Botanica Pacifica. A journal of plant science and conservation. 2025. 14(2): 45–54
DOI: 10.17581/bp.2025.14212

RESEARCH PAPER

Features of morphology and ultrasculpture of fruits of some rare xerophytic Asteraceae species

Alexander K. Mamontov, Marianna A. Zueva, Andrey S. Ryabchenko* & Alexandra V. Stogova

Alexander K. Mamontov
e-mail: veidelev@rambler.ru

Marianna A. Zueva
e-mail: marianna-ko@yandex.ru

Andrey S. Ryabchenko*
e-mail: marchellos@yandex.ru

Alexandra V. Stogova
e-mail: a.stogova85@gmail.com

N.V. Tsitsin Main Botanical Garden RAS,
Moscow, Russia

* corresponding author

Manuscript received: 19.03.2025
Review completed: 02.10.2025
Accepted for publication: 30.10.2025

ABSTRACT

Ultrastructure of the achenes surface in seven rare Asteraceae taxa: *Artemisia alpina* Pall. ex Willd., *A. hololeuca* M. Bieb. ex Besser., *Jurinea cretacea* Bunge, *Klasea radiata* (Waldst. & Kit.) Á. Löve & D. Löve subsp. *tanaitica* (P.A. Smirn.) L. Martins, *Pentanema salicinum* (L.) D. Gut. Larr., Santos-Vicente, Anderb., E. Rico & M.M. Mart. Ort., *Ptilostemon echinocephalus* (Willd.) Greuter. and *Xeranthemum annum* L., were examined using scanning electron microscopy (SEM). The study reveals key structural features of the seed coat in species with diverse ecological adaptations. Various morphological adaptations are shown, such as thickening of the pericarp and the presence of a waxy coating.

Keywords: achene, Asteraceae, micromorphology, scanning electron microscopy

РЕЗЮМЕ

Мамонтов А.К., Зуева М.А., Рябченко А.С., Стогова А.В. Особенности морфологии и ультраскульптуры плодов некоторых редких ксерофитных видов семейства Asteraceae. Ультраскульптура поверхности семянки 7 редких таксонов семейства Asteraceae: *Artemisia alpina* Pall. ex Willd., *A, hololeuca* M. Bieb. ex Besser., *Jurinea cretacea* Bunge, *Klasea radiata* (Waldst. & Kit.) Á. Löve & D. Löve subsp. *tanaitica* (P.A. Smirn.) L. Martins, *Pentanema salicinum* (L.) D. Gut. Larr., Santos-Vicente, Anderb., E. Rico & M.M. Mart. Ort., *Ptilostemon echinocephalus* (Willd.) Greuter. и *Xeranthemum annum* L., исследована методами сканирующей электронной микроскопии (СЭМ). Выявлены основные особенности строения семенной кожуры у видов с разной экологической приуроченностью. Показаны различные морфологические адаптации, такие как утолщение околоплодника и наличие воскового налета.

Ключевые слова: семянка, сложноцветные, микроморфология, сканирующая электронная микроскопия

Representatives of the Asteraceae family are distributed across all continents except Antarctica, and are widely represented in all floristic regions of the Earth, ranging from coastal areas to highland environments. This extensive distribution is likely attributable to their notable adaptive capacity, which enables them to colonize diverse ecotopes (Tadesse 2014). The Asteraceae family is one of the largest and most evolutionarily advanced families of dicotyledonous plants, comprising more than 23,600 species, which represent approximately 8 % of all angiosperms (Stevens 2007). A distinctive feature of the entire family is the uniformity of fruit type, allowing for objective comparison of samples in scientific studies. However, micromorphological research on the seeds of most Asteraceae genera is still in its early stages.

The ultrastructural characteristics of Asteraceae seeds are crucial not only for taxonomic classification but also for understanding the adaptive capacities of these species. Morphologically, the achene is a dry, indehiscent, one-seeded fruit formed from a two-lobed ovary (Polyakov 1967). The seed coat (testa) remains intact in all family members until the achene reaches full ripeness. The pericarp, testa, and endosperm collectively serve to protect the ovary. The pericarp consists of the exocarp, mesocarp, and endocarp. The ratio between the thickness of the pericarp and the seed coat varies among species. Typically, one of these layers plays a predominant role in protecting the embryo from environmental stress. In species inhabiting arid environments, the pericarp is typically dense and composed of thick-walled cells, whereas species in mesophytic conditions tend to have a pericarp with thinner-walled cells. The surface of the exocarp cells can be either smooth or textured, with granules, scales, or flakes of epicuticular wax (Boyko 2015).

The achenes of many Asteraceae species exhibit a grooved surface on the exocarp cells. These grooves are formed by the folding of the cuticle on the outer periclinal walls of the fruit or seed coat (Velez 1981, Boyko & Novozhilova 2018). The surface may also contain mucus-producing cells, which are grouped into complexes and interspersed among the main exocarp cells. The mucus content and the structure of these cells are influenced by the thickness of the cuticle and the nature of their contents. Mucus is rarely found in specialized trichomes, such as those in *Senecio* sect. *Senecio* and species of the tribe *Gnaphalieae*. In the pericarp, mucus-containing cell complexes are easily distinguishable from the epidermal cells. These complexes extend along the axis of the achene and vary in length, occasionally reaching the length of the entire achene (Boyko 2011).

The colour of the achenes in Asteraceae species can range from straw yellow to dark brown, with some species displaying white (e.g., *Artemisia stelleriana* Besser), reddish-brown shades (e.g., pink in *Taraxacum* species), dark burgundy (e.g., *Pterocypsela*), or black (e.g., certain species of *Helianthus*, *Hieracium*). The colouration is attributed to the presence of tannin-like phenolic substances, which can stain the pericarp cell walls or specific rows of cells, resulting in yellow or brown hues. In species such as *Crepis hokkaidoensis* Babc., pigmentation affects individual mesotesta cell rows. The presence of phlobaphenes in the exocarp cells of species in the tribe *Lactuceae* (e.g., *Crepis*, *Hieracium*, *Lactuca*, *Sonchus*) imparts a dark brown colour. Tannins, believed to have a protective function, are common in species from open habitats (Kravtsova 2007). The mature seed coat consists of a layer of thin-walled or variably thickened exotesta cells, which are covered by a cuticle (Boyko & Novozhilova 2018).

Many species of Asteraceae are currently listed in various lists of endangered species. The fruits of these rare taxa (Table 1) have not yet been extensively examined using scanning electron microscopy (SEM). Therefore, it is important to explore the structural characteristics of these species from an ecological and regional perspective. For instance, T.G. Buch (1989) investigated the relationship between epidermal outgrowths and their ecological significance in several families, including Saxifragaceae. Modern research on Asteraceae species covers a wide range of biological aspects, with increasing attention to ultrastructural features. Consequently, the taxonomic classification of the Asteraceae family has undergone significant revisions, with the number of subfamilies expanding from two to twelve and the number of tribes increasing from 13 (or 15) to 38 (Panero & Funk 2008). Comparative carpological studies have identified several key adaptive traits of achenes that contribute to the widespread and localized distribution of Asteraceae species, revealing how adaptations shift when transitioning from xerophytic to mesophytic habitats.

The ultrasculptural diversity of achenes in Asteraceae species is determined by differences in the structure of the pericarp, testa, and additional outgrowths. Based on the classification system proposed by Barthlott (1981) and Georgiadou Tvrtkovic-Šahin (1982), the key structural features of achene ultrasculpture include the shape and arrangement of exocarp cells, the relief of the outer cell walls, and epicuticular deposits. Studies have shown that when exocarp cells are thin-walled, the underlying cell layers influence the surface structure. In species with a pericarp consisting of few layers of thin-walled cells, the surface sculpture is primarily determined by the structure of the testa cells (Boyko, personal communication). According to Belyaev (1984), the epidermal cell surface structure is characterized by thickenings in the anticlinal walls of epidermal cells that protrude to the surface, with outer periclinal walls often recessed, creating unique mesh-like or pitted textures.

The aim of this study was to investigate the main morphological characteristics of Asteraceae fruits and their surface features using SEM, to examine the diversity of epidermal projections some species of arid and petrophytic habitats.

MATERIAL AND METHODS

Seed samples of the studied taxa were collected during expeditions to various regions in the European part of Russia, including Belgorod, Volgograd and Crimea. Taxon names are provided according to GBIF data. Since numerous studies have noted that the size and shape of achenes can vary depending on their position on the receptacle and within the inflorescence (Kotlyarova 2016), we collected seeds from different parts of the inflorescence.

