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SHORT COMMUNICATION

Atypical cristae in bundle sheath mitochondria in leaves of *Atriplex tatarica* (*Chenopodiaceae* s. str. / *Amaranthaceae* s. l.)

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Abstract. Electron microscopic analysis of leaf ultrastructure patterns of *Atriplex tatarica* (*Chenopodiaceae* s. str. / *Amaranthaceae* s. l.) revealed a prominent feature in mitochondria in bundle sheath cells (BSCs). Our studies of developing leaves of *A. tatarica* collected in the Novobilychi neighborhood of Sviatoshyn District (Kyiv City, Ukraine) demonstrated that the internal mitochondrial structure in BS cells is significantly different from that in other cells. Many BSc mitochondria have two types of cristae, normal and atypical ones. The atypical cristae represented with curved lamellae are oriented along the longitudinal axis of a mitochondrion or at some angles to it. Such mitochondria appear to be widely distributed within the BS cells in leaves of *A. tatarica* and are highly abundant (probably between 70 and 90%), but have not been observed in mitochondria from cells of other chlorenchymal and epidermal tissues. These abnormal mitochondria can only be identified by the presence of atypical cristae; no other differences in their fine structure have been observed. In many cases, such mitochondria are found in close proximity to chloroplasts. A functional connection between the architecture of atypical cristae and their physiological function in BS cells is possible. The close proximity of these mitochondria to chloroplasts indicates that they may play an important role in cellular energy or metabolite transport.

Keywords: *Atriplex tatarica*, bundle sheath cells, C_4 photosynthesis, cristae, mitochondria, ultrastructure

Atriplex L. is a plant genus with about 250 currently recognized species belonging to the family *Amaranthaceae* s. l., subfamily *Chenopodioideae* (often recognized as a separate family *Chenopodiaceae* s. str.) (see Kadereit et al., 2010; Žerdoner Čalasan et al., 2022; POWO, 2025–onward). The genus is quite diverse and widely distributed. It includes many desert and seaside plant species, halophytes, and often plants of anthropogenic plant communities. Representatives of *Amaranthaceae* subfam. *Chenopodioideae* (*Chenopodiaceae* s. str.) are important components of the flora and vegetation in arid and saline regions; they also often occupy arable fields, roadsides, wastelands, and other disturbed habitats (Akhani et al., 1997; Kocháneková, Mandák, 2008; Šerá et al., 2023).

Only a few clades of *Atriplex* are represented by C_3 plants, but most species of the genus are C_4

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plants (one of the largest C_4 clades in eudicots, according to Žerdoner Čalasan et al., 2022), with a characteristic leaf anatomy known as Kranz anatomy (Hatch, 1987). The C_4 pathway of photosynthesis is thought to have played an important role in the evolutionary success of the genus *Atriplex*, as most successful of its species that now are distributed almost throughout the world use the C_4 metabolism (see Rudov et al., 2020; Žerdoner Čalasan et al., 2022, and references therein). A representative of this family belonging to the C_4 type clade, *Atriplex tatarica* L., is considered a weedy plant that is native throughout a wide area of Middle and Western Central Asia, Asia Minor, southeastern Europe, and North Africa (Akhani et al., 1997), as well as Ukraine (Skripnik, 1987). Based on flow cytometry data, the biochemical type of photosynthesis in *A. tatarica* is classified as NAD-ME, resembling that of the related NAD-ME species *A. rosea* L. (Pfundel et al., 1996).

