the detachments of the outermost pericarp layer at cross sections (including the wing area) appeared to be obligatory. Large and undulate, they give the fruit a "crumpled paper" look at the large-scale view (Fig. 3A).

Seed coat. – The seed coat is (3-)5-10 μm thick, formed by 2 layers of markedly compressed, crushed tannin-containing cells. Only in some fruits of *Corispermum patelliforme* 3-layered spermoderm was found. There are reasons to believe that the spermoderm in the genus is derived from the inner integument of the ovule (Netolitzky 1926, Wunderlich 1967). Usually intercellular spaces between spermoderm cell layers are unnoticeable, but in a number of taxa of different taxonomic positions *(C. hilariae, C. intermedium, C. ulopterum)* they can be well seen at high magnification at certain spots. The innermost spermoderm cell layer is covered with a well developed cuticle from inside.

Perisperm and embryo. – The perisperm is copious. The embryo appeared to be well developed, with two cotyledons, located parallel to the seed surface, or slightly oblique in relation to the fruit surface (see also Volkens 1893). Such position of cotyledons is considered rare in the family (Ulbrich 1934). However, this character should not be treated as genus-specific because in

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Table 1. Species groups in *Corispermum* based on carpological characters and comparative carpology of *Corispermum* species.

Taxa	Fruit shape (outline)	Fruit length × width [mm]	Hairs (= h)/ papillae (= p)	Wing shape and width in cross section [mm]	Ultrasculp-turing of peri-carp surface	Width of outer pericarp layer [µm] without papillae	Detachment of outer pericarp layer	Macrosclereid layers (i = inner, o = outer) in median part
I. *Patelliforme* group								
C. patelliforme	round	3-3.7 × 0.5-0.9(-1)	–	broadly triangular, 0.15-0.3	+	(62-)70-90	small	0-1(-2) o, 1-2 i
II. *Ulopterum* group								
C. ulopterum	broadly elliptical	3.5-4.5 × 0.6-0.8[1]	+ (h)	narrowly triangular, 0.65-0.85	+	30-50(-60)	wave-like, up to 350 µm	1-2(-3) i
III. *Puberulum* group								
C. puberulum	broadly elliptical	3.5-4.2 × 0.3-0.55[2]	+ (h)	narrowly triangular, 0.4-0.6	+	(25-)30-50(-60)	wave like, up to 100-130 µm	1 i (interrupted)
IV. *Aralocaspicum* group								
C. aralocaspicum	broadly elliptical or round	3.2-4(-5) × (0.26-)0.4-0.6	–	narrowly triangular, 0.6-0.8(1.2)	–	(25-)40-65	small	–
C. laxiflorum	broadly elliptical or round	3.2-4.5 × 0.4-0.55	–	(narrowly) triangular, 0.4-0.7	–	35-50(-62)	small	–
C. caucasicum	broadly elliptical or round	3-3.5 × 0.4-0.55	–	narrowly triangular, 0.3-0.4	–	25-45(-60)	small	(1i)
V. *Nitidum* group								
C. americanum	broadly elliptical	2.5-3 × 0.4-0.55	–	triangular, 0.3-0.45	–	25-40	small	1-2 i
C. nitidum aggr.[3]	broadly elliptical or round	2.4-3(-3.5) × 0.4-0.7(-0.8)	–	triangular, 0.26-0.5 (0.4- 0.6 in *C. ucrainicum*)	–	(20-)25-37(-50)	small	1-2 i
C. filifolium	broadly elliptical or round	3.5-5 × 0.35-0.55	–	triangular, (0.5-)0.6-0.9	–	(20-)25-45(-50)	small	1(-2) i
C. korovinii	elliptical	2.5-3.3 × (0.25-)0.3-0.52	+ (h)	(broadly) triangular, 0.2-0.5	–	25-40	small	1(-2) i

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C. lehmannianum	broadly elliptical	2.8-3.2 × 0.40-0.55	–	triangular, 0.3-0.45	–	25-40(-50)	small	1(-2) i
C. papillosum	(broadly) elliptical	3-4 × (0.25-)0.35-0.55	+ (p)	(narrowly) triangular, 0.33-0.65	–	(25-)30-50	small	1(-2) i
VI. *Heptapotamicum* group								
C. chinganicum	elliptical	2.3-3(-4) × (0.5-)0.6-0.8	–	broadly triangular, 0.1-0.2(-0.35)	–	20-37(-50)	small	1(-2) i
C. heptapotamicum	elliptical	1.4-2(-2.5) × 0.4-0.55	–	broadly triangular, 0.13-0.26(-0.4)	–	25-30	invisible	1(-2) i
C. mongolicum	elliptical	1.5-2(-2.2) × 0.3-0.4(-0.55)	–	broadly triangular, (0.08-)0.1-0.15(-0.2)	–	25-30(-37)	small	1(-2) i
C. pamiricum	elliptical	2.2-2.7(-3) × 0.45-0.6	–	broadly triangular, 0.15-0.25(-0.3)	–	20-30	small	1(-2) i
VII. *Piliferum* group								
C. piliferum	(oblong) elliptical	2.2-2.8 × (0.6-)0.7-0.9	+ (h)	broadly triangular, 0.12-0.22	–	20-28	invisible	0-1 o, 3-4 i
VIII. *Dutreuilii* group								
C. dutreuilii	elliptical	2.8-3.5(-4) × (0.25-)0.3-0.5 (-0.65)	–	narrowly triangular, 0.45-0.7	–	25-40(-50)	up to 100 µm	1-2 i
C. gelidum	elliptical	3-3.5 × 0.45-0.65	+ (h)	narrowly triangular, 0.25-0.45	– (epicuticular wax granules)	20-30	small	1 o (interrupted)
C. hilariae	(broadly) elliptical	(2.2-)2.6-3.2 × 0.5-0.65	–	narrowly triangular, 0.3-0.4	–	(20-)25-40(-50)	up to 75 µm	1(-2) i
IX. *Marschallii* group								
C. algidum	broadly elliptical	3.5-4.2 × (0.45-)0.6-0.95	–	(narrowly) triangular (0.3-)0.4-0.6	–	12-25(-30)	small	0-1(-2) o, 1-2 i
C. crassifolium	broadly elliptical or round	3.5-4(-5) × 0.6-0.9	–	narrowly triangular, 0.45-0.65	–	12-30(-35)	small	0-1(-2) o, 1-2(-3) i
C. gallicum	broadly elliptical	2.5-3 × 0.7-0.8	–	triangular, 0.25-0.35	–	25-38(-45)	small	0-1 o, (1-)2-3 i
C. intermedium	broadly elliptical	3.7-4.5 × 0.8-0.9	–	triangular, 0.3-0.5	–	18-25(-32)	small	2-3 o, 2-3 i
C. marschallii[4]	broadly elliptical	3.5-4.8 × (0.45-) 0.55-0.9(-1)	–	narrowly triangular, (0.4-)0.5-0.8(-1.3)	–	12-30(-37)	small	(0-)1(-2) o, 1-2(-3) i