The surface of the seeds was examined using a LEO 1430 VP scanning electron microscope (Germany). Observations were conducted in high vacuum mode at an accelerating voltage of 20 kV and a working distance of 9 mm. Following air drying, specimens were mounted on copper plates, coated with gold via cathode sputtering in an argon environment, and subsequently examined in high vacuum mode. Since air drying was employed, standard fixation procedures for biological materials in SEM were not applied, thus preserving the native structure of the biological samples.

Seed weight was measured using an OHAUS Adventurer electronic balance with a precision of 0.01 g. The following morphometric parameters were recorded: weight (for dried seeds), length, width, color, presence of projections, and seed and fruit shape. Terminology from Terehin (1996) was applied for the descriptions. To assess the presence of mucilage on the seed surface, samples were soaked for 12 hours and examined under backlight.

The ultrasculpture of the seed surface was described following the methodology of Barthlott (Barthlott 1981, Barthlott & Ziegler 1981, Boesewinkel & Bauman 1984, Jeffrey et al. 1985). This approach identifies three levels of sculpture: primary, secondary, and tertiary.

At the primary level, the focus is on the shape of the exotesta cells, including their outline, the type of anticlinal walls (cell boundaries), relief of the cell boundaries, and the curvature of the outer periclinal walls. The secondary level considers the characteristics of the cell wall surface, including the presence of different types of cuticular sculptures (e.g.,

Table 1. Macro- and micromorphological characteristics of the studied species.

Genus	Average length, mm	Average width, mm	Weight, mg	Structural elements of achenes	Pappus lenght, mm	Colour
Artemisia alpina	1.22	0.62	0.19	carpopodium	–	greyish dark brown
A. hololeuca	1.22	0.56	0.22	none	–	grayish brown, silver
Jurinea cretacea	3.52	2.01	5.1	carpopodium absent, attachment area lateral	7.81	dark brown, along the ribs light brown
Pentanema salicinum	1.15	0.31	0.0035	carpopodium symmetrical	5.68	light brown, glossy
Ptilostemon echinocephalus	4.33	2.69	15.32	none	–	dark grey-brown with 4–5 black-brown stripes
Klasea radiata	4.24	1.66	3.545	carpopodium asymmetrical	–	from brown to dark brown
Xeranthemum annum	4.05	0.93	1.033	carpopodium asymmetrical	3.28	grey-brown

linear, reticulate, tuberculate) and the visibility of secondary thickenings on the inner side of the walls, which become more noticeable as the exotesta cells dry. The tertiary level of sculpture, less commonly observed, is characterized by the presence of various epicuticular secretions, such as micropapillae, granules, or films, primarily composed of waxes. Six types of epicuticular waxes are found on the surface of Asteraceae achenes: papillary nodules, mounds, scales, flakes, fine granules, and granules of indeterminate shape (Boyko 2015).

RESULTS

Artemisia alpina Pall. ex Willd.

A Near Eastern and Eurasian steppe species, lithophyte, euxerophyte, shade-tolerant, grows on non-saline soils (Golubev 1996).

The achenes are elliptic-ovate, dark brown, occasionally greyish, and relatively light in weight. The pappus is absent (Table 1). Fine, disordered folds on the surface of achenes in *Artemisia* species are formed by the unevenness of the outer walls of the exocarp cells (Fig. 1a) in the apical region of the achene. In the basal region, a carpopodium is present, consisting of four rows of cells that form a ring structure (Fig. 1b).

At the primary level of sculpture, the cell boundaries create a complex, wavy, ribbed relief on the exocarp of *A. alpina*, with long longitudinal complexes of mucilaginous cells alternating with 2–4 rows of main exocarp cells, which do not release mucus when wetted (Fig. 1d). Secondary sculpture is characterized by the presence of reticulate and folded-ribbed projections on the tangential surfaces of the cells. At the tertiary level, papillary projections, granular secretions, and wax flakes are observed in certain areas (Fig. 1c).

Artemisia hololeuca M. Bieb. ex Besser.

Associated with underlying limestone layers and pure chalk outcrops, isolated populations are found on gravelly placers at the base of slopes. It can reproduce both vegetatively and by seeds (Volodina 1982, Korobkov 2024).

The fruits are oval to ovoid, finely grooved achenes, and are gray-brown or silvery in color (Table 1). The primary sculpture of the epidermal surface consists of alternating complexes of mucilaginous cells and the main epidermal cells, creating a distinct, longitudinally ribbed relief with irregular, oblong tubercles (Fig. 1e). The secondary sculpture features small ribbed protuberances and pits with irregular outlines (Fig. 1f). The tertiary sculpture exhibits a relatively abundant secretion of epicuticular wax in the form of granules and flakes of indeterminate shape. Unlike the previous species, the seeds produce a pectinaceous mucilage when wet.

Jurinea cretacea Bunge

Regional endemic of the Donets Ridge and southern Volga Upland, calcephite (Radygina 2014). Petrofilous steppe species (Mazina 2018). It inhabits chalk outcrops on slopes and chalk hills in the valleys of the Volga and Don tributaries (Lukonina et al. 2017).

Achenes are 4-sided, dark brown, with a descending tuft preserved in some specimens (Table 1). The structural elements of the pappus (setae) are densely arranged in the apical part of the fruit, are belt-shaped and have a coarsely serrated edge (Fig. 2a). Visually distinguishable is the ribbed epidermis with small spines concentrated in longitudinal rows (Fig. 2b). When examined by SEM, on the surface of the pericarp, they are clearly distinguished by three cylindrical tubercles covered with hooked spines, located in the axial part of each face. The primary ultrasculpture of the exotesta is formed by polygonal cells forming a folded-cellular-tuberous surface (Fig. 2c). The peculiarity of the secondary sculpture is determined by the presence of a thin ribbed relief of the cell walls. Tertiary sculpture is caused by the presence of flocculent wax secretions on the apices of the spines and occasionally in other areas of the epidermis (Fig. 2c,d).

Klasea radiata (Waldst. & Kit.) Á. Löve & D. Löve subsp. *tanaitica* (P.A. Smirn.) L. Martins. (=*Serratula tanaitica* P.A. Smirn.)

Pontic species, xeromesophyte heliophyte, grows on non-saline soils. (Golubev 1996). It inhabits grassy chalk and marl slopes, carbonate sandstone outcrops with areas of feather grass and mixed grass steppes, sometimes on relatively flat areas, more often on north-facing slopes. Reproduction is seed-based (Reshetnikova 2023).

The achenes are four-sided, dark brown, with a descending tuft present in some specimens (Table 1). The structural elements of the pappus (setae) are densely arranged in the apical part of the fruit, are belt-shaped, and have a coarsely serrated edge (Fig. 2a). The ribbed epidermis, which is visually distinguishable, contains small spines concentrated in longitudinal rows (Fig. 2b). When examined by SEM, the surface of the pericarp clearly shows three cylindrical tubercles covered with hooked spines, located in the axial part of each face. The primary ultrasculpture of the exotesta consists of polygonal cells, forming a folded-cellular-tuberous surface (Fig. 2c). The secondary sculpture is characterized by the presence of a thin ribbed relief on the cell walls. The tertiary sculpture is characterized by flocculent wax secretions on the apices of the spines and occasionally in other areas of the epidermis (Fig. 2c,d).

Pentanema salicinum (L.) D. Gut. Larr., Santos-Vicente, Anderb., E. Rico & M.M. Mart. Ort. (=*Inula salicina* L.)

Calcephilous species. Grows along the banks of streams and temporary watercourses on south-facing slopes (Kostina 2014).

The achenes are 1.5–2 mm long, brown, bare, and finely ribbed, with a well-developed pappus, 7–8 mm long, composed of dirty white hairs fused at the base (Table 1) (Fig. 4a). The achene has a well-defined carpopodium consisting of irregular elliptical cells arranged in indistinct rows (Fig. 4b). The pappus consists of paired hairs (Fig. 4a,d). The primary and secondary sculpture are not expressed because the surface of the exocarp is completely covered by a layer of prismatic calcium oxalate crystals (Fig. 4c). The tertiary sculpture is very weakly expressed in the form of rare flocculent and granular wax deposits.

Ptilostemon echinocephalus (Willd.) Greuter.