In contrast to many other groups of C_4 *Chenopodiaceae*, *Atriplex* exhibits a typical Kranz anatomy, characterized by a layer of bundle sheath cells (BSCs) surrounding each vascular bundle and radially arranged palisade cells, and relatively little variation in C_4 leaf types (Kadereit et al., 2010). The outer layer is comprised of mesophyll cells (MCs), which are not differentiated into spongy and palisade parenchyma. A distinguishing feature of MCs and BSCs is their structural and functional heterogeneity. MCs are characterized by their diminutive size, dispersed arrangement, and the presence of grana in their chloroplasts. In contrast to BSCs, MCs rarely contain starch. The BSCs are characterized by their larger size, thickened cell walls, and close proximity to leaf veins. The chloroplasts within BSCs may lack grana and frequently contain starch grains. The Rubisco enzyme is localized within BSCs, and the typical Calvin cycle occurs. Primary photosynthetic CO_2 fixation is performed in the cytosol of the MC. The resulting C_4 acid is then converted to either malate or aspartate, which are transported to the BSCs where they are decarboxylated, releasing CO_2 in the vicinity of Rubisco. The cooperative functioning of the two photosynthetic cells, which are biochemically and ultrastructurally distinct (Hatch, 1987), results in a multiple elevation in substrate (CO_2) concentrations around the carboxylating enzyme Rubisco (Sage, 2004), thereby minimizing photorespiration (von Caemmerer, Furbank, 2003).

The C_4 cycle necessitates additional biochemical steps, leading to higher energy consumption as compared to C_3 photosynthesis. The fixation of one CO_2 molecule requires 5 ATP and 2 NADPH for C_4 plants, which drive the NAD-ME photosynthetic subtype, whereas for the C_3 cycle this energy requirement is 3 ATP and 2 NADPH (Edwards, Voznesenskaya, 2010; Walker et al., 2020). However, available research on the mechanisms that regulate energy balance in these different subtypes of C_4 plants is limited, and in particular the ultrastructural features of mitochondria in MCs and BSCs have received little attention. The aim of this study was to examine the internal structure of mitochondria in BSCs of *A. tatarica* leaves collected on the suburbs of Kyiv.

Field experiments were carried out in June 2023 in the region of the western suburbs of Kyiv. Seven plants were collected in the Novobilychi neighborhood, Sviatoshyn District of Kyiv City (50°28'37.0"N, 30°21'29.0"E), between the railway and the roadside (Fig. 1A); we then selected for sampling three leaves from each plant (Fig. 1B).

For ultrastructural analysis of leaf mitochondria, 2 × 2 mm sections were cut from the middle zone of the leaves (Fig. 1C). A pre-fixation of the material was carried out at room temperature (18–22 °C) as described earlier (Fediuk et al., 2017). After vacuum infiltration with 2.5% glutaraldehyde in 0.1 M phosphate buffer (pH 7.2) for 8 h at 4 °C, the samples were buffer-washed (2 × 20 min) and postfixed with 1% OsO_4 in 0.1 M cacodylate buffer, pH 7.2, overnight at 4 °C. The prepared plant materials were dehydrated in a graded ethanol series and infiltrated via acetone series. Then, samples were soaked in epoxy resin mixtures and acetone, embedded in Epon-araldite resin and transferred to a thermostat for polymerization at 37 and 60 °C. Ultra-thin sections were made with a LKB-V ultramicrotome (LKB, Sweden), stained with Pb citrate, and examined in a JEM-1300 transmission electron microscope (JEOL, Japan) with magnification of 50 000 or 100 000×. The images of 50 mitochondria were analyzed as described earlier (Fediuk et al., 2018) for each variant. Morphometric image analysis of the mitochondria and determination of transverse dimension of the grana were carried out using an ImageJ computer program (NIH Image, USA).