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C. redowskii	broadly elliptical	4-5 × (0.4-)0.55-0.9	+ (h)	narrowly triangular, 0.4-0.7	–	(17-)20-35(-50)	up to 85 (-125) µm	1-2 o, 1-2(-3) i
C. stenopterum	(broadly) elliptical	3-4 × 0.55-0.7	–	triangular, 0.25-0.35	–	17-25	small	0-1 o, 2-3 i
C. uralense	(broadly) elliptical	2.5-3.2 × 0.6-0.9	–	triangular, 0.15-0.25(-0.3)	–	(20-)25-30(-37)	small	0-1 o, 1(-2) i
X. *Macrocarpum* group								
C. komarovii	broadly elliptical	3.2-3.7 × 0.45-0.7	–	narrowly triangular, 0.45-0.65	–	15-30(-37)	small	0(-1) o, 1(-2) i
C. macrocarpum	broadly elliptical	4.5-5.5 × (0.3-)0.4-0.6(-0.65)	–	narrowly triangular, 0.65-1.3	–	25-38	small	0-1 o, 0-1 i
C. navicula	elliptical or broadly elliptical	4-5 × 0.75-1.1	–	narrowly triangular, 0.3-0.45	–	20-35(-40)	small	0-1 i (interrupted)
C. ochotense	broadly elliptical	3-3.7 × 0.5-0.7	–	narrowly triangular, 0.5-0.7	–	(25-)30-40	small	1(-2) i (interrupted)
C. pacificum	broadly elliptical	3.2-4 × 0.4-0.55	–	narrowly triangular, 0.55-0.7	–	(20-)25-35	small	0-1 i (interrupted)
C. pallidum	broadly elliptical	3-3.5 × 0.3-0.4	–	narrowly triangular, 0.3-0.65	–	12-25(-30)	small	0-1(-2) i
C. welshii	broadly elliptical	4-4.5 × 0.45-0.65	–	narrowly triangular, 0.45-0.6	–	35-55(-62)	small	1(-2) i
XI. *Declinatum* group								
C. bardunovii	oblong elliptical	3.5-4 × 0.6-0.8	–	triangular, 0.35-0.5	–	20-37	up to 50 µm	2-3 o, 2-3 i
C. declinatum	oblong elliptical	2.8-3.5(-4.1) × 0.4-0.8	–	triangular, 0.2-0.4	–	12-30(-38)	small	0-1(-2) o, 1-2(-3) i
C. gmelinii	oblong elliptical	3.2-3.8 × 0.4-0.6	+ (h & p)	triangular, 0.15-0.3	–	17-25	up to 50 µm	(0-)1 o, 1-2 i
C. tylocarpum	oblong elliptical	3-3.5 × 0.5-0.8	+ (p)	triangular, 0.1-0.2	–	20-37	up to 100 µm	0(-1) o, 1-2 i
XII. *Hyssopifolium* group								
C. altaicum	elliptical	2.7-3.2 × 0.55-0.7	–	triangular, 0.35-0.5	–	25-37	small	1-2(-3) o, 2(-3) i
C. hyssopifolium	elliptical	2.5-3 × 0.5-0.85	–	triangular, 0.25-0.4	–	(15-)20-30	small	1-2 o, 2-3 i
C. krylovii	(broadly) elliptical	2.2-2.7(-3) × 0.45-0.55	–	broadly triangular, 0.2-0.35	–	25-38	small	1-2 or, 1-2 i
C. orientale	elliptical	2.3-3 × 0.35-0.65	–	triangular, 0.16-0.3(-0.35)		25-50	small	1-2 o, (1-)2-3 i
C. pallasii	(broadly) elliptical	3-3.6 × 0.55-0.8	–	triangular, 0.4-0.7	–	20-45(-50)	up to 100 µm	0-1(-2) o, 1-2 i

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C. sibiricum subsp. *sibiricum*	elliptical	3-3.5 × 0.7-0.9	–	triangular, 0.35-0.6	–	(20-)25-40	small	1-2 o, 2-3(-4) i
C. sibiricum subsp. *jenissense*	elliptical	3-3.5 × 0.4-0.55	–	triangular, 0.25-0.35	–	20-38	small	0-1 o, 1-2 i
XIII. *Hookeri* group								
C. hookeri	(broadly) elliptical	3.5-4 × 0.4-0.6	–	broadly triangular, 0.13-0.26	–	17-30(-45)	small	(1 i, interrupted)
Species of unclear status								
C. candelabrum	elliptical	3.5-5 × 0.6-0.7	+ (h)	triangular, 0.35-0.45	–	25-37	wave-like, up to 160 µm	0-1(-2) o, 2-4 i
C. falcatum	elliptical	3.8-4.5 × 0.45-0.65	–	(narrowly) triangular, 0.5-0.8	–	(25-)30-50	small	1-2 o, (1-)2-3 i
C. grubovii	elliptical	4-4.7 × 0.4-0.6	–	(narrowly) triangular, 0.5-0.7	–	30-50	small	0(-1) o, 1-2 i
C. lepidocarpum	(broadly) elliptical	4-5 × 0.6-0.75	+ (h)	narrowly triangular, 0.85-1.1	–	20-37	invisible	1-2 o, (1-)2-3 i
C. retortum	elliptical	4-5 × 0.45-0.65	+ (h)	narrowly triangular, 0.6-0.8	–	25-37(-50)	small	1-2 o, 2 i

[1-2)] In the parts where pericarp is not detached.
[3)] The same structure in *C. calvum, C. coloratum, C. glabratum, C. insulare,* syn. nov.; *C. nitidulum, C. ucrainicum*.
[4)] The same structure in *C. borysthenicum, C. ×klokovii.*

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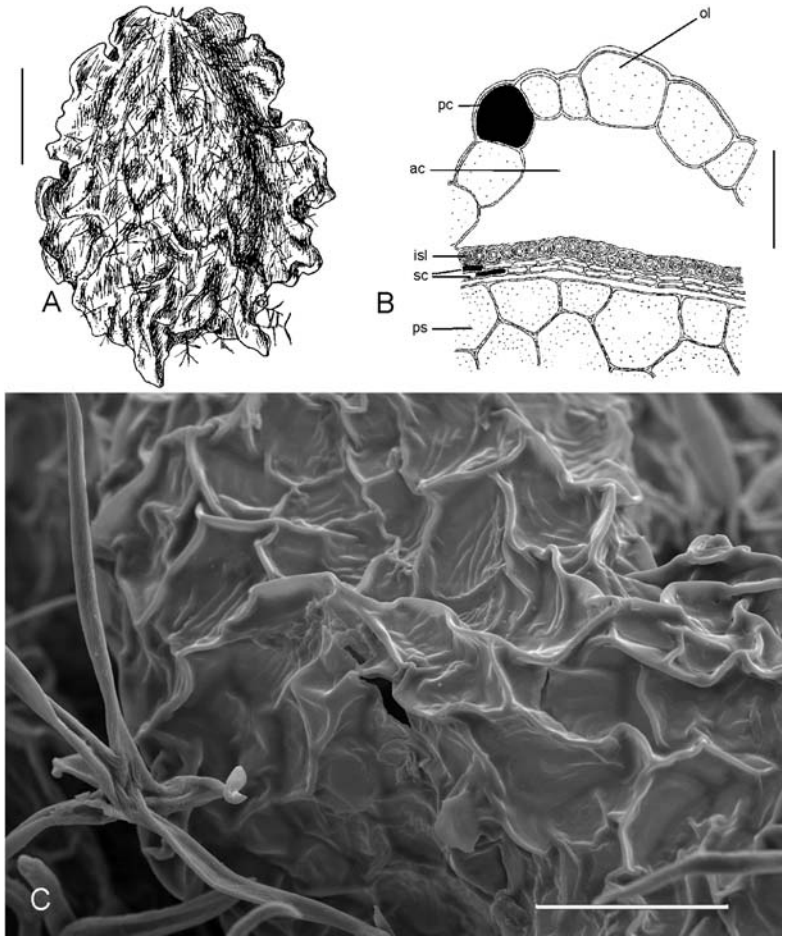


Fig. 3. *Corispermum ulopterum* – A: fruit; B: cross section in the medium part of fruit; C: pericarp surface. – Scale bars: A = 1 mm, B = 50 μm, C = 100 μm; abbreviations: pc = pigment cell, others see caption of Fig. 1.

