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An Overview on Anatomy of Jerusalem Artichoke (*Helianthus tuberosus* L.)

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JERUSALEM artichoke (JA) is a promising crop, classified as a foodstuff (tubers), animal feed (fodder or silage), and an energy crop (for bioethanol production). This crop has several economic benefits including the production of inulin, fructose, and proteins, as well as raw materials for the chemical, pharmaceutical and food industries. The present review mainly focus on the anatomical structure of unstressed JA which has distinguished features for stems, leaves, stomata and trichomes. Anatomy of JA plant may support its responses to harsher conditions including the physiological and metabolic changes. Under stress conditions, JA may undergo some biochemical and anatomical adaptations to survive depending on the kind of stress, abiotic (e.g., drought, salinity, waterlogging, heat stress, etc.) and biotic (insects, microbes, herbivorous, etc.). Hence, due to the rare or may be no studies on anatomical structure of cultivated JA under stress, many futures studies are strongly required to reflect the real anatomical situation of stressed JA plants.

Keywords:Jerusalem artichoke; Stomata; Stem; Trichomes; Leaf anatomy

Introduction

The phytotomy or plant anatomy as an important discipline in plant biology started from hundred years ago (may be the late 17thcentury) and still includes enormous reports in the literature based on the great efforts of several scientists like The ophrastus (Greek scientist), Gaspard Bauhin (Swiss physician and botanist) and Marcello Malpighi (Italian botanist). The first edition of the classic plant anatomy was published by Katherine Esau in 1953 and recently many distinguished books have been published such as Cutler et al. (2007), Beck (2010), Maiti et al. (2012), Steeves and Sawhney (2017), Schweingruber and Börner (2018) and Fitzgerald (2020). The anatomical data could be applied for better understanding of the interrelationships of plants with the surrounding environment. Therefore, the concepts of plant anatomy may help us getting enough knowledge of the behavior of cultivated plants under changing environments (Crang et al. 2018). The applied plant anatomy is considered a powerful tool that has been employed to realize the nature of many baffling responses of plants particularly under stress in many recent studies (e.g., Ghazy et al. 2017; Amer and El-Emary, 2018; Ribeiro et al. 2019; Bákonyi et al. 2020; Bueno et al. 2020; dos Santos et al. 2020; Lobato et al. 2020; El-Ramady et al. 2021).

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Jerusalem artichoke (*Helianthus tuberosus* L.), as a herbaceous perennial plant belongs to the family of sunflower plant (Compositae or Asteraceae), is cultivated for tubers (as a vegetable), for feeds or silage (as a fodder crop) and for producing the high biomass as a bioenergy crop (Qiu et al. 2018). This crop also has high ecological value, which represents in its growing well under harsher conditions such as marginal land, waterlogging, saline-alkali soils and coastal shoals (Qiu et al. 2018; Yan etal. 2018). Jerusalem artichoke also known as topinambur or sunchoke, as a non-grain crop, has a lot of desirable characteristics including strong ecological adaptability, rapid growth, low management cost, and high biomass yield as well as high energy conversion efficiency (Lv et al. 2019 and Yue et al. 2020). Jerusalem artichoke is well known as a hexaploid crop, and the main researches on this crop have been focused on fructan synthesis and its nutrition value as well as the dormancy of tubers (Yang et al. 2019). It is well established that, the JA tubers are the main organ of this plant for human foods, animal feeds, and inulin processing. The JA tubers have four distinguished changes during different period of growth including the forming of creeping stem, the forming of tubers, the swelling of tubers and the maturation of tubers, which needs 9, 17, 22 and 24 weeks, respectively (Zhao et al. 2020).

The morphological structure of JA plant includes the leaves and stems as shoots or the above-ground biomass as well as the tubers (Fig. 1). The yield of JA tubers may record up to 75.5 Mg ha^{-1} and above-ground fresh green matter up to 120 Mg ha^{-1}. JA plants grow from 2 to 4 m in height and can be cut 3–4 times a year. The JA shoots including both leaves and stems, which could be used for making good high value silage and forage for animals. The optimal quality of JA forage could be obtained by harvesting plant tops early when the leaves ratio is more than 50% of the above ground biomass and protein levels are at their maximum level. Concerning the JA leaves, they are main source of proteins (particularly that rich in amino acids methionine and lysine) which make JA nutritionally comparable to better known forage crops. The level of calcium content in the aerial parts of JA may be around 8-times higher than that found in the tubers, whereas the potassium and phosphorus contents about 4- and 5-times lower, respectively, and equivalent magnesium levels (Papi et al. 2019). The structure of JA leaves may guarantee the using of this areal part of JA in feeding the animals and might also control the tolerance of this plant to different stressful conditions.