It grows on open denudation slopes (found on dry slopes, steep scree slopes, unsuitable for the growth of other species). Heliophyte, xerophyte, grows on non-saline soils. It reproduces by seeds (Korzhenevsky & Bondareva 2018).

The achenes are large, downward-tapering, and obliquely pear-shaped. The tuft consists of several rows of thin, white bristles, which are completely absent or fallen. The fruits of this species are the heaviest of all the species studied (Table 1). On the surface of the achene, there are fairly evenly distributed, not clearly expressed longitudinal grooves (Fig. 5a). In the primary sculpture, the surface is finely cellular, formed by rows of cells oriented along the axis of the achene, with irregular contours ranging from rectangular to rounded, with thickened anticlinal walls and concave periclinal walls (Fig. 5b,c). In the secondary sculpture, fine ribbing of the tangential surfaces of the cells and the presence of additional depressions in their relief are noted. The secondary sculpture of the surface is wavy. In the tertiary sculpture, the surface is covered with large foci

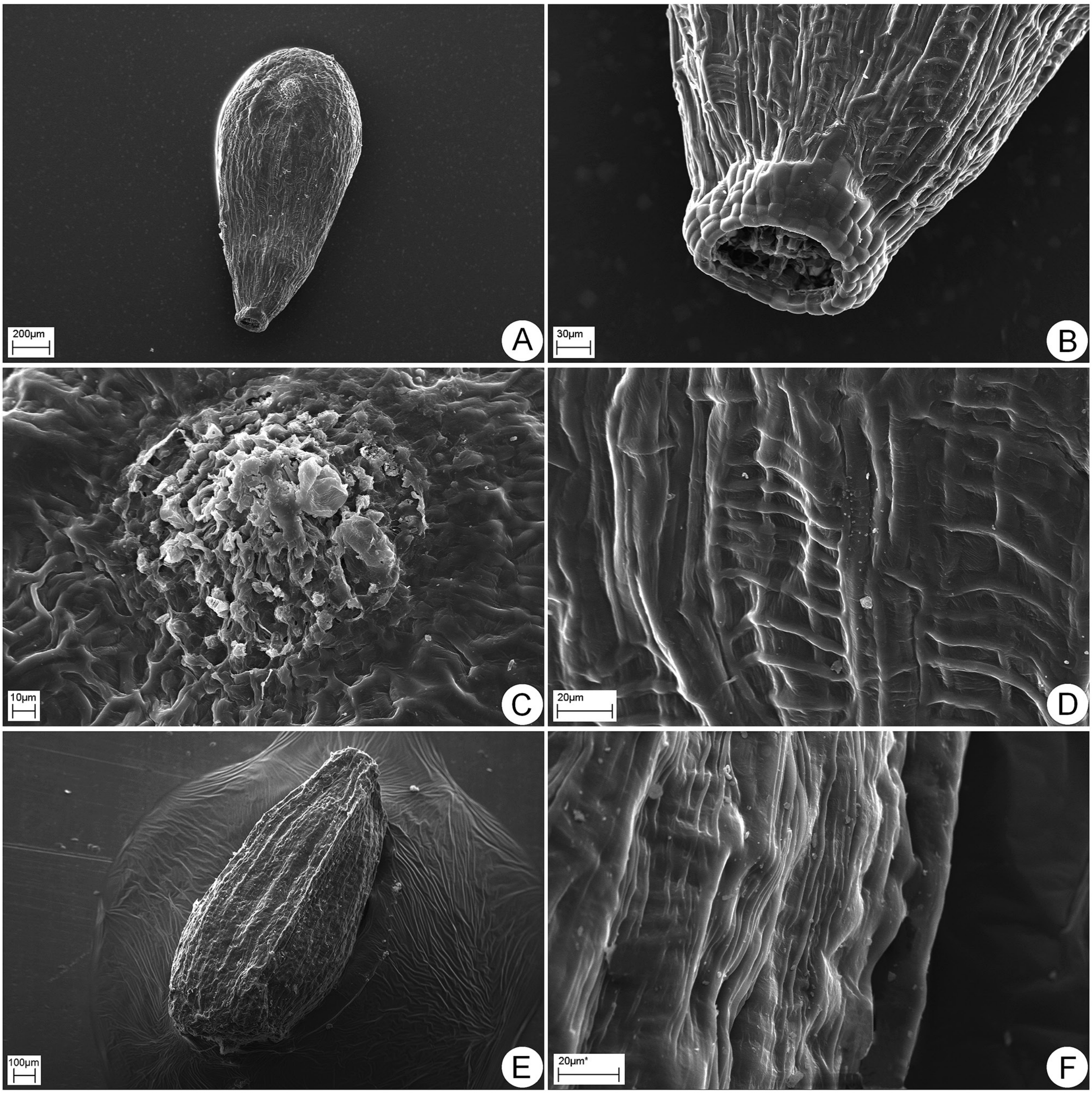

Figure 1 The structure of the achene of *Artemisia alpina* Pall. ex Willd. (A–D); *Artemisia hololeuca* M. Bieb. ex Besser. (E, F): A – general view of the achene; B – basal part (carpopodium); C – accumulation of wax granules in the apical part; D – complexes of mucilaginous cells elongated along the axis of the achene; E – general view of the achene; F – complexes of mucilaginous cells elongated along the axis of the achene. Scale bars: A – 200 μm; B – 30 μm; C – 10 μm D, F – 20μm; E – 100 μm

of wax fields; at higher magnification, abundant papillary tubercles, granular wax secretions, and a few flakes are visible (Fig. 5c,d).

Xeranthemum annuum L.

Mediterranean-Near Eastern and Eurasian steppe. Euxerophyte, heliophyte, grows on non-saline soils (Golubev 1996). Grows in steppes, in arid conditions. Seeds germinate quickly without any special requirements for germination (Ruprecht et al. 2024).

The fruit is an achene of dark grey-brown color. The pappus is formed by five unequal setae, widened at the base and filiform at the top, slightly shorter than the achene (Fig. 6a). The surface of the exocarp is abundantly covered with trichomes (Fig. 6a, b, d), and only in some places can the peculiarities of its ultrasculpture be observed (Fig. 6c). In the primary sculpture, a cellular surface is observed, composed of cells with rectangular outlines (Fig. 6c). In the secondary sculpture, the outer periclinal walls are concave, and the anticlinal walls are sharply raised and thickened (Fig. 6c). The covering trichomes are represented by the following types: long, double with a forked end (on the surface of the fruit) (Fig. 6b); club-shaped with a depressed end; and spindle-shaped (Fig. 6e). The tertiary sculpture is formed by fairly frequent flocculent and granular wax deposits (Fig. 6b,e).

DISCUSSION

The species under consideration are adapted to the arid conditions of rocky steppes, and many of them are rare. Microstructural seed traits in arid environments provide valuable insights into plant adaptations to dry climates and