In higher plants, mitochondria are usually spherical, sausage-shaped, or linear, and their morphology is highly variable (Logan, 2003). They are usually

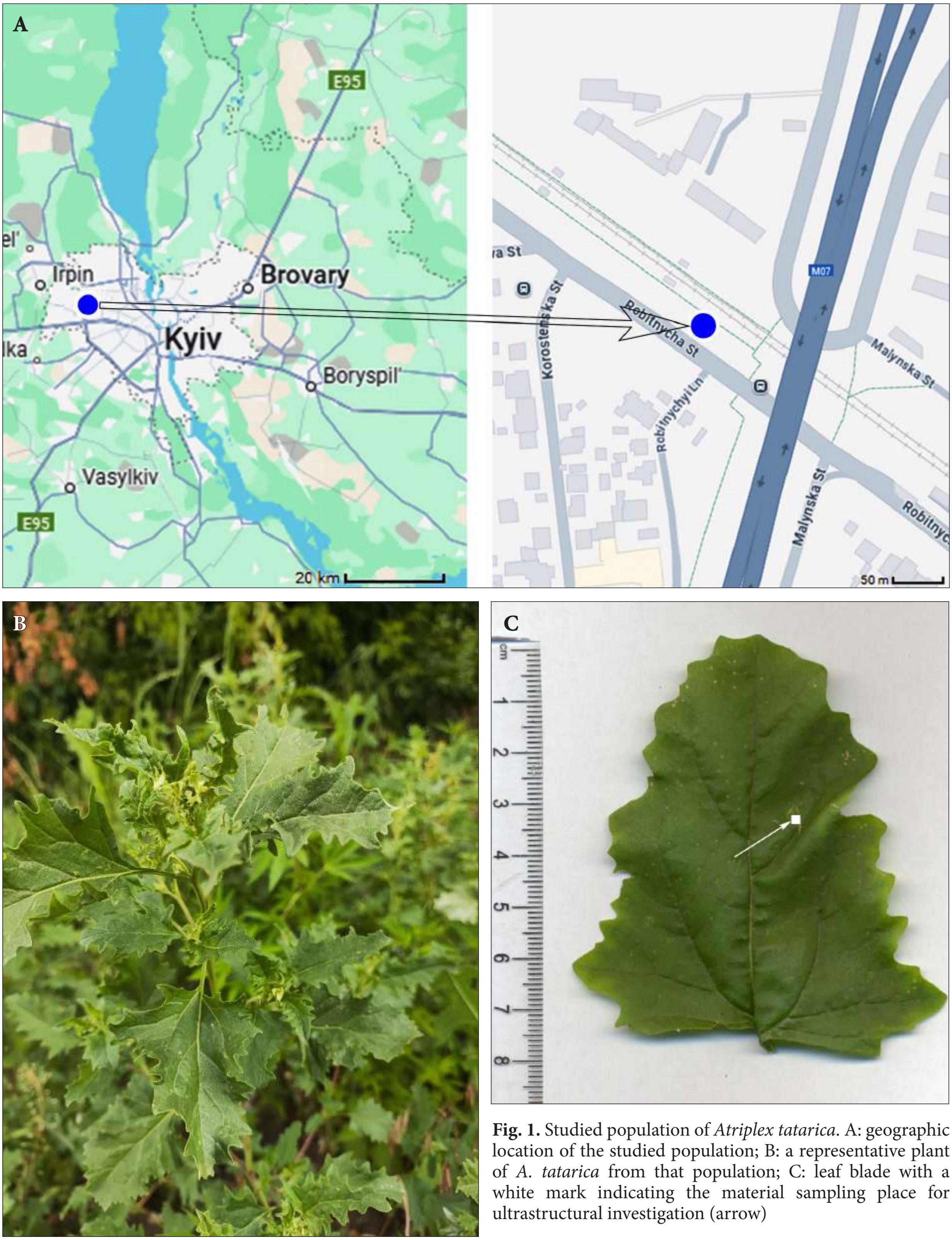

Fig. 1. Studied population of *Atriplex tatarica*. A: geographic location of the studied population; B: a representative plant of *A. tatarica* from that population; C: leaf blade with a white mark indicating the material sampling place for ultrastructural investigation (arrow)

distributed in the cytoplasm (Stickens, Verbelen, 1996) with diameters ranging from 0.2 to 1.5 µm (Jaipargas et al., 2015).