Therefore, this current review represents an attempt to highlight the anatomy of JA in different fractions including leaves and stems as well as the stomata and trichomes as a first report. The separts might have a promising role in explaining the tolerance of the cultivated JA to abiotic and biotic stresses.

Anatomical structure of stem

In general, the stem organ is considered a typically above ground part that grows toward light as a positive phototropism and negative gravitropism or away from the ground. This plant organ has a vital function which is the long-distance transport of photosynthetically derived sugars, minerals, water, and hormones (Crang et al. 2018).It has to be differentiated between stem and shoot; stem is the axis of plant whereas the shoot is the stem plus any leaves, flowers, or buds that may be exist. The stem organized into nodes where leaves are attached and internodes, the regions between nodes (Mauseth, 2017).

Some investigations have been published regarding the stem of JA to be focused on the potential applications of JA stems (Li et al. 2016; Wang et al. 2020), as a valuable feedstock for biorefinery (Qiu et al. 2018; Gao and Yuan 2019; Kotsanopoulos et al. 2019), or industrial purposes (Chen et al. 2019 and Shao et al. 2019) and for sustainable protein supply (Kaszás et al. 2020), but the anatomical studies of JA still need more concern particularly under changing and stressed environments.

The anatomy of JA stem from outside to inside is illustrated in Fig. 2. A. Cuticle is a pure layer of cutin which is a fatty substance that makes the wall impermeable to water. Cutin resists digestive enzymes and provide defense against pathogens like fungi and bacteria. B. Epidermis is the outermost layer of herbaceous plants stem which found in a single layer of living parenchyma cells. Its critical function is preventing water loss from plants to air. Also, the epidermis works as a barrier against invasion by bacteria and fungi as well as small insects. It protects internal cells from abrasion by dust particles, passing animals, rubbing leaves and stems and it is a shelter in bright sunlight from overheating (Mauseth, 2017). C. Cortex is the interior to the epidermis. It mainly composed of photosynthetic parenchyma and sometimes collenchyma.

Fig. 1. Normal unstressed JA plant at vegetative stage; as a source of stem and leaf samples which were taken at the end of June 2019 for anatomy. Demonstration Garden, Agricultural Botany, Plant Physiology and Biotechnology Dept., Debrecen Uni., Hungary