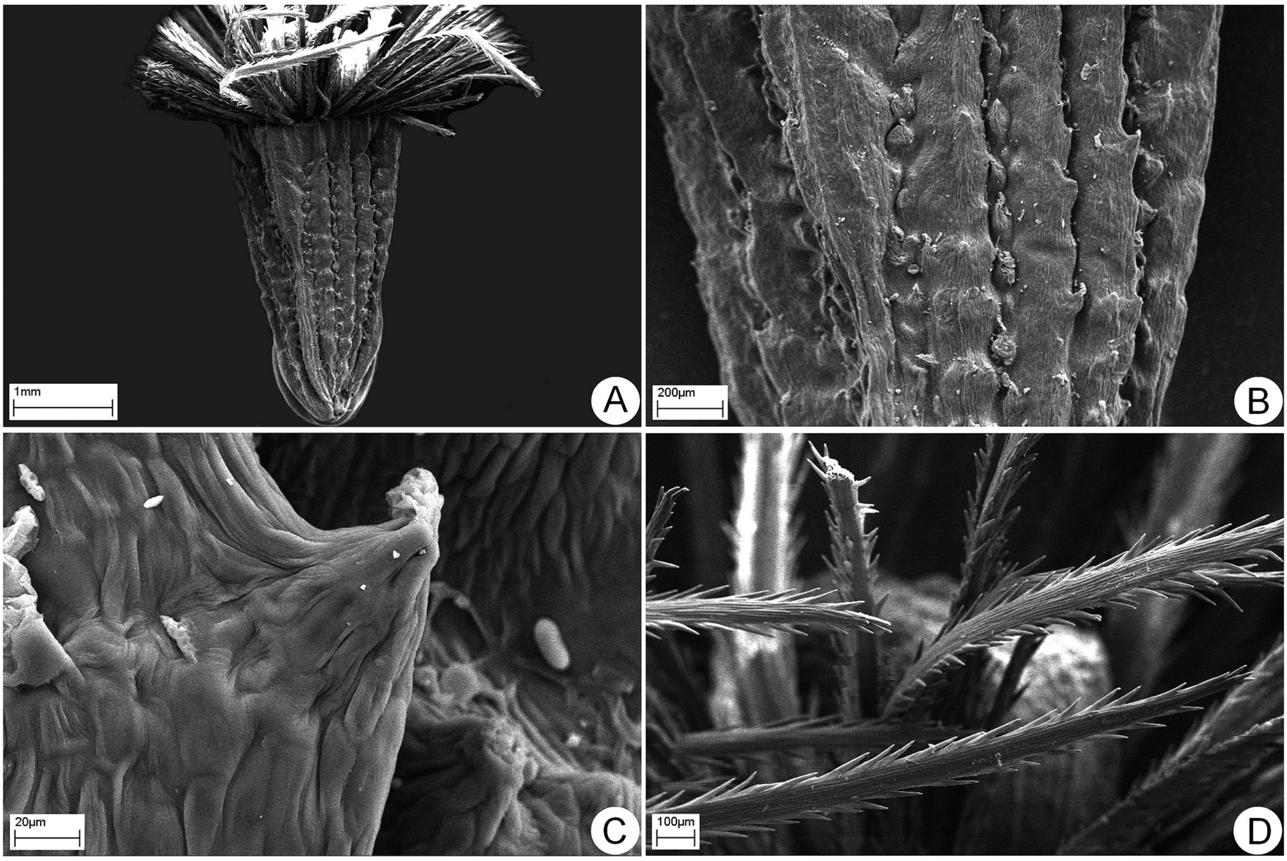

Figure 2 The structure of the achene of *Jurinea cretacea* Bunge: A – general view of the achene; B – structure of the exotesta; C – hook-shaped spine on the surface of the exotesta with waxy secretions; D – pappus setae with spines. Scale bars: A – 1 mm; B – 200 µm; C – 20 µm; D – 100µm

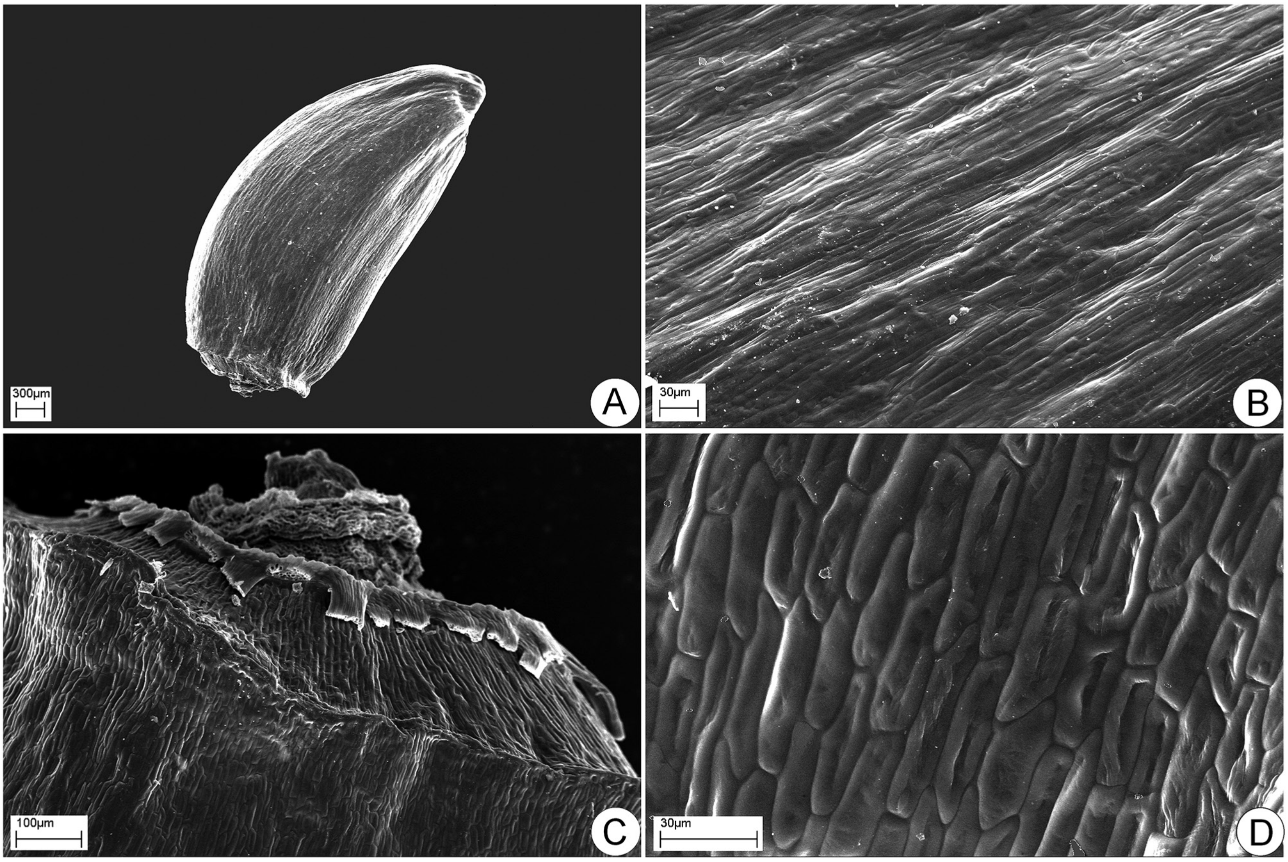

Figure 3 The structure of the achene of *Klasea radiata* subsp. *tanaitica* (P.A. Smirn.) L. Martins.: A – general view of the achene; B – wavy-tuberculate surface of the exotesta; C – pronounced crown in the apical part of the seed; D – rectangular-trapezoid and unevenly thickened cells of the exocarp. Scale bars: A – 300 µm; B – 30 µm; C – 100 µm; D – 30µm