In the BSCs of *Atriplex tatarica* leaves, a significant proportion of the mitochondria appear elongated; moreover, we found that they contain not only normal cristae, but also atypical cristae, which form specific structures that occupy a considerable fraction of the volume of these organelles (Fig. 2A). Atypical cristae are curved lamellae that are often arranged parallel to each other along the longitudinal axis of the mitochondrion. When viewed longitudinally, these structures appear as a series of curved lamellae that are connected at some points. The diameter of these structures has been measured to be 10–15 nm, with lengths reaching 500–700 nm. The ultrastructure of these mitochondria consists of interconnected sectors with widened electron-transparent zones resembling normal cristae, and narrower sectors with electron-dense membranes and an electron-opaque central layer (Fig. 2B). Typically, their terminal sectors are occluded; numerous intramitochondrial granules are often observed between them (Fig. 2C). The number of elements in each structure varies considerably (from a few to more than 10 per section), as does their number in a mitochondrial section (1–3 per organelle). Such mitochondria appear to be widely distributed within the BSCs of *A. tatarica* leaves (Fig. 2A) and are highly abundant (probably between 70 and 90%), but have not been observed in mitochondria from cells of other chlorenchymal and epidermal tissues. The abnormal mitochondria can only be identified by the presence of atypical cristae; no other differences in their fine structure are observed. In many cases, such mitochondria are found in close proximity to chloroplasts (Fig. 2A).

Mitochondria represent the energy center of eukaryotic cells and the main site of ATP synthesis during aerobic respiration producing various metabolites involved in programmed cell death, oxidative stress, and other important cellular processes (Tang, Zhu, 2023). Most of the ATP required by the cell is produced by ATP synthases localized on the inner membranes of mitochondria. These membranes of a typical mitochondrion have numerous deep folds or indentations called cristae (*singular*: crista). In addition to their function in energy transduction, the F_1F_0-ATP synthase supercomplexes play a structural role in determining cristae morphology (Giraud et al., 2002; Paumard et al., 2002; Bornhövd et al., 2006; Davies et al., 2012). This depends on their ability to form dimeric and higher oligomeric supracomplexes. The use of electron microscopy and cryo-electron tomography techniques has revealed the very precise organization of these enzymes in eukaryotic species, from yeasts to vertebrates (Strauss et al., 2008; Velours et al., 2009; Davis et al., 2012; Anselmi et al., 2018). ATP synthases have been shown to form dimers, organized in ribbon-like rows of dimers, that induce curvature along tubule and lamellar edge rows extending over hundreds of nanometers. These rows are observed only in cristae, particularly along their sharply curved edges. Cristae are thought to increase the membrane area available for oxidative phosphorylation, and thus they play an important role in optimizing ATP synthesis (Strauss et al., 2008; Davis et al., 2012). When ATP synthase oligomers disintegrate, the internal structure of mitochondria is disrupted, the cristae decay, and abnormal intramembrane morphologies are observed (Venkatraman et al., 2023). It has been shown that the contents of dimeric F_1F_0-ATPase in the mitochondria of human placenta correlates with the atypical cristae morphology (Castillo et al., 2011).

In addition, the IF_1 inhibitory protein, which suppresses ATP synthase activity, plays a critical role in its oligomerization and, consequently, in the structure of mitochondrial cristae (Campanella et al., 2008). *In vivo* studies have shown that IF_1 expression in various mammalian cells promotes an increase in the number of oligomeric aggregates of ATP synthase. Conversely, its ablation reduces the content of ATP synthase oligomers, leading to changes in the structure of mitochondrial cristae (Romero-Carramiñana et al., 2023).

Thus, the critical role of ATP synthase oligomers and its IF_1 subunit in maintaining the typical cristae structure of yeast and mammalian mitochondria has been established.

Unlike the mitochondria of these organisms, the mechanisms of cristae formation and the factors responsible for the atypical structures of plant mitochondria, including C_4-pathway mitochondria, have been the focus of only limited research.