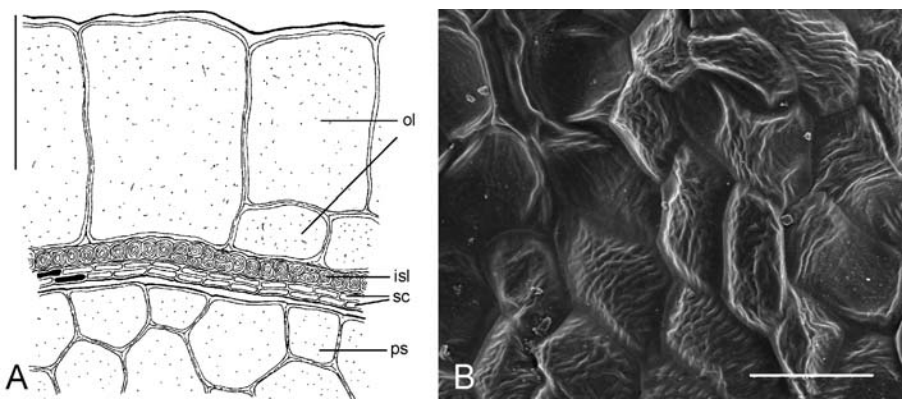


Fig. 4. *Corispermum patelliforme* – A: cross section in the medium part of fruit; B: pericarp surface. – Scale bars: A = 50 μm, B = 100 μm; abbreviations see caption of Fig. 1.

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Corispermum puberulum and large-fruited forms of *C. chinganicum* a perpendicular position of the cotyledons (in relation to the seed and, correspondingly, the fruit surface) was found along with the oblique one.

Regardless that the fruit structure in the genus is generally rather uniform, it proved possible to group the species carpologically. These groups mainly differ in the fruit size and shape, the number of macrosclereids in the median part of the fruit, wing shape, less often in the presence of trichomes and/or papillae, ultrasculpture of the pericarp surface, detachment type and thickness of the outer pericarp layer. The data obtained are summarized in Table 1.

3.2. Key to the species groups of *Corispermum* based on fruit anatomical characters

For a better understanding of the most significant traits of the species groups in the genus, a key for their identification is offered below, which includes also other important diagnostic reproductive and, whenever appropriate, vegetative characters. The key may also be useful in cases where identification of species by gross morphological characters remains ambiguous. The species with unclear status (see Table 1) are omitted from the key.

1. Pericarp detachments (including those in the wing area) large, (40-)60-350 µm, present in all fruits, undulate (Fig. 3A, B); ultrasculpture of pericarp surface usually pronounced (undulated folds, see Fig. 3C); fruits pubescent; innermost layer of zone 1 usually well distinguished along the fruit perimeter . . . . . *Ulopterum* group
– Pericarp detachments seemingly optional and always outside the wing area, small in size (up to 130 µm) or absent 2
2. Isodiametric cells of the outer pericarp layer (62-)70-90 µm thick (Fig. 4A), their outer cell walls with secondary cuticle deposits (Fig. 4B); fruits round, 3-3.7 mm in diameter; wing up to 0.3 mm wide, broadly triangular in cross section; leaves >1 cm wide . . . . . *Patelliforme* group
– Isodiametric cells of the outer pericarp layer ≤ 60(-65) µm thick; outer cell walls only with papillae (if present) up to 90 µm; leaves up to 0.8(-1) cm wide 3
3. Ultrasculpture of pericarp surface plicate, pericarp detachments up to 100-130 µm high; fruits pubescent, widely elliptical, 3.5-4 mm long; wing narrowly triangular in cross section shape, c. 0.4-0.6 mm wide; outermost pericarp layer (25-)30-50(-60) µm thick . . . . . *Puberulum* group
– Ultrascultpure of pericarp surface not plicate (Fig. 5A), sometimes epicuticular wax granules present *(C. gelidum* and *C. papillosum)*; other features different 4
4. Median fruit part lacking macrosclereids (Fig. 5B), or less often, with one interrupted inner layer of sclereids 5
– Median fruit part possessing macrosclereids 7
5. Wing (narrowly) triangular in cross section, ≥ 0.3 mm wide 6
– Wing broadly triangular in cross section, up to 0.26 mm wide; cells of the outer pericarp layer 17-25(-30) µm thick . . . . . *Hookeri* group
6. Outer pericarp cell layer 25-55(-65) µm thick; fruit round or broadly elliptical (Fig. 6A), wider than bracts; inflorescence axes slightly coiled . . . . . *Aralocaspicum* group
– Outer pericarp cell layer (12-)20-30(-38) µm thick; fruit different, narrower than bracts; inflorescence axes straight . . . . . *Macrocarpum* group (p.p.)
7 One sclereid layer only (rarely 2, very rarely 3), usually of the “inner” type (round at cross section) 8
– Two or more sclereid layers, often sclereids differently oriented 11
8. Wing usually conspicuous, triangular or narrowly triangular in cross section; fruits (2-)2.5-4 mm long 9
– Wing mostly inconspicuous, broadly triangular in cross section (Fig. 1A); fruits minute, 1.5-3 (rarely 3.5-4) mm long, elliptical (Fig. 6B); bracts usually covering the fruits completely, only sometimes fruit slightly wider than bracts . . . . . *Heptapotamicum* group

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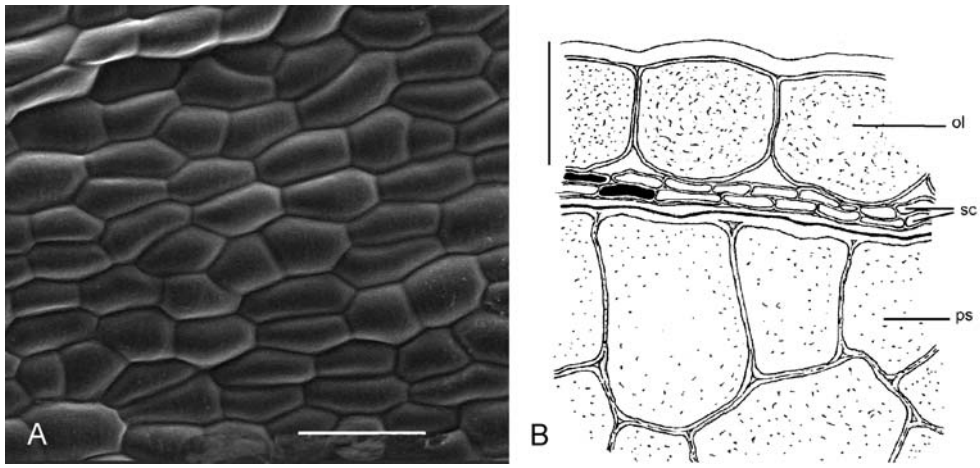


Fig. 5. A: *Corispermum filifolium* – ultrastructure of pericarp surface. – B: *C. aralocaspicum* – cross section in the median part of the fruit. – Scale bars: A = 100 µm, B = 50 µm; abbreviations see caption of Fig. 1.

9. Bracts covering fruit completely; wing in cross section narrowly triangular 10
– Bracts (at least in the upper part of the inflorescence) not covering fruit entirely (i.e. fruit exceeding bracteole); wing in the upper part of the fruit (in the stylodia area) round or with a small excision (Fig. 6C); wing in cross section triangular, with usually well developed inner zone 1 layer . . . . . *Nitidum* group (Fig. 6D)
10. Fruit up to 3.5 mm long, wing in its upper part acute-triangular in cross section without excision (Fig. 6E); outer walls of the outer pericarp layer slightly convex in cross section; supporting tissue represented by 1 to 2 inner layers . . . . . *Dutreuilii* group
– Fruit 3.2-5.5 mm long, wing in its upper part round or with an excision; outer walls of the outer pericarp layer straight in cross section; supporting tissue represented by both inner (Fig. 2) and (sometimes) outer layers . . . . . *Macrocarpum* group (p.p.)
11. Perianth usually missing; fruit wing usually undulate (Fig. 6F), rarely entire; wing narrowly triangular or, more rarely, triangular in cross section; outer pericarp layer with straight (but not convex) outer cell walls . . . . . *Marschallii* group
– Perianth in all or the majority of flowers with 1-3 white, filmy tepals; wing (if visible) entire, triangular or widely triangular in cross section; outer walls of the outer pericarp layer cells not straight 12
12. Wing inconspicuous, broadly triangular in cross section, 0.12-0.22 mm wide; fruits pubescent, 2.2-2.8 mm long; supporting tissue in the median fruit part represented usually by the inner layers (round at cross sections) . . . . . *Piliferum* group
– Wing commonly easily distinguishable, usually ≥ (0.1-)0.15 mm wide; fruits usually ≥ 2.5 mm long; supporting tissue represented by both outer and inner layers (i.e. different in orientation) 13
13. Fruits oblong-elliptical (Fig. 7A), their length exceeding width by factor 2-2.5; wing restricted to the upper part of the fruit (in the stylodia area); outer walls of the outermost pericarp layer cells markedly convex (Fig. 7B) . . . . . *Declinatum* group
– Fruits elliptical to globose; wing restricted to the upper part of the fruit, of round shape or with a small excision; outer walls of the outermost pericarp layer cells insignificantly convex . . . . . *Hyssopifolium* group