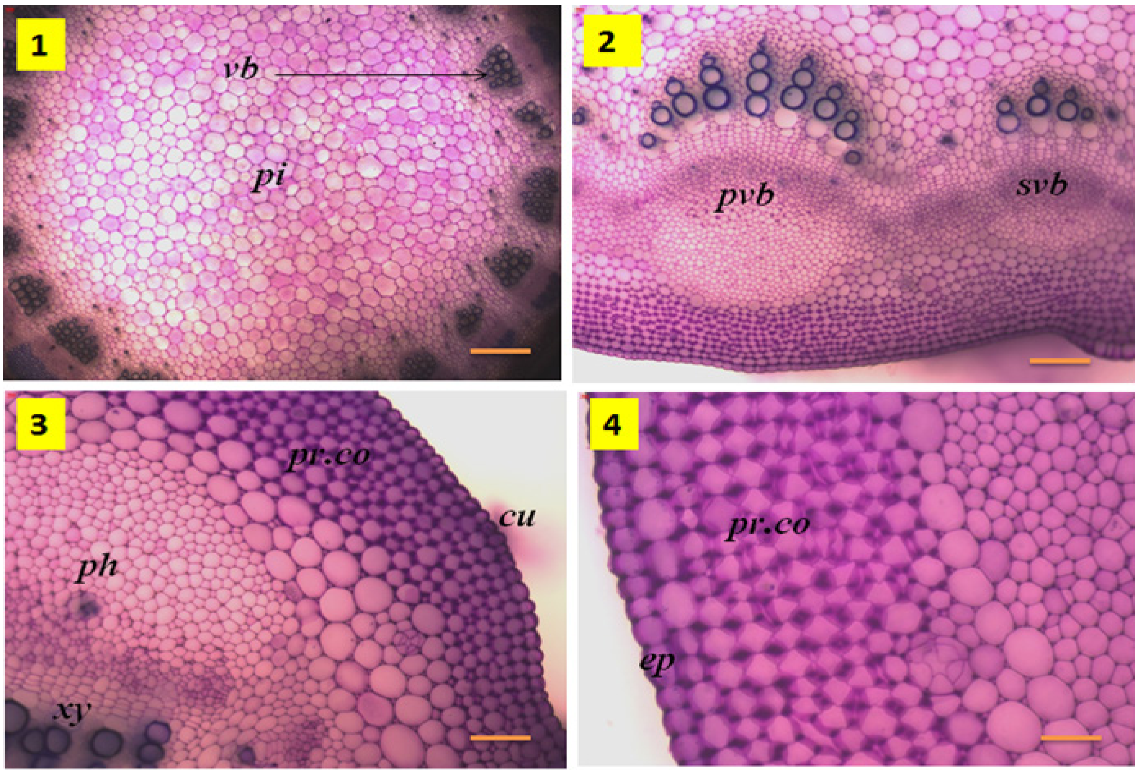

Fig. 2. Cross sections of Jerusalem artichoke stem.*vb* vascular bundle, , *Pi pith pvb* primary vascular bundle, *svb* secondary vascular bundle, *pr.co* primary cortex, *cu* cuticle, *ph* phloem, *xy* xylem, *ep* epidermis. Scale bar = 50, 20, 10 and 5 µm for photos 1, 2, 3 and 4, respectively. The cross sections have been prepared, stained by toluidine blue (0, 2%), examined using Electronic Microscope (Axioskop 2 plus, Carl Seiss Technika Kft, Hungary) and photographed using Scop-Photo software by Neama Abdalla

D. Vascular tissues that found in two types of tissues; xylem, which conducts water and minerals from the soil to roots, stem and leaves to make photosynthesis and phloem which distributes sugars and carbohydrates produced in leaves all over plant parts. In JA, xylem and phloem located together just interior to the cortex in form of primary and secondary vascular bundles. F. These vascular bundles arearranged in one ring surrounding the pith; consist of parenchyma cells (Mauseth, 2017).

Anatomical structure of leaf

Plant leaves are considered the lateral organs of the shoot, which have several or multiple functions in the plant. The main task of plant leaves is the photosynthesis or the harvesting light energy and the transpiration (Crang et al. 2018). Concerning leaves of JA, they have a high photosynthetic efficiency (Shao et al. 2016). Several physiological and morphological changes could be occurred during the JA leaf development. These changes might include increasing the accumulation of chlorophyll, leaf thickness and its area, enlargement in stomatal conductance and synthesis of CO_2 assimilation enzymes and photosynthetic apparatus (Yan et al. 2012).The anatomical structure of JA leaves is shown in Fig. 3 and 4.

The stomata and trichomes

The epidermis layer of the plant leaf contains pairs of cells (guard cells) with a hole (stomatal pore) between them. Guard cells and a stomatal pore together constitute a stoma (plural, stomata). Stomatal pores can be opened during the daytime, permitting needed carbon dioxide to enter the plant for photosynthesis. All leaves surface have stomata exception of spines, but their density, distribution and relative number on each surface vary greatly. Only the floating leaves have stomata on the upper surface or adaxial surface, which called epistomatic, whereas the distribution of leaf stomata only on the lower surface is called hypostomatic. When the leaves contain stomata on both the abaxial and adaxial surfaces then called amphistomatic (Crang et al. 2018).

In case of JA, the stomata represent the primary sites for gas exchange and the stomata size ranges between 323 and 343µm^2 for the abaxial and adaxial surfaces, respectively (Fig. 5), the stomata shape varies from rounder for the lower stomata and oval shape for the upper surface (Kays and Nottingham, 2008).