Mitochondria are well known to be directly or indirectly involved in the C_4 pathway (Fan et al., 2022), although it is important to note that their role varies between different C_4 subtypes (Yin et al., 2018). Changes in the mitochondrial dynamics and cristae structure can be viewed as a mechanism by

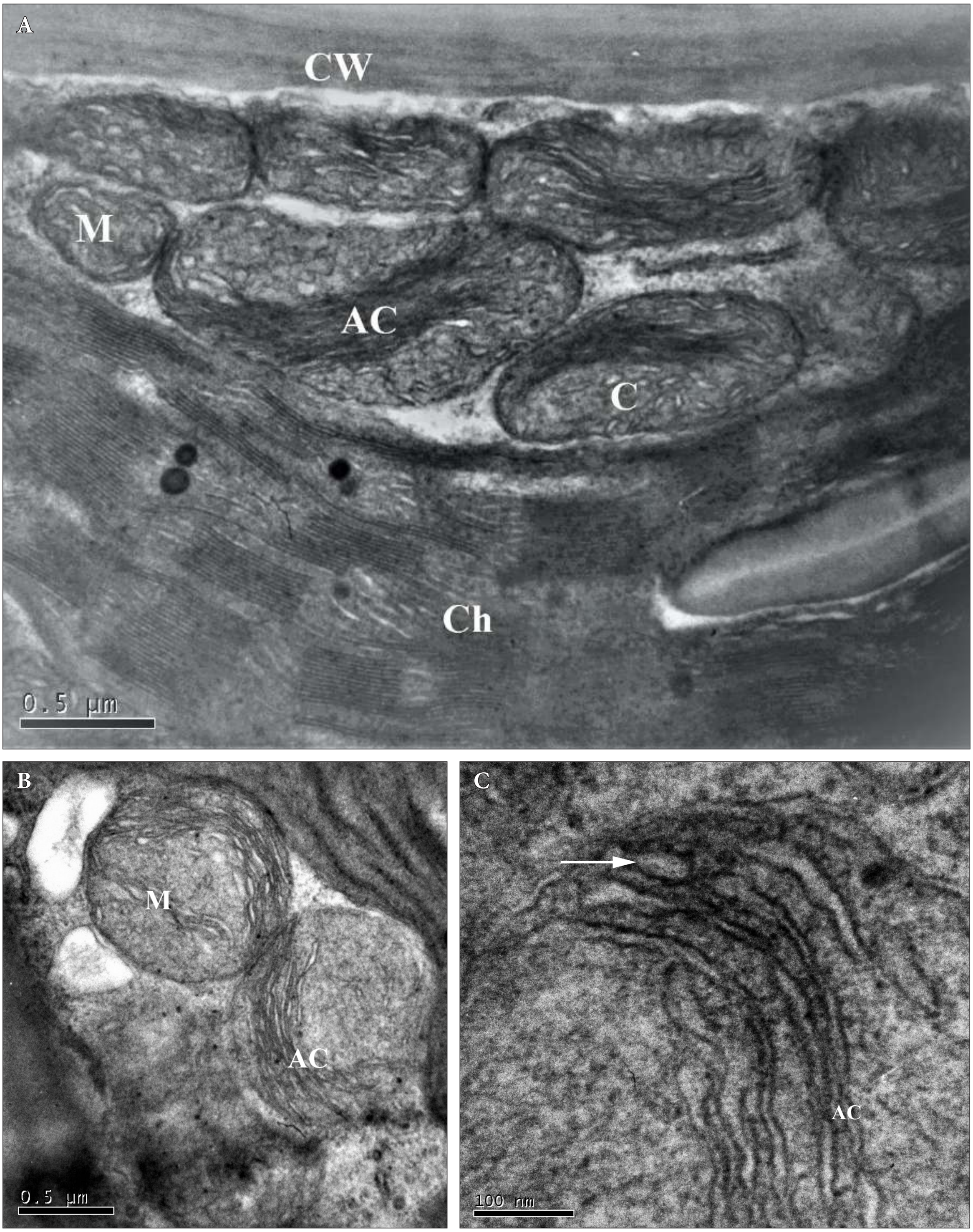

Fig. 2. Ultrastructure of mitochondria in BS cells of leaves of *Atriplex tatarica*. A: a group of mitochondria (longitudinal section) located between a cell wall and a chloroplast, in which normal cristae and atypical cristae are distinctive; B: a transverse section of mitochondria with curved atypical cristae; C: terminal sites of atypical cristae (arrow). Abbreviations: AC — atypical cristae, C — normal cristae, Ch — chloroplast, CW — cell wall, M — mitochondria

which the cell regulates mitochondrial functional efficiency and respiratory capacity (Baker et al., 2019). The presence of specific cristae in BSC mitochondria has previously been reported in two *Cleome* s. l. species with different forms of cristae anatomy (Koteyeva et al., 2014), although the present research seems to be the first to identify atypical intramembrane structures that differ from normal cristae in BS cells.

In conclusion, the mitochondrial population in BSCs of *A. tatarica* leaves is not homogeneous; many of the mitochondria have two types of cristae, both normal and atypical ones. Atypical cristae are represented by curved plates, which are often arranged parallel to each other in the central part of such a structure and are connected in some places; they are oriented along a longitudinal axis or at some angles to it in these organelles. The mitochondria have both similar features with analogues in other species and significant differences from them, such as the high frequency of occurrence, curved contours and uneven formation of plates. The close proximity of such mitochondria to chloroplasts suggests that they may play an important role in the transport of metabolites. It is possible that there is a morphological and functional connection between the atypical cristae architecture and their physiological function in BS cells. We believe that these structures require further investigations, especially regarding their functions in the cells of the BS tissue at the subcellular and molecular level.