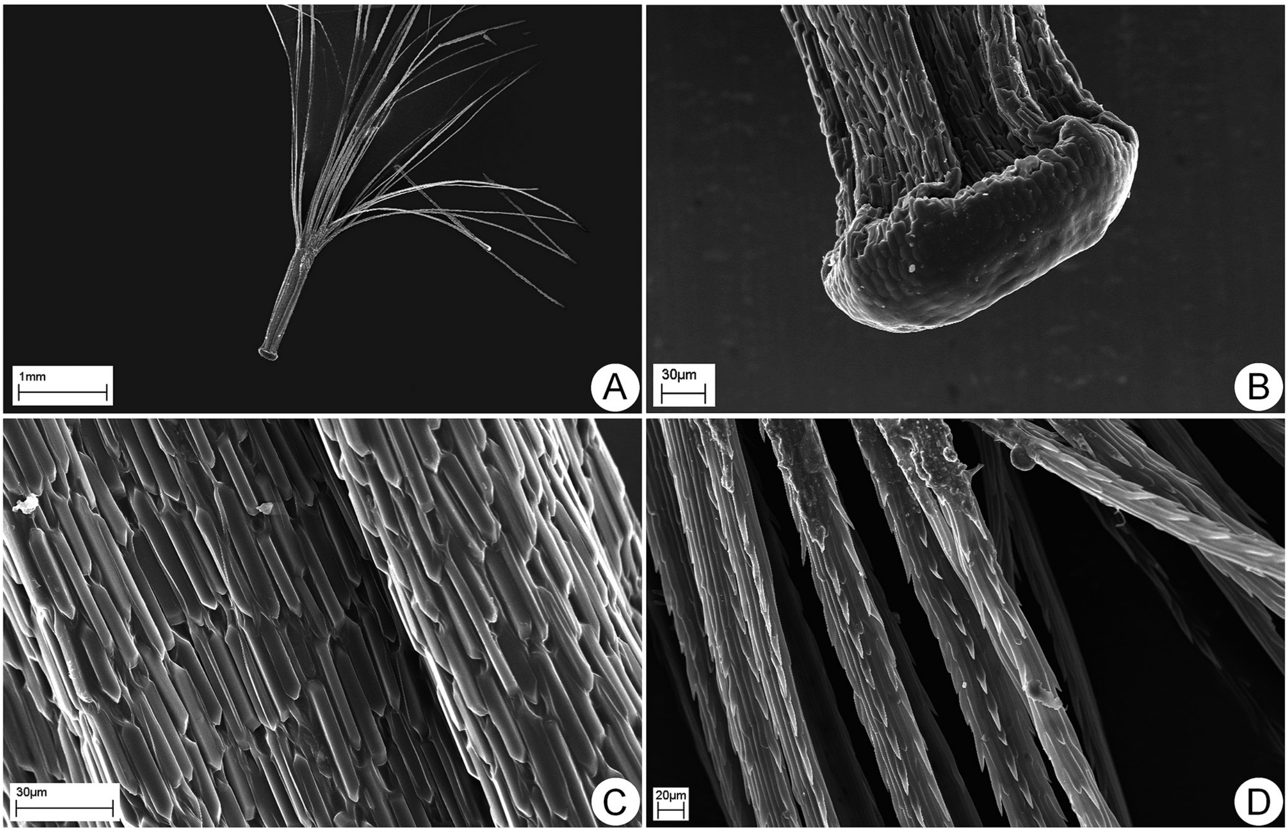

Figure 4 The structure of the achene of *Pentanema salicinum* (L.) D. Gut. Larr., Santos-Vicente, Anderb., E. Rico & M.M. Mart. Ort. A – general view of the achene; B – carpopodium; C – calcium oxalate crystals covering the coarsely ribbed surface of the exocarp; D – pappus bristles with spines. Scale bars: A – 1 mm; B, C – 30 µm; D – 20µm

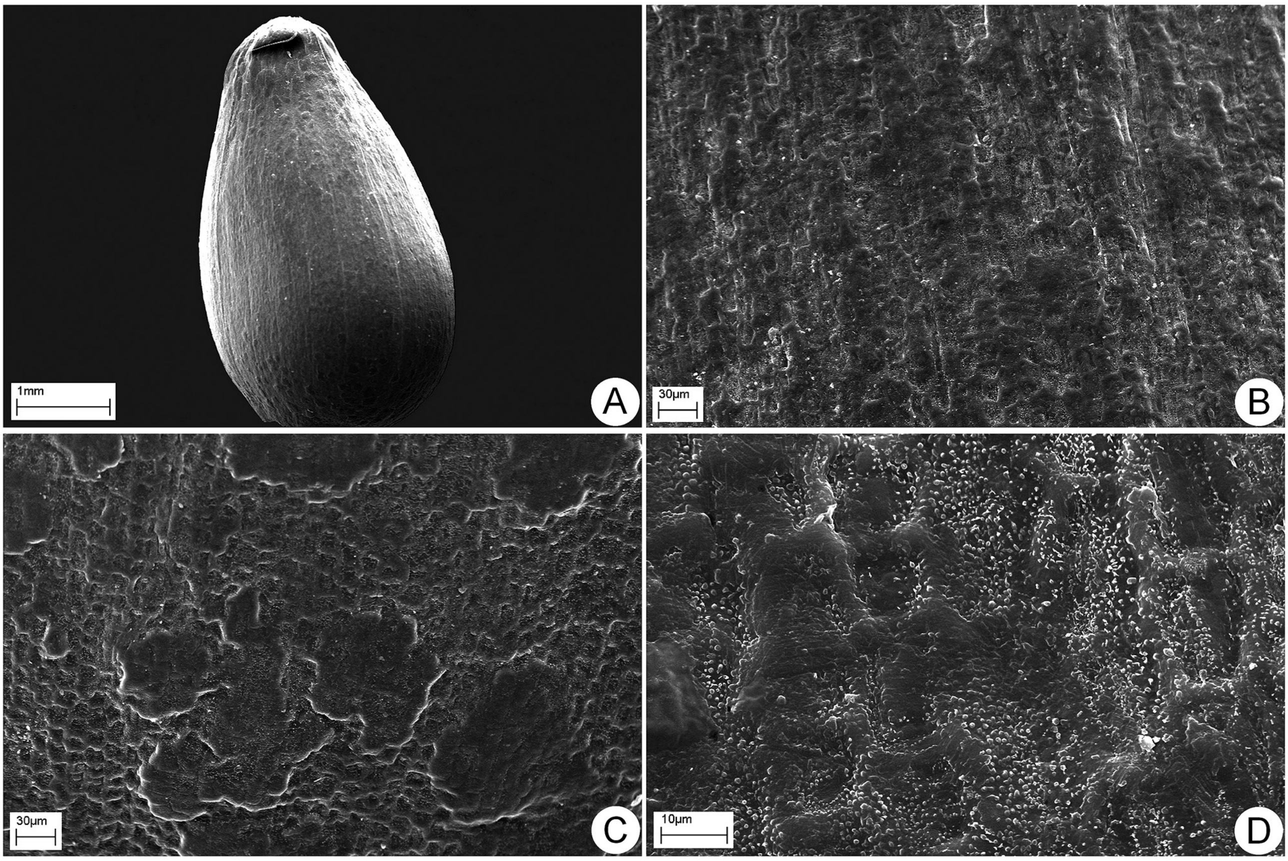

Figure 5 The structure of the achene of *Ptilostemon echinocephalus* (Willd.) Greuter: A – general view of the achene; B – finely cellular surface of the exocarp; C – clusters of large wax spots in the basal part; D – fields of small wax granules. Scale bars: A – 1 mm; B, C – 30 µm; D – 10µm

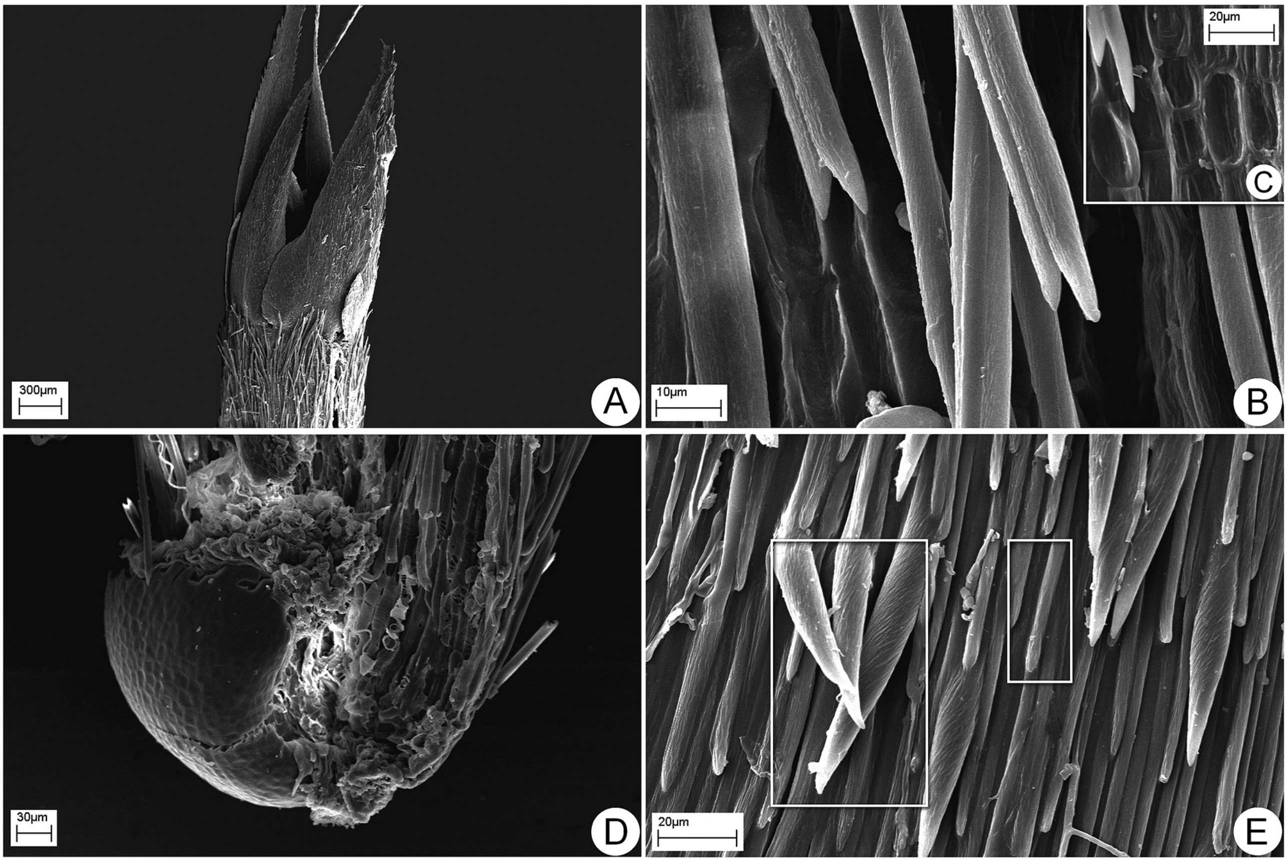

Figure 6 The structure of the achene of *Xeranthemum annuum* L.: A – fragment of the achene with pappus; B – long paired trichomes with forked ends on the surface of the fruit; C – fragment of the cellular surface of the primary sculpture of the exocarp; D – carpopodium; D – spindle-shaped and club-shaped trichomes on the surface of the exocarp. Scale bars: A – 300 μm; B – 10 μm; C – 20 μm; D – 30μm; E – 20 μm