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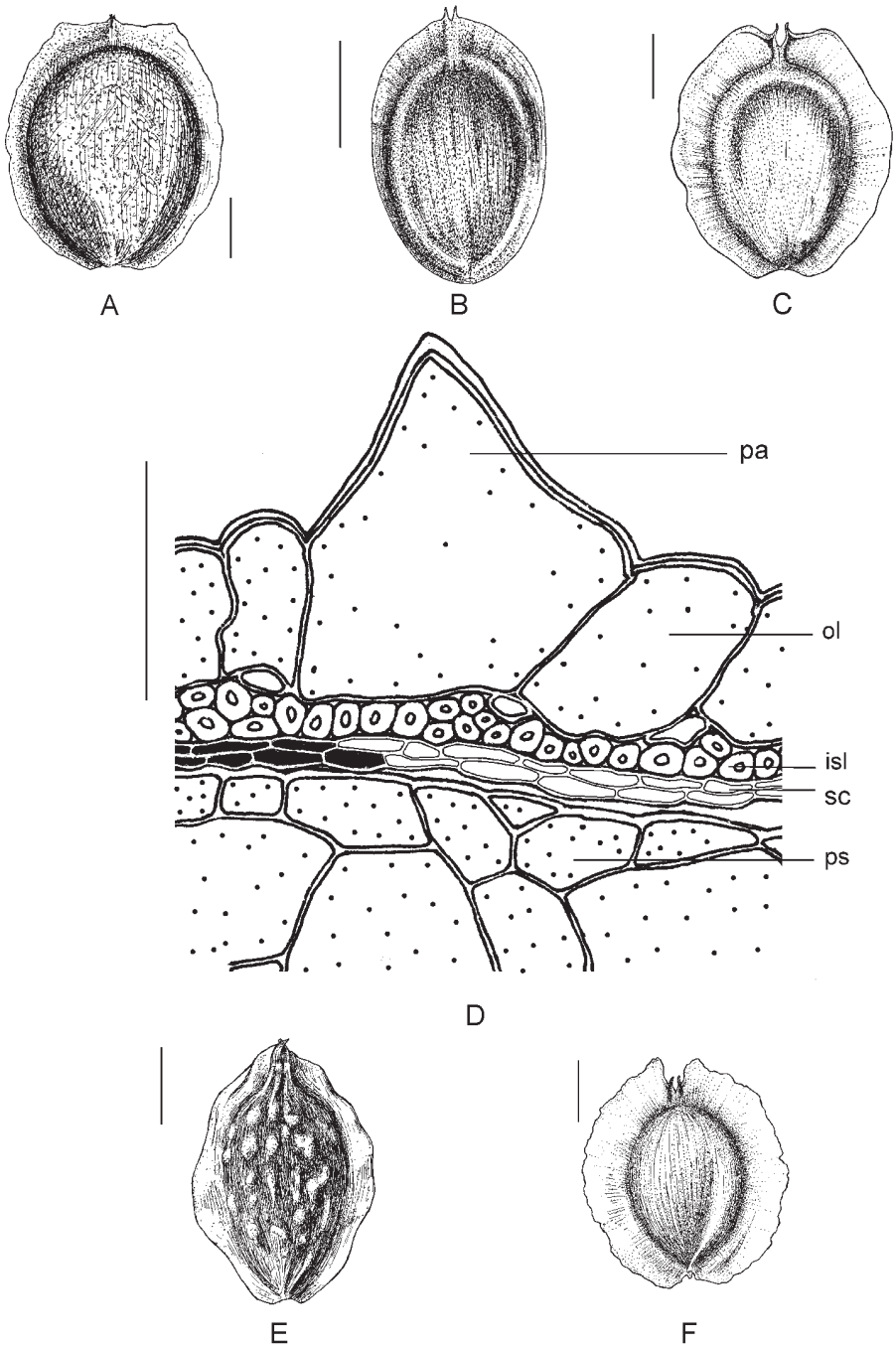


Fig. 6. A: *Corispermum aralocaspicum* – fruit; B: *C. chinganicum* – fruit; C: *C. filifolium* – fruit; D: *C. papillosum* – cross section in the median part of the fruit; E: *C. dutreuilii* – fruit; F: *C. marschallii* – fruit. – Scale bars: A-C, E-F = 1 mm, D = 50 µm.

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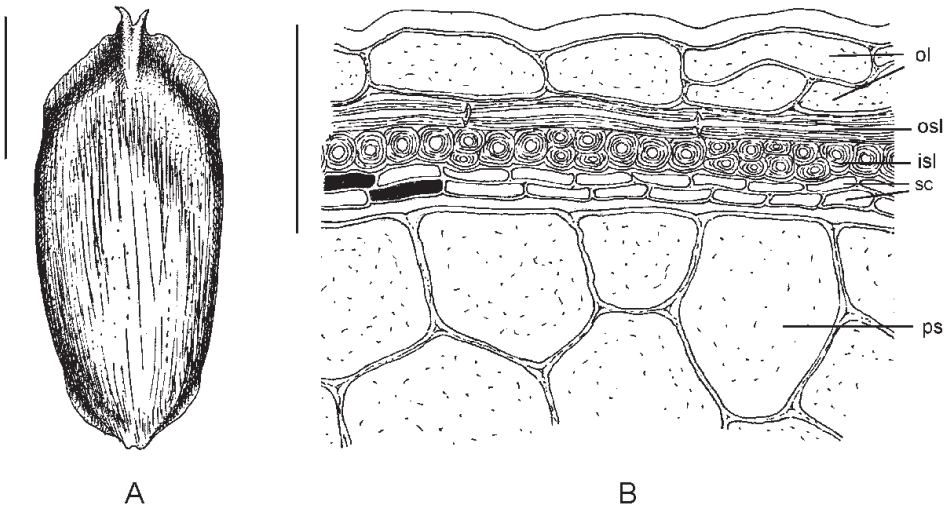


Fig. 7. *Corispermum declinatum* – A: fruit; B: cross section in the median part of the fruit. – Scale bars: A = 1 mm, B = 50 µm.

3.3. Comparative carpology of the *Corispermoideae*

Two diaspore types are known in *Corispermoideae*. One of them is an indehiscent fruit with the pericarp tightly adjoining the spermoderm (represented by *Corispermum* and *Anthochlamys),* with a continuous wing-shaped projection along the fruit margin. Sometimes this diaspore type is interpreted as a fruit surrounded by a "bracteolar involucre" (Butnik 1991). However, the wing-shaped projection lacks any features of a foliar structure, unlike, for instance, diaspores of *Ceratocarpus arenarius* L. (Takhtajan 1934). Smirnova (1984) also used the term "involucre" when characterizing the *Corispermum* fruit, but to name the structural unit consisting of a bract and the tepals, which does not fuse with the fruit. It would be more correct, however, to restrict the term "involucre"to the bract, which covers the flower and, subsequently, the fruit.