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ETHICS DECLARATION

The authors declare no conflict of interest.

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Атипові кристи в мітохондріях обкладинок судинних пучків в листках *Atriplex tatarica* (*Chenopodiaceae* s. str. / *Amaranthaceae* s. l.)

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Реферат. Електронно-мікроскопічний аналіз ультраструктури листків *Atriplex tatarica* (*Chenopodiaceae* s. str. / *Amaranthaceae* s. l.) виявив характерну особливість мітохондрій у клітинах обкладинки судинного пучка (BS). Дослідження листків *A. tatarica*, що розвиваються, зібраних у Новобіличах Святошинського району міста Києва (Україна), показали, що внутрішня структура мітохондрій у клітинах BS значно відрізняється від інших клітин. Багато мітохондрій BS мають два типи крист (нормальні та атипові). Атипові кристи представлені вигнутими пластинками, орієнтованими вздовж поздовжньої осі або під деякими кутами до неї. Такі мітохондрії, як видається, широко розповсюджені в клітинах BS листків *A. tatarica* і є дуже поширеними (ймовірно, від 70 до 90%), але не були виявлені в мітохондріях клітин інших хлоренхімних та епідермальних тканин. Аномальні мітохондрії можна ідентифікувати лише за наявністю атипових крист; інших відмінностей у тонкій структурі не спостерігається. У багатьох випадках такі мітохондрії знаходяться в безпосередній близькості до хлоропластів. Можливо, існує зв'язок між архітектурою атипових крист та їхньою фізіологічною функцією, враховуючи те, що клітини BS мають додаткові потреби в енергії порівняно з клітинами мезофілу. Близьке розташування мітохондрій до хлоропластів у клітинах BS вказує на те, що вони можуть відігравати важливу роль у транспорті енергії або метаболітів.

Ключові слова: *Atriplex tatarica*, C_4 фотосинтез, клітини оболонки судинного пучка, кристи, мітохондрії, ультраструктура