have significant implications for crop breeding programs and ecological restoration efforts (Mustafa & Rizwana 2025). The seed must take up moisture from the substrate faster than it is lost to the atmosphere and this problem is particularly acute in dry conditions (Harper et al. 1965).

The protective function of the endosperm is further supported by the cuticle that covers it (Yakovleva et al. 2002). Several *Artemisia* species have been extensively studied regarding the ultrasculpture of their achenes (Boyko & Novozhilova 2018, Mamontov & Ryabchenko 2017), revealing distinct types and subtypes of surface structures. The ribbing pattern of achenes in many *Artemisia* species varies. It may result from the presence of large mucilaginous cells in the exocarp or from the loose adhesion of the pericarp to the seed, which leads to the formation of folds that do not align with the distribution of vascular bundles. The seeds of many *Artemisia* species are adapted to germinate in arid and semi-arid conditions. Thus a significant characteristic of *Artemisia* species is the presence of mucilaginous cells in the exocarp (Kreitschitz & Vallès 2007, Yakovleva 2002). The mucilage in the achenes is indicative of an adaptation to arid growing conditions. Achenes of *A. austriaca* Jacq. and *A. absinthium* L., which thrive in similar environments, also contain long mucilaginous cells and exhibit high mucilage content. The morphology of the mucus-containing cells and the main cells of the exocarp is difficult to ascertain due to the influence of the exotesta's structure on the ultrasculpture of the achenes (Boyko 2013a).

We identified significant similarities in the ultrastructural features of *A. senjavinensis* Besser (Boyko 2013a), a rare species from the northern Far East, and *A. alpina*. However, neither species exhibited mucus secretion from the mucus-containing cell complexes. Other Far Eastern wormwood species, such as *A. feddei* subsp. *arschantinica* (Darijma) Gubanov & Kamelin, *A. rubripes* Nakai, and *A. selengensis* Turcz. ex Besser, contain cells similar to mucilaginous cells, but no mucilage is observed in their achenes, even when wetted. The "mucification" or "non-mucification" of cells and cell complexes is linked to the thickness of the cuticle covering the mucus-containing cell complexes and the nature of the cellular contents (Boyko 2013b). The loss of mucilage secretion in wet conditions (as observed in *A. rubripes*, *A. feddei*) likely occurred when wormwoods colonized mesophilic habitats or when certain species reached coastal areas, facilitating seed dispersal by water (*A. stelleriana* Besser, *A. opulenta* Pamp.) (Boyko 2013b). Our *A. alpina* sample appears to follow a similar strategy. In contrast, *A. hololeuca* secretes abundant mucus when wet, likely enhancing its seed dispersal efficiency. The seed coat mucilage envelope is also present in *A. annua* L. and *A. leucodes* Schrenk (Kreitschitz & Gorb 2018).

Additionally, plants from other families common in arid regions, such as the Brassicaceae, have developed various adaptations to withstand harsh growing conditions. These adaptations are not only evident in the leaves (e.g., thickening of the outer epidermal cell walls, presence of mucilaginous substances in the vacuoles of mesophyll cells, and sclerenchymatous sheaths around vascular bundles) but also in the fruits. For example, in the pericarp of species in the genus *Stroganowia*, there is thickening of the exocarp's outer cell walls, the presence of mucus-like substances in intercellular spaces, and sclerenchymatous sheaths around the bundles. The seed coat also contains mucus-producing cells in the exotesta (Karpova & Yakovleva 2012).

Different Asteraceae taxa exhibit distinct patterns of cell wall thickening. Häffner (2000), who studied the cell wall thickening of the exotesta in achenes of species within the subtribe *Carduinae*, identified four distinct types, including the "*Jurinea*" type, in which the outer and inner tangential walls of the exotesta cells are thin, while the radial walls are strongly thickened. This type of ultrasculpture has been observed in several *Jurinea* species, such as the mesh-like structure in *Jurinea alpigena* K. Koch (Ozcan & Akinci 2019). The "*Jurinea*" type of secondary sculpture is also characteristic of other genera, such as *Serratula manshurica* Kitag. (Häffner 2000) and *Klasea centauroides* (L.) Cass. ex Kitag. (Boyko & Novozhilova 2018). We identified this type of cell wall thickening in the closely related species *Klasea radiata*. When the adjacent exotesta cells exhibit varying elongations, a wave-like sculpture forms. In cases of primary sculpture with a thin pericarp, this waviness can create a relief surface. A similar type of exotesta cell thickening is also characteristic of several taxa from xerophytic habitats, including *K. centauroides* (L.) Cass. ex Kitag., *Olgaea nidulans* (Rupr.) Iljin, and *Onopordum acanthium* L. (Boyko & Novozhilova 2018). The thickened testa, particularly the exotesta, of *Ptilostemon echinocephalus* (Willd.) Greuter is considered a relict feature, as noted by Netolitzky (1926) and confirmed by researchers studying various angiosperm families (Reese 1989). Within the tribe, however, the testa structure exhibits considerable variation, likely related to the ecology of the species and their methods of diasporic dispersal.

The thickest testa is found in species of the tribe *Cardueae*, whose origin and greatest species diversity are associated with the arid habitats of the Mediterranean. In these species, a thick testa with a thin pericarp serves as the primary adaptation for protecting the embryo (Boyko 2015). As noted by researchers, the presence of wax on the surface of the fruit is influenced by the plant's growing conditions. In a comparison of two sunflower (*Helianthus annuus* L.) hybrids, it was found that the surface of the achenes is covered with granular wax, the quantity and quality of which vary under different water regimes (Franchini et al. 2010). According to Boyko (2015), the achenes of *H. annuus*, collected from plants in the Primorsky Territory, lack epicuticular wax altogether. Achenes of species in the tribe Inuleae are similar in that they never have mucilaginous trichomes (Anderberg 1991). Notably, achenes of grassland species such as *Inula japonica* Thunb., *I. britannica* L. and *I. linariifolia* Turcz. (Boyko 2012), as well as halophytic species like *I. tuzgoluensis* M. Ozturk & O. Cetin, bear simple trichomes across their entire surface (Şeker & Çetin 2013). In contrast, the fruit of the xerophytic species *I. salicina*, under consideration here, lacks trichomes. The widespread occurrence of the large-cell type of seed coat surface in a number of taxa from different families suggests that these seeds have a high capacity for moisture absorption and evaporation, due to the extensive contact between the epidermal cells and the soil. This structure facilitates wind dispersal of the seeds, aiding in species preservation and rapid spread (Butch 1989). The carpopodium is asymmetrical, as noted by other researchers (Jana & Mukherjee 2014, Ozcan & Akinci 2019).

The morphological characteristics of the achenes in the listed taxa reveal patterns in terms of optimal dispersal strategies in similar ecotopes. As noted by Häffner (2000), genera primarily confined to mountainous regions do not exhibit clear adaptations for long-distance dispersal of achenes. This pattern is interpreted as a strategy for risk minimization, where reproductive efforts are concentrated on ensuring the persistence of the growth site under unfavorable conditions. The propagules of *Xeranthemum annuum* are well-adapted to be dispersed over long distances by sheep. Furthermore, seeds may also be dispersed by wind (Ruprecht et al. 2024). Morphological features that limit long-distance dispersal include a fragile pappus, reduced length of pappus setae, and increased seed weight (Häffner 2000). This trend is also evident in our sample. Notably, plants from both mountainous habitats and lowland petrophytic species tend to lack adaptations for long-distance dispersal, with 4 out of 7 samples not having a persistent pappus.