The other (represented by *Agriophyllum*) is an adaxially dehiscing (sometimes on both sides) fruit (Fig. 8A) with a more or less round opening, irregular in outline (so-called "dehistentia fenestralis": see Kaden 1964, Smirnova 1972). The way of dehiscence due to a dramatic decrease of pericarp cell layers is a very rare phenomenon in *Chenopodiaceae,* and in this case the seed serves as a dissemination unit. The wing in *Agriophyllum* species is pronounced in the upper fruit part and consists of cells with non-lignified walls, which are round in cross section; supporting tissue are present outside the wing. The cotyledons located perpendicularly to the seed surface (in contrast to *Anthochlamys* and most *Corispermum* species). The seed coat is 3-layered, the outer layer is thicker, not compressed and its cells are rectangular.

Despite the listed differences in fruit structure of *Corispermum* and *Anthochlamys* on the one hand and *Agriophyllum* on the other hand, they have in common that the fruits are more or less flattened, the number of pericarp layers increases toward the fruit margins, the seed coat consists of (1-)2-3 layers and that fruit and seed dimorphism is absent.

The fruits of *Anthochlamys* and *Corispermum* look rather alike, although, unlike those of *Corispermum*, the fruits of *Anthochlamys* are convex both on adaxial and abaxial sides at the large-scale view (Fig. 8B). The convexity of fruit sides is not that well seen at cross sections, however.

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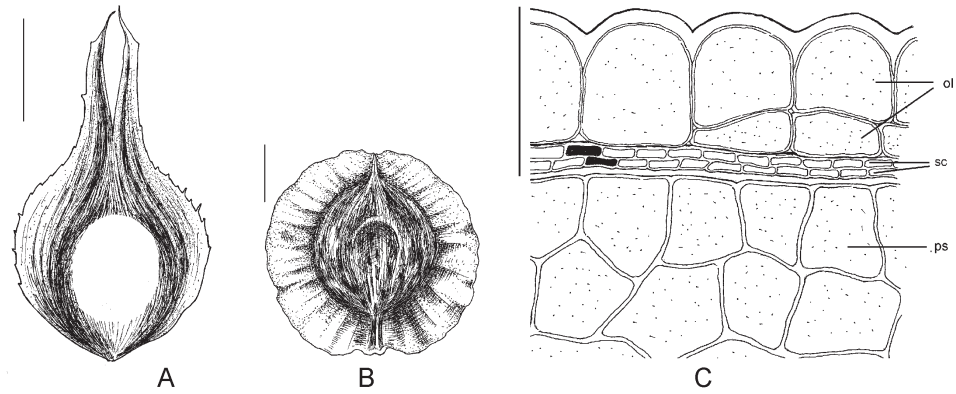


Fig. 8. A: *Agriophyllum squarrosum* (L.) Moq. – fruit. – B-C: *Anthochlamys tianschanica* Aellen – fruit (B), cross section in the median part of fruit (C). – Scale bars: A-B = 1 mm, C = 50 µm.

There are a few clear-cut distinguishable features in fruit anatomy of *Anthochlamys* and *Corispermum*. The pericarp in *Anthochlamys,* as mentioned above, has sclereids only in its marginal part, the median one possessing one to several layers of cells with non-lignified walls. Moreover, at cross sections the outer walls of the outermost pericarp cell layer are semi-circular along the entire fruit perimeter (Fig. 8C). All investigated species demonstrated resemblance in fruit anatomy, so they are diagnosed primarily on the basis of minor morphological traits (Aellen 1950, Hedge 1997).

4. Discussion

4.1. Interpretation of fruit traits for the taxonomy and systematics and of *Corispermum* species

From the first half of the 19th century until today it can be noticed that macromorphological similarity of species (formerly described as separate taxa) has been frequently the reason for authors to consider carpologically actually distant taxa as closely related or even to unite them into very widely circumscribed species such as *Corispermum hyssopifolium, C. lehmannianum, C. marschallii, C. sibiricum* (Moquin-Tandon 1849, Bunge 1880, Kuntze 1887, Ascherson & Gräbner 1913, Iljin 1936a, Aellen 1961, Grubov 1966, Maihle & Blackwell 1978, Voroshilov 1982, Zhu & al. 2003). Fruit anatomy makes it obvious that there is a sufficiently wider range of carpological features that could be used for species identification. Therefore it is desirable to include in identification keys anatomical features as was proposed for the species of the middle and lower Volga region by Sukhorukov (2006c). Fruit anatomy is especially relevant in cases where fruits are very similar (Krylov 1930) and where other features of reproductive organs also intergrade or overlap (*C. filifolium – C marschallii,* see Fig. 6C, 6F; *C. uralense – C. hyssopifolium; C. orientale – C. chinganicum, C. pallasii – C. komarovii,* etc.).

Taxonomic position and/or status of some taxa are often contradictory. For instance, *Corispermum laxiflorum* was allied either with *C. aralocaspicum* (Iljin 1929, Mosyakin 1996), or with *C. lehmannianum* (Mosyakin 1997). Fruit anatomy shows that *C. laxiflorum* is apparently allied with *C. aralocaspicum.* It is also obvious that *C. intermedium* should neither be merged with *C. gallicum* or *C. pallasii* [= *C. leptopterum* (Asch.) Iljin] (Jalas & Suominen 1980). Fruit anatomy supports the treatment of these taxa as independent species, as was proposed by Mosyakin (1995), Gudzhinskas (2000) and Kurtto (2001).

The hypothesis on a hybrid origin of *Corispermum filifolium* (Mosyakin 1996) is not confirmed on the basis of carpological data. The alleged presence of fertile intersectional (and/or intersub-

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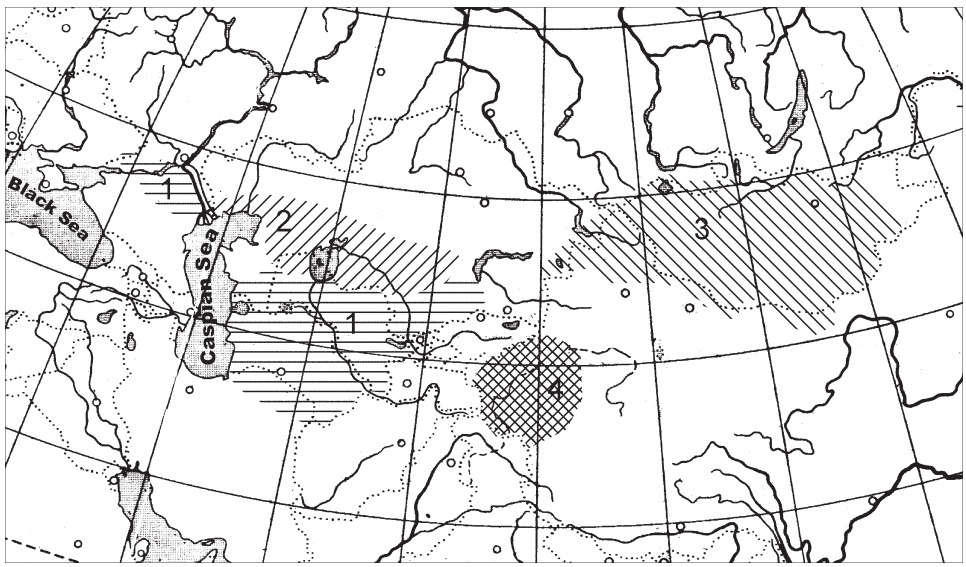


Fig. 9. Initial ranges of some *Corispermum* species groups – 1: *Nitidum* group; *2: Aralocaspicum* group; 3: *Declinatum* and *Heptapotamicum* groups; 4: *Dutreulii* group.

sectional) hybrids indicated in the literature (Klokov 1960, Aellen 1960-61, Strazdinsh 1993) needs further studies.

According to the anatomical studies *Corispermum* ×*klokovii* (= *"calvo-borysthenicum"*) and *C. ucrainicum* most likely represent morphological variants of *C. marschallii* and *C. hyssopifolium,* respectively.

A classification of *Corispermum* species based on carpological features corresponds with the original geographical ranges of these groups (Fig. 9). The species of the *Aralocaspicum* group and the *Nitidum* group (except *C. americanum,* which is believed to be a species native to North America and differs from *C. nitidum* in having larger leaves and narrower fruits) are Turanian elements. Origin and development of species of the *Aralocaspicum* group are probably connected with the Aralo-Caspian province. Central Asian origin can be postulated for both the *Declinatum* group and the *Heptapotamicum* group. Large modern ranges of several species (i.e. *C. declinatum* and *C. nitidum*) undoubtedly resulted from their spreading during the last 100 years (Iljin 1928, Stankov & Taliev 1949, Iljin 1954, Sukhorukov 1999) and are not the result of mosaic-like distribution within the limits of the initial natural range (Skvortsov 1973). The collective range of species of the *Macrocarpum* group is disjunctive, though two American taxa are somewhat different from other species of that group (*C. welshii* has thicker cells of the outer pericarp layer, and *C. navicula* differs in having thicker fruits). The distribution areas of the species of both the *Marschallii* group and the *Hyssopifolium* group range almost entirely north of 43° latitude.

Within the limits of each of the described carpological groups, the anatomic fruit features usually do not allow a confident species identification, but, usually, taxa can be identified on the basis of macromorphological fruit features, especially when papillae or trichomes are present on an unripe fruit. Thus in uncertain cases a combined analysis of macromorphological and anatomical fruit structures is extremely useful. Studies of pericarp structure, e.g., allowed a correct solution in selecting a neotype of *Corispermum papillosum* (Sukhorukov 2006b).

The problem of the various local endemics (related to *Corispermum hyssopifolium, C. nitidum* and *C. marschallii*) described from Ukraine and later accepted by some Ukrainian authors (Skripnik 1987) still remains unsolved. *C. stenopterum* is the most remarkable among the Ukrainian *Corispermum* species allied to *C. marschallii*. It is close to *C. gallicum* according to the fruit anatomy and probably merits species rank as was proposed earlier (Mosyakin 1988).

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From the data analysed so far, it appears that fruit anatomy may be also a valuable source for a natural classification of the *Corispermum* species into infrageneric units. The author has, however, deliberately refrained from any attempt to revise the existing classification prior to the results of a molecular study of the genus.

4.2. Carpological traits and their significance for the taxonomy and systematics of the subfamily representatives

It was considered that *Corispermum patelliforme* and *Anthochlamys* retained some ancestral traits shared with their common ancestor, which both have large spathulate leaves and rather large fruits (Mosyakin 2003a). The results of the present study does not confirm this hypothesis.

A tendency of reduction of pericarp layers in *Corispermum* can be stated, provided that several layers of supporting tissue are a primitive feature as is assumed here. There are some data in favour of this consideration such as a prevalence of several pericarp layers in the median part of fruits in some groups of *Corispermum* with vast ranges and in the species of *Anthochlamys*. In addition, some *Corispermum* species with reduced sclereid layers (i.e. *C. aralocaspicum, C. caucasicum, C. filifolium, C. laxiflorum,* etc.) originated from the Aralo-Caspian and Irano-Turanian floristic provinces (Takhtajan 1978) and should be regarded as phylogenetically younger taxa (Iljin 1952) when taking into consideration the geological history of the region (Wulf 1944, Yakubov 1955) and the small ranges of some taxa today *(C. caucasicum, C. filifolium)*. Otherwise, a tendency of supporting tissue elimination occurred probably independently in several chorologically unrelated groups (*Aralocaspicum* group and *Hookeri* group).

4.3. A survey of the most important carpological features in the family *Chenopodiaceae*

Currently, according to Kadereit & al. (2003), the family *Chenopodiaceae* is subdivided into 6 subfamilies: *Chenopodioideae* Ulbr., *Betoideae* Ulbr., *Corispermoideae* Ulbr., *Salicornioideae* Ulbr., *Suaedoideae* Ulbr. and *Salsoloideae* Ulbr. Along with molecular data, these authors used for their phylogenetic hypothesis such important characters and traits as the ovary position (inferior or semi-inferior in subfamily *Betoideae* and superior in almost all other taxa of the family), leaf anatomy and photosynthetic pathways. Carpological features as the most constant ones among the reproductive traits were not used sufficiently for taxonomic and evolutionary research due to the lack of comprehensive data for many taxa of *Chenopodiaceae*. Detailed information on fruit and seed envelope structure is available only for representatives of subfamily *Salicornioideae* (Shepherd & al. 2005)

The most obvious feature that allowed splitting the family into two large groups, *Cyclolobeae* C. A. Mey. and *Spirolobeae* C. A. Mey., is the embryo position and the presence of perisperm in the seed (Meyer 1829). Moreover, it was believed that the first group is known to have a ring-shaped (or horseshoe-shaped) embryo along with the nutritive tissue, while *Spirolobeae* appeared to possess spiral embryos and no perisperm. Some researchers (Pratov 1970, Blackwell 1977) until recently adhered to this concept of the family subdivision, recognizing, correspondingly, the subfamilies *Chenopodioideae* and *Salsoloideae* sensu latissimo. However, more often the family was subdivided into 3 to 4 subfamilies, with recognition of more or less widely circumscribed tribes (Williams & Ford-Lloyd 1974, Kühn & al. 1993).

Revealing differences in seed structure in various representatives of the family, shown, e.g., in Martin's (1946) paper, researchers paid attention to other traits, too. In particular, these were heterocarpy and heterospermy as evolutionary adaptations playing an important role in the dissemination process, conservation of soil seed banks and seed germination in different years (Levina 1981). Today heterospermy, expressed morphologically (different colours and shapes of seeds) and anatomically (different number and thickness of spermoderm layers) has been proven for many taxa. In particular, the majority of Eurasian species of *Suaeda* Forssk., *Atriplex* L. (Becker 1913, Sukhorukov 2006a) are shown to have heterospermy, as well as some *Chenopodium* species (Baar 1913, Baygosina & al. 1984). Heterocarpy was reported for representatives

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of the genera *Axyris* L. (Crocker 1906, Sukhorukov 2005) and *Halogeton* C. A. Mey. (Zappetini 1953, Sukhorukov unpubl. data), a number of annual species of *Salsola* L. (Rilke 1999), *Halothamnus* Jaub. & Spach [= *Aellenia* Ulbr.] (Werker & Many 1974) and also for *Atriplex* sect. *Atriplex*. Despite the fact that research on heterocarpy and heterospermy are not completed, it can be surely stated that this feature is a good one to be used in the systematics of certain *Chenopodiaceae* groups, in particular, for classifying Eurasian species of the genus *Atriplex* (Sukhorukov 2003). It is also meaningful for the identification of "suaedoid" representatives of the family (Iljin 1936c, Schütze & al. 2003).

Studies of heterocotyly that started quite recently are of great interest. They are connected with different quantity of chloroplasts in embryos (Yamaguchi & al. 1990), the colour of cotyledons (Smirnova 1972) and correlation of this trait with a certain fruit type (Werker & Many 1974), as well as with the presence of phytoecdysteroids in seeds (Dinan & al. 1998).

An interesting fact significant for the classification of the *Chenopodiaceae* was revealed in subfamilies *Chenopodioideae* s. str. (*Chenopodium* L., *Roubieva* Moq., *Atriplex* L., *Cycloloma* Moq., *Monolepis* Schrad., etc.) and *Suaedoideae*. Given all the known structural diversity of fruits and seeds within the taxa investigated, it is still striking and therefore should be pointed out: in the thumping majority of these taxa, widely distributed and considered to be the most primitive in the family (Zhu 1996), all seeds (or at least one of their heteromorphic types) are found to have rather thick spermoderm. The cells of its outer layer usually deposit tannins in their outer walls, substances that are darker in colour than those in the and project into the cell lumens (so-called "stalactites"). Depending on the seed coat thickness, such seeds vary from red to black in colour, and their structure in the representatives of these subfamilies differs markedly from that of most taxa of the other ones. Sometimes (e.g., in *Atriplex pedunculata* L., *A. verrucifera* M. Bieb., *A. portulacoides* L.) fruit and seed covers may be reduced to 1-2 cell layers and the fruit itself can be surrounded by two bracteoles, fused up to the top and tightly adhering to the pericarp, but the anatomical structure of such diaspore is still much more different from that of wing-shaped *Corispermoideae* fruits than it was believed earlier (Al-Turki & al. 2003). In subfamily *Chenopodioideae* the reduction of seed-covering layers occurs rather rarely, whereas (e.g., in *Salsoloideae* as well as in the tribe with unclear systematic position *Camphorosmeae* Moq. = *Camphorosmioideae* A. J. Scott, or, to a certain extent, in *Salicornioideae*) the pericarp and the spermoderm consists only of 1-3 tannin-free cell layers (Butnik 1962, Roth 1977, Sukhorukov unpubl. data).