CONCLUSION

Our study allowed us to assess the diversity of carpological features in the achenes of xerophytic species within the family Asteraceae. In the primary sculpture, no uniformity in the shape of exocarp cells was observed: cellular sculpturing is noted in *Xeranthemum annum*, *Ptilostemon echinocephalus*, and *Jurinea cretacea*, characterized by a combination of concave periclinal and convex anticlinal outer walls. A wavy, ribbed surface is characteristic of *Artemisia alpina* and *A. hololeuca*, with two types of cells: those with convex and concave periclinal walls. In our sample, *Pentanema salicinum* is notable for its unique coating of calcium oxalate crystals. Secondary sculpture is generally poorly defined, appearing as microrelief on the cell walls. The tertiary sculpture of the taxa examined shows a variety of wax secretions, including papillary tubercles, flakes of indeterminate shape, and granulated wax, which are most characteristic of *Ptilostemon echinocephalus*. Upon examining the achenes of Asteraceae species, we observed an ordered folding of the achene surface, likely reflecting the structure of protuberances on the outer walls of the exocarp cells. The fine, disordered folding of the achene surface in *Artemisia* species is similarly caused by the unevenness of the outer periclinal walls of the exocarp. The morphological diversity of the cells is related to their shape, size, spatial orientation relative to the seed axis, and the nature of the thickening of the cell walls. Exocarp cells are oval or round in shape, covered with a layer of cuticle, with concave outer walls. The epicuticular wax is composed of granules of various shapes and sizes.

ACKNOWLEDGEMENTS

The work was supported by assignments № 122042700002-6 and № 124030100058-4, both to MBG RAS, of the Ministry of Science and Higher Education of the Russian Federation.

LITERATURE CITED

Anderberg, A.A. 1991. Taxonomy and phylogeny of the tribe *Plucheeae* (Asteraceae). *Plant Systematics and Evolution* 176:145–177.

Barthlott, W. 1981. Epidermal and seed surface characters of plants: systematic applicability and some evolutionary aspects. *Nordic Journal of Botany* 1(3):345–355.

Barthlott, W. & B. Ziegler 1981. Micromorphology of seed coats as systematic marks in orchids. *Berichte der Deutschen Botanischen Gesellschaft* 24:267–273.

Belyaev, A.A. 1984. Surface ultrastructure and some morphological characteristics of seeds of representatives of the Campanulaceae family. *Botnicheskii Zhurnal* 69(7):890–898 (in Russian). [Беляев А.А. 1984. Ультраструктура поверхности и некоторые морфологические характеристики семян представителей семейства Campanulaceae // Ботанический журнал. Т. 69, №7. С. 890–898].

Boesewinkel, F.D. & F. Bouman 1984. *The seed: structure. Embryology of angiosperms.* Springer, Berlin, Heidelberg.

Boyko, E.V. 2011. *Taxonomy and resources of Far Eastern species of the family Asteraceae: Doctor Diss abstract.* Vladivostok (in Russian). [Бойко Э.В. 2011. Таксономия и ресурсы дальневосточных видов семейства Asteraceae: автореферат дис. доктора биологических наук. Владивосток. 42 с.].

Boyko, E.V. 2012. Trichomes of achenes of Asteraceae species. *Turczaninowia* 15(2):85–95 (in Russian). [Бойко Е.В. 2012. Трихомы семянок видов семейства Asteraceae // Turczaninowia. Вып. 15, № 2. С. 85–95].

Boyko, E.V. 2013a. Micromorphology of achenes of the *Artemisia* species (*Anthemideae* – Asteraceae). *Turczaninowia* 16(2):91–105 (in Russian). [Бойко Е.В. 2013. Микроморфология семянок видов *Artemisia* (*Anthemideae* – Asteraceae) // Turczaninowia. Вып. 16, № 2. С. 91–105].

Boyko, E.V. 2013b. Papillae on the surface of the seeds of species of Asteraceae. *Turczaninowia* 16(3):86−95 (in Russian). [Бойко Е.В. 2013. Папиллы на поверхности семянок видов Asteraceae // Turczaninowia. Вып. 16, № 3. С. 86−95].

Boyko, E.V. 2015. Cuticle of the cypselas of the Asteraceae species. *Turczaninowia* 18(4):80–90 (in Russian). [Бойко Е.В. 2015. Кутикула семянок видов Asteraceae // Turczaninowia. Вып. 18, № 4. С. 80–90].

Boyko, E.V. & E.V. Novozhilova 2018. The structure of the seed coat of Asteraceae species. I. Tribes *Arctotideae*, *Cardueae*, *Mutisieae*, *Vernonieae*. *Turczaninowia* 21(4):44–62 (in Russian). [Бойко Е.В., Новожилова Е.В. 2018. Строение семенной кожуры видов Asteraceae. I. Трибы *Arctotideae*, *Cardueae*, *Mutisieae*, *Vernonieae* // Turczaninowia. Вып. 21, № 4. С. 44–62].

Buch, T.G. 1989. Ultrastructure of the seed coat surface and morphological characteristics of seeds of some species of vascular plants of the Soviet Far East. *V.L. Komarov Memorial Lectures* 36:3–19 (in Russian). [Буч Т.Г. 1989. Ультраструктура поверхности семенной кожуры и морфологическая характеристика семян некоторых видов сосудистых растений Дальнего Востока СССР // Комаровские чтения. Вып. 36. С. 3–19].

Franchini, M.C., L.F. Hernández & L.I. Lindström 2010. Cuticle and cuticular wax development in the sunflower (*Helianthus annuus* L.) pericarp grown at the field under a moderate water deficit. *Phyton-Revista Internacional de Botanica Experimental* 79(2):153–161.

Georgiadou Tvrtkovic-Sahin, E. E. 1982. *The systematics of the genus Helichrysum* Miller *in the countries bordering the Mediterranean*. Doctoral dissertation, University of Reading.

Golubev, V.N. 1996. *Biological Flora of Crimea*. NBS-NNC, Yalta, 126 pp. (in Russian). [Голубев В.Н. 1996. Биологическая флора Крыма. Ялта: НБС-ННЦ. 126 с.].

Häffner, E. 2000. On the phylogeny of the subtribe *Carduinae* (tribe *Cardueae*, Compositae). *Englera* 21:1–208.

Harper, J.L., W.T. Williams & G.R. Sagar 1965. The behavior of seeds in soil. Part 1. The heterogeniety of soil surface and its role in determining the establishment of plants from seed. *Journal of Ecology* 53:273–286.

Jana, B.K. & S.K. Mukherjee 2014. Exomorphology and internal structure of cypselas of seven species of the tribe *Cardueae* (Compositae). *Journal of the Indian Botanical Society* 93(1–2):50–59.

Jeffrey, C., V.H. Heywood & D.M. Moore 1985. Current concepts in plant taxonomy. *Kew Bulletin* 40(4):95–105.

Karpova, A. & O. Yakovleva 2012. The comparative analysis of species of genus *Stroganowia* (Cruciferae). *Biological Communications* 1:14–37.

Korzhenevsky, V.V. & L.V. Bondareva 2018. *Ptilostemon echinocephalus* (Willd.) Greuter [*Lamyra echinocephala* (Willd.) Tamamsch.]. In: *Red Book of the City of Sevastopol* (S.Yu. Samoilov, ed.), p. 104, ROST-DOAFK, Kaliningrad, Sevastopol (in Russian). [Корженевский В.В., Бондарева Л.В. 2018. Птилостемон ежеголовый (Ламира ежеголовая). *Ptilostemon echinocephalus* (Willd.) Greuter [*Lamyra echinocephala* (Willd.) Tamamsch.] // Красная книга города Севастополя / предс. ред. колл. С.Ю. Самойлов. Калининград, Севастополь: ИД РОСТ-ДОАФК. С. 104].

Korobkov, A.A. 2024. *Artemisia hololeuca* M. Bieb. ex Besser. In: *Red Book of the Russian Federation* (D.V. Geltman, ed.), p. 132, VNII Ekologiya, Moscow (in Russian). [Коробков А.А. 2024. Полынь беловойлочная *Artemisia hololeuca* M. Bieb. ex Besser. // Красная книга Российской Федерации / отв. ред. Д.В. Гельтман. Москва: ВНИИ Экология. С. 132].