Therefore, recognizing a number of subfamilies within the *Chenopodiaceae* as also revealed from the molecular data seems more justified than recognizing just *Chenopodioideae* sensu latissimo (= *Cyclolobeae*) and *Salsoloideae* sensu latissimo (= *Spirolobeae*) based only on embryo position type and perisperm presence.

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Appendix – Origin of the material of the *Corispermum* species investigated:

C. algidum Iljin – (1) Russia, prov. Arkhangelsk, Shenkursk, Vaga River, 9.1922, *Yu. Zinserling* (LE, typus); (2) Russia, Komi Republic, Syktyvkar, Sysola River, 9.1985, *A. K. Skvortsov* (MHA); (3) Russia, Arkhangelsk, railway station, 9.2003, *A. V. Kravchenko & M. A. Fadeeva 12868* (MW)

C. altaicum Iljin – Russia, Altai, Kosh-Agach, Tchuya River, 8.1931, *B. K. Shishkin* (LE)

C. americanum (Nutt.) Nutt. – (1) America, [sine loc.], *E. Hall 1562* (LE); (2) Canada, Ontario, distr. Thunder Bay, Rossby village, 9.1969, *C. E. Garton 12648* (H)

C. aralo-caspicum Iljin – (1) Russia, prov. Astrakhan, Nizhniy Baskunchak, 9.1926, *M. M. Iljin* (LE); (2) Kazakhstan, Buzachi peninsula, 9.1926, *I. M. Krasheninnikov* (LE); (3) Russia, Astrakhan, 9.2002, *A. Seryogin & A. Sukhorukov NR-113* (MW)

C. bardunovii Lomon. – Russia, Tuva, distr. Ersin, road Ersin-Samagaltai, 9.1989, *M. Lomonosova & O. Shdanova* (MHA)

C. borysthenicum Andrz. – Ukraine, Kiev, Truhanov island, 9.1953, *M. Klokov* (KW)

C. ×*klokovii* Mosyakin [= "*C. calvo-borysthenicum* Klokov"] – Ukraine, Kiev, Truhanov island, *M. Klokov* (LE, typus)

C. calvum Klokov – Ukraine, prov. Kiev, mouth of the Desna River, 9.1957, *M. Klokov & al.* (KW, LE)

C. candelabrum Iljin – China, prov. Chshili, Bejing [Beijing], Pohuashan Mountains, 1850-58, *S. I. Bazilevsky* (LE)

C. caucasicum (Iljin) Iljin – Azerbaidzhan, Velvey-chai River, 9.1954, *E. M. Iljina & A. A. Theodorov* (MW)

C. chinganicum Iljin – (1) Kazakhstan, prov. Semipalatinsk, distr. Karakaralinsky, N Balhash, 9.1910, *S. E. Kucherovskaya* (LE); (2) Mongolia, prov. Zabhan, valley of Dzabhan River, 9.1978, *I. A. Gubanov* (MW); (3) Mongolia, Buir-Nor, 9.1980, *I. A. Gubanov 5727* (MW)

C. crassifolium Turcz. – (1) Russia, Krasnoyarsk, 1838, *N. Turczaninow* (MW); (2) Russia, Siberia, distr. Turukhansk, Kureyka River, 9.1914, *N. I. Kuznetzov & V. V. Reverdatto* (LE);

C. declinatum Iljin – (1) Russia, Siberia, distr. Verhneudinsk, Zolotuhino, 8.1913, *G. Poplavskaya & al.* (MW); (2) Russia, Bashkiria, 9.1942, *D. Afanasyev,* (KW); (3) Russia, Moscow, Kuryanovo, 8.1997, *A. Sukhorukov* (MW); (4) Russia, Saratov, Zhasminnaya, 8.1998, *M. Beresutsky* (MW)

C. dutreuilii Iljin – (1) China, Kashgaria, Polour, VII.1892, *Dutreuil-de-Rence* (LE); (2) Tadzhikistan, East Pamir, Rang-kul, 8.1935, *I. Raikova* (LE)

C. falcatum Iljin – China, Tibet, Gyangtse, 1904, *P. Watson* (LE)

C. filifolium Becker – (1) [Russia, prov. Volgograd], Sarepta, *A. Becker* (MW); (2) Russia, Volgograd, Krasnaya Sloboda, 9.2005, *A. Sukhorukov* (MW)

C. gallicum Iljin – France, Avignon [sine coll. & anno] (LE; paratypus)

C. gelidum Iljin – Tadzhikistan, East Pamir, Rang-kul, 8.1935, *I. Raikova* (LE; isotypus)

C. glabratum Klokov – Ukraine, prov. Kiev, mouth of the Desna River, 9.1918, *Yu. M. Semenkevich* (LE)

C. gmelinii Bunge – (1) China, prov. Inner Mongolia, Ordos australis, 1877, *P. Verlinden* (LE; lectotypus); (2) China, prov. Inner Mongolia, Dshasakachi, 8.1957, *M. P. Petrov* (LE); (3) France, Gruissan, 10.1994, *W. Belotte 16834* (MHA)

C. grubovii Chien & Ma – China, Tibet, Lhasha, *K. S. Fu 658* (LE, type fragment)

C. heptapotamicum Iljin – (1) Kazakhstan, Heptapotamia, distr. Kopalsk, between Chingyldy & Iliysky, 8.1909, *A. Mikhelson* (LE; typus); (2) Kazakhstan, Heptapotamia, prov. Taldy-Kurgan, Matai, 9.2000, *M. Lomonosova & A. Sukhorukov* (MW)

C. hilariae Iljin – (1) [Tadzhikistan], Murgab, Boguchi, valley of Ak-su River, 8.1934, *H. Raikova 247* (LE, typus); (2) Tadzhikistan, East Pamir, Ak-Baital, 9.1955, *S. Ikonnikov* (MW)

C. hookeri Mosyakin – (1) Canada, Saskatchewan, distr. de Moose Jaw, dune eventree, 9.1960, *B. Boivin & G. F. Ledingham 14079* (LE; isotypus); (2) [Canada], Saskatchewan [sine. loco, anno & collect.] (LE)

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C. hyssopifolium L. – (1) Hungaria, Budapest, *Staub 3841* (MW); (2) Kazakhstan,. prov. Turgai, 1929, *V. Kutyeva* (MW); (3) USA, Wisconsin, Lake Superior, Barksdale, 9.1959, *P. Weber & al.* (LE); (4) Russia, prov. Ryasan, distr. Spassk, 8.1975, *V. N. Tikhomirov* (MW); (5) Russia, prov. Tambov, 20 km W from Tambov, 8.2005, *A. Sukhorukov* (MW)

C. insulare Klokov – Ukraine, Kiev, Truhanov island, 9.1955, *M. Klokov 127* (MHA)

C. intermedium Schweigg. – 1) Latvia, Riga, *T. Bienert 644* (LE); (2) [Russia], Pillau [now prov. Kaliningrad, Baltiysk], ex herb. Schrader [sine anno] (LE)

C. komarovii Iljin – Russia, Buryat-Mongolia, Sayany Mts, distr. Tunkinsky, Mt Belaya, Tunka, 9.1902, *V. Komarov 3522* (H; isotypus)

C. korovinii Iljin – (1) Kazakhstan, Heptapotamia, Iliyskoye, 6.1903, *V. Lipsky* (LE); (2) Turkmenistan, Uzboi, 6.1929, *Minervan* (LE); (3) Kazakhstan, Heptapotamia, prov. Taldy-Kurgan, Matai, 9.2000, *M. Lomonosova & A. Sukhorukov* (MW)

C. krylovii Iljin – Russia, Altai, Chulyshman, [sine anno & collect.] (MW)

C. laxiflorum Schrenk – (1) Kazakhstan, Karsakpai, Sary-su, 6.1929, *N. V. Pavlov* (MW); (2) Kazakhstan, Karsakpai, Kara-Kum sands, 8.1929, *S. Lipschiz* (MW); (3) Kazakhstan, prov. Kzyl-Orda, 8 km SE Aralsk, saline sands, 18.10.2003, *A. Sukhorukov* MW)

C. lehmannianum Bunge – (1) Turkmenistan, Farab, 5.1900, *N. Androssow* (LE); (2) Kazakhstan, prov. Kzyl-Orda, Tele-kul, 6.1929, *N. Pavlov* (MW)

C. lepidocarpum Grubov – China, SE Tibet, Temo, 9.1938, *F. Ludlow & al. 6227* (LE, type fragment)

C. macrocarpum Bunge – (1) Russia, Amur River, Sugu, A. Bunge (LE, original material); (2) Russia, prov. Khabarovsk, Sofiysk, 9.1970, *N. Shagu* (MHA); (3) Russia, Udmurtiya, Ishevsk, Raketnaya str. 9.1993, *A. N. Puzyryov* (MHA)

C. marschallii Steven – (1) Russia, prov. Volgograd, Tsaritsa River, 9.1992, *V. D. Bochkin & al.* (MHA); (2) Russia, Volgograd, Krasnaya Sloboda, 9.2005, *A. Sukhorukov* (MW)

C. mongolicum Iljin – (1) N Mongolia, between Tugurik and Bain-huduk, 8.1896, *E. Klementz 129* (LE, lectotypus); (2) Mongolia, Gobi, Haldzan-Ula, 9.1983, *I. A. Gubanov 7246* (MW); (3) Mongolia, Altai Mountains, 60 km NW from village Altai, 9.1983, *I. A. Gubanov 7255* (MW)

C. navicula Mosyakin – USA, Colorado, Jackson Co., North Park, north sand dunes, 9.1976, *F. Martin Brown* (KW: lose fruits from the holotype [COLO])

C. nitidulum Klokov – Ukraine, Sea of Azov, Biryuchiy island, 8.1953, *M. Klokov* (LE)

C. nitidum Schult. (= *C. coloratum* Andrz.) – (1) Hungary, near Budapest, 10.1928, *B. A. Fedtschenko* (LE); (2) Russia, prov. Krasnodar, Anapa, 8.1998, *A. Zernov 264* (MOSP); (3) Russia, prov. Tambov, Sherdevka, 7.1999, *A. Sukhorukov* (MW); (4) Ukraine, Kiev, Truhanov island, 9.1987, *S. L. Mosyakin* (KW)

C. ochotense Ignatov – Russia, prov. Magadan, distr. Olsky, Talom, 7.1971, *A. P. Khokryakov* (MW; isotypus)

C. orientale Lam. – (1) Russia, Daghestan, distr. Derbent, Mollakend, 9.1990, *N. V. Kostyleva* (MW); (2) Russia, prov. Volgograd, distr. Ilovlya, Berdiya, 8.1999, *A. Sukhorukov* (MW); (3) Russia, prov. Tambov, distr. Muchkap, Chashino, 8.2003, *A. Sukhorukov* (MW)

C. pacificum Mosyakin – USA, Washington, Wawawai, apparently introduced, 10.1893, *C. V. Piper 1770* (KW: lose fruits from the holotype [GH])

C. pallasii Steven (Syn.: *C. leptopterum* (Asch.) Iljin = *C. bielorussicum* Klokov) – (1) Canada, Neepawa, Delta Agassiz, 9.1960, *B. Boivin 14181* (H); (2) Netherlands, Goeree & Overflakkee, 9.1981, *D. Podlech 36514* (MHA); (3) Ukraine, Kiev, Obolon, 8.1988, *S. Mosyakin* (MHA); (4) Russia, prov. Kaluga, distr. Kozelsk, 7.2005, *N. M. Reshetnikova & A. V. Krylov* (MHA); Ukraine, Kiev, Rybalsky peninsula, 9.1987, *S. L. Mosyakin* (KW)

C. pallidum Mosyakin – USA, Washington, Douglas Co., in drifting sands, 7.1893, *J. H. Sandberg & J. B. Leiberg 309* (LE, isotypus; KW: lose fruits from the holotype [MO])

C. pamiricum Iljin – Tadzhikistan, prov. Vakhan, Pamir, Lingar-Gisht, 7.1901, *T. Alexeenko 3217* (LE, typus)

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C. papillosum (Kuntze) Iljin – (1) Turkmenistan, Kara-Kum, Repetek, 5.1897, *D. I. Litvinov 3527* (MW); (2) Uzbekistan, Karakalpakia, SW Kyzyl-Kum, 6.1932, *S. A. Nikitin & N. A. Mikhailova* (LE); (3) Tadzhikistan, Vakhsh valley, Burgo-tau, 6.1936, *V. A. Nikitin 210* (LE)

C. patelliforme Iljin – (1) China, prov. Inner Mongolia, Alashan, 9.1871, *N. M. Przevalsky* (LE; typus); (2) Mongolia, prov. Dzabhan, 9.1984, *I. A. Gubanov 9111* (MW)

C. piliferum Iljin – (1) Uzbekistan, prov. Fergana, distr. Andizhan, Shin-say, 7.1911, *O. Knorring & Z. Minkvitz* (LE, typus); (2) Kirghizia, Central Tien Shan, Ketmen-Tyube, 7.1927, *R. I. Abolin 522* (LE); (3) Ukraine, Kiev, Bortnichi, *S. Mosyakin* (LE)

C. puberulum Iljin – China, prov. Inner Mongolia, S Ordos, *P. Verlinden 1877* (LE; lectotypus)

C. redowskii Steven – (1) Russia, Baikal, *Adams* (MW); (2) Russia, Krasnoyarsk, Yenisey River, 8.1932, *M. M. Iljin 286* (MW)

C. retortum W.Wang & P. Y. Fu – China, Inner Mongolia, *V. I. Grubov* (LE)

C. sibiricum Iljin – (1) subsp. *jenissense* Iljiin: Russia, distr. Minusinsk, Lugovskoye, 9.1931, *M. Iljin & P. Ovchinnikov 437* (MW); (2) subsp. *sibiricum:* Russia, Krasnoyarsk, 8.1932, *M. M. Iljin* (LE)

C. stenopterum Klokov – Ukraine, Kiev, Truhanov island, 9.1953, *M. Klokov* (KW)

C. tylocarpum Hance – China, prov. Shehe, distr. Chifin, Laofu, 1952, *Liou Tchen-ngo 5227* (MHA)

C. ucrainicum Iljin – Ukraine, Dzharylgach island, 9.1947, *E. Pobedimova* (LE)

C. ulopterum Fenzl – (1) [Russia], Baikal, *Redovsky* (LE); (2) Russia, Lake Baikal, Olhon island, Peschanka, 9.1969, *G. Peshkova* (LE)

C. uralense (Iljin) Aellen – (1) Russia, prov. Orenburg, Sakmarsky gorodok, 1878, *Trautvetter* (LE); (2) Russia, Tomsk, 8.1925, *Zandakureva* (TK)

C. welshii Mosyakin – USA, Utah, Kane Co., sand dunes, 9.1992, *S. L. Welsh & K. H. Thorne 25170* (KW: lose fruits from the isotype [NY])

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