Kostina, V.A. 2014. *Red Book of the Murmansk Region. 2nd edition, revised and expanded.* Aziya-print, Kemerovo, 584 pp. (in Russian). [Костина В.А. 2014. Красная книга Мурманской области. Изд. 2-е, переработанное и дополненное. Кемерово: Азия-Принт. 548 с.].

Kotlyarova, I.A., G.A. Tereshchenko & O.I. Voloshina 2016. Variability of achenes within the basket by morphometric characteristics and seed productivity in modern sunflower varieties. *Maslichnye Kultury* 1(165): 29–37 (in Russian). [Котлярова И.А., Терещенко Г.А., Волошина О.И. 2016. Изменчивость семянок в пределах корзинки по морфометрическим признакам и семенной продуктивности у современных сортов подсолнечника // Масличные культуры. Вып. 1, № 165. С. 29–37].

Kravtsova, T.I. 2007. The system of the Urticaceae family. *Botanicheskii Zhurnal* 92(1):3–28 (in Russian). [Кравцова Т.И. 2007. Система семейства Urticaceae // Ботанический журнал. Вып. 92, № 1. С. 3–28].

Kreitschitz, A. & J. Vallès 2007. Achene morphology and slime structure in some taxa of *Artemisia* L. and *Neopallasia* L.(Asteraceae). *Flora* 202(7):570–580.

Kreitschitz, A. & S.N. Gorb 2018. The micro- and nanoscale spatial architecture of the seed mucilage –Comparative study of selected plant species. *PLoS ONE* 13(7):e0200522.

Lukonina, A.V., N.G. Volodina & V.A. Sagalaev 2017. *Jurinea cretacea* Bunge. In: *Red Book of the Volgograd Region. Vol. 2. Plants and Other Organisms* (V. E. Sazonov, ed.), p. 87, Izdat-Print, Voronezh (in Russian). [Луконина А.В., Володина Н.Г., Сагалаев В.А. 2017. Наголоватка меловая – *Jurinea cretacea* Bunge. Красная книга Волгоградской области. Том 2. Растения и другие организмы / под ред. В.Е. Сазонова. Воронеж: Издат- Принт. С. 87].

Mamontov, A.K. & A.S. Ryabchenko 2017. Peculiarities of seed and fruit morphology of some rare calciphilic species of European Russia. *Vestnik Voronezhskogo gosudarstvennogo universiteta. Seriya: Himiya. Biologiya. Farmaciya* 4:54–61 (in Russian) [Мамонтов А.К., Рябченко А.С. 2017. Особенности морфологии семян и плодов некоторых редких кальцефильных видов Европейской России // Вестник Воронежского государственного университета. Серия: Химия. Биология. Фармация. № 4. С. 54–61].

Mazina, O.V. & E.N. Sokhina 2018. Representation of rare plant species in the floristic complexes of the Shcherbakovsky Nature Park. In: *Steppes of Northern Eurasia: proceedings of the VIII International Symposium* (A.A. Chibilev, ed.), pp. 606–609, IS UrO RAS, Orenburg (in Russian). [Мазина О.В., Сохина Э.Н. 2018. Представленность редких видов растений во флористических комплексах природного парка «Щербаковский» // Степи Северной Евразии: материалы VIII международного симпозиума / под ред. А.А. Чибилёва. Оренбург: ИС УрО РАН. С. 606–609].

Mustafa, A.E.Z.M. & H. Rizwana 2025. Micromorphological traits of seed stratification for optimizing biodiversity conservation. *Plant Species Biology* 40(1):42–53.

Netolitzky, F. 1926. Anatomie der Angiospermen-Samen. In: *Handbuch der Pflanzenanatomie* (ed. K. Linsbauer), pp. 1–364, Gebrüder Borntraeger, Berlin.

Ozcan, M. & N. Akinci 2019. Micromorpho-anatomical fruit characteristics and pappus features of representative *Cardueae* (Asteraceae) taxa: Their systematic significance. *Flora* 256:16–35.

Panero, J.L. & V.A. Funk, 2008. The value of sampling anomalous taxa in phylogenetic studies: major clades of the Asteraceae revealed. *Molecular Phylogenetics and Evolution* 47(2):757–782.

Polyakov, P.P. 1967. *Taxonomy and origin of Asteraceae*. Nauka Kazakhskoi SSR, Alma-Ata, 336 pp. (in Russian) [Поляков П.П. 1967. Систематика и происхождение сложноцветных. Алма-Ата: Наука Казахской ССР. 336 с.].

Radygina, V.I. 2014. Endemism of calcephites of the central Russian and Volga uplifts. *Uchenye zapiski Orlovskogo gosudarstvennogo universiteta. Seriya: Estestvennye, tekhnicheskie i meditsinskie nauki* 6:83–85 (in Russian). [Радыгина В.И. 2014. Эндемизм кальцефитов Среднерусской и Приволжской возвышенностей. Ученые записки Орловского государственного университета. Серия: Естественные, технические и медицинские науки. № 6. С. 83–85.]

Reese, H. 1989. Development of pericarp and testa in *Calenduleae* and *Arctotideae* (Asteraceae). *Botanische Jahrbücher fur Systematik* 110(3):325–419.

Reshetnikova, N.M. 2024. *Serratula tanaitica* P.A. Smirn. [*Klasea radiata* (Waldst. et Kit.) Á. Löve et D. Löve subsp. *tanaitica* (P.A. Smirn.) L. Martins]. In: *Red Book of the Russian Federation* (D.V. Geltman, ed.), p. 146, VNII Ekologiya, Moscow (in Russian). Решетникова Н.М. 2024. Серпуха донская – *Serratula tanaitica* P.A. Smirn. [*Klasea radiata* (Waldst. et Kit.) Á. Löve et D. Löve subsp. *tanaitica* (P.A. Smirn.) L. Martins] // Красная книга Российской Федерации / отв. ред. Д.В. Гельтман. Москва: ВНИИ Экология. С. 146].

Ruprecht, E., F. Essl, C.A. Mot, B. Balaji, T. Kuhn, A. Fenesi, ... & Z. Miholcsa 2024. Ecological attributes promoting intra-continental range-expansion of a native annual forb triggered by intensified land-use. *Flora* 310:152416.

Şeker, M. & Ö. Çetin 2013. *Inula tuzgoluensis* (Asteraceae), a new species from Central Anatolia, Turkey. *Turkish Journal of Botany* 37(5):825–835.

Stevens, P.F. 2007. *Angiosperm Phylogeny Website. Version 14, July 2007 (and more or less continuously updated since)*. http://www.mobot.org/MOBOT/research/APweb/. Last accessed on 28.10.2024.

Tadesse, M. 2014. How to study the Asteraceae (Compositae) with special reference to the Asteraceae of fee. *Ethiopian Journal of Biological Sciences* 13(Supp.):91–101.

Terekhin, E.S. 1996. *Seed and seed propagation*. Mir i Semja-95, Saint-Petersburg. 376 pp. (in Russian). [Терехин Е.С. 1996. Семя и семенное размножение. Санкт-Петербург: Мир и Семья-95. 376 с.].

Velez, M.C. 1981. Carpological studies on American *Astereae* (Compositae). *Mitteilungen der Botanischen Staatssammlung München* 17:1–170.

Volodina, N. G. 1982. Flora of Cretaceous outcrops in the Volgograd region. In: *Flora of steppes and semi-deserts (based on the example of the Lower Volga region)* (Yu.Ya. Anikin, ed.), pp. 34–46, VGPI, Volgograd (in Russian). [Володина Н.Г. 1982. Флора меловых обнажений Волгоградской области // Флора степей и полупустынь (на примере Нижнего Поволжья) / под. ред. Ю.Я. Аникина. Волгоград: ВГПИ. С. 34–46].

Yakovleva, O.V., A.A. Korobkov & E.V. Boyko 2002. The structure of mucus-containing cells in the pericarp of achenes of some *Artemisia* species (Asteraceae). *Botanicheskii Zhurnal* 87(9):1–9 (in Russian) [Яковлева О.В., Коробков А.А., Бойко Е.В. 2002. Строение слизесодержащих клеток околоплодника семянок некоторых видов *Artemisia* (Asteraceae) // Ботанический журнал. Т. 87, № 9. С. 1–9].