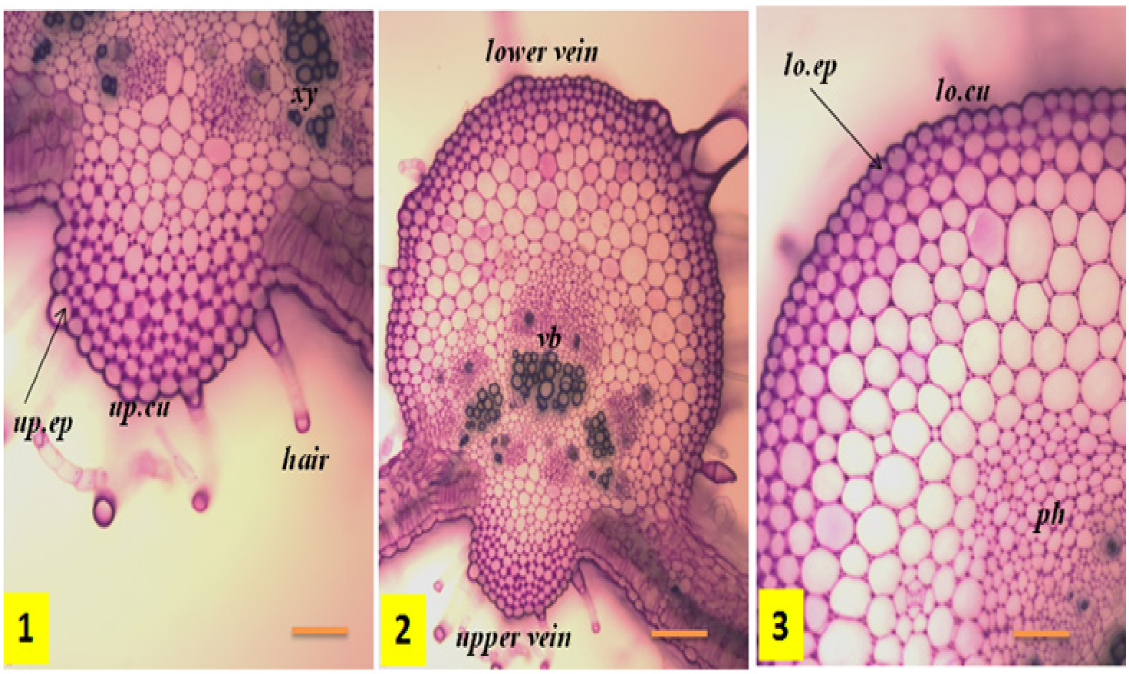

Fig. 3. Transverse sections of the middle vein of the leaf of Jerusalem artichoke. *up.cu* upper cuticle. *up.ep* upper epidermis, *xy* xylem, *vb* vascular buddle, *lo.cu* lower cuticle, *lo.ep* lower epidermis, *ph* phloem. Scale bar = 20 µm for photo (2), 10 µm for photos (1, 3). The cross sections have been prepared, stained by toluidine blue (0, 2%), examined using Electronic Microscope (Axioskop 2 plus, Carl Seiss Technika Kft, Hungary) and photographed using Scop-Photo software by Neama Abdalla

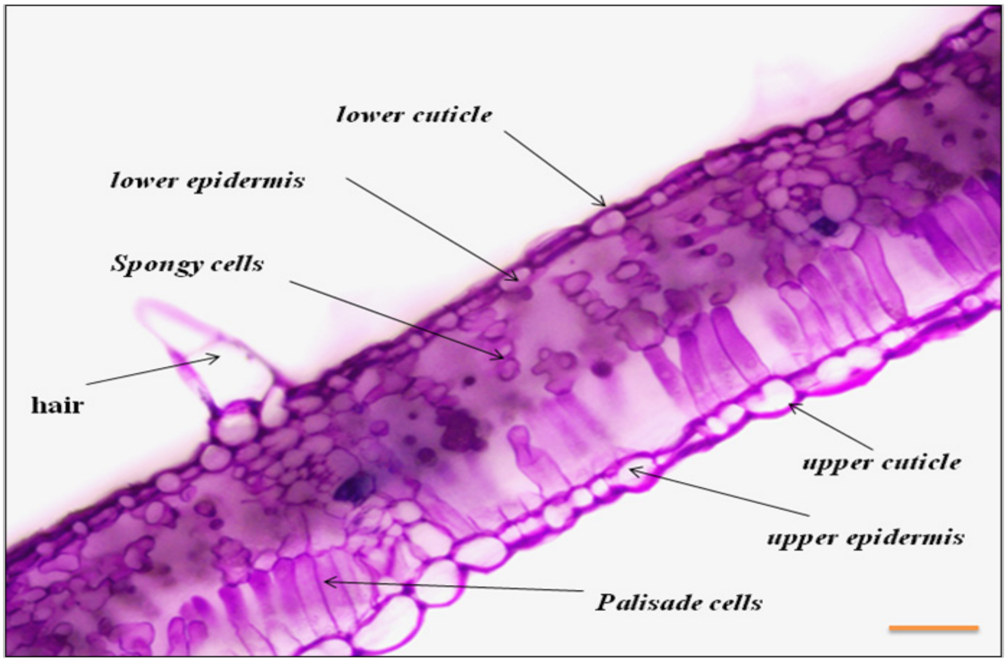

Fig. 4. Transverse section of the arm of the leaf of Jerusalem artichoke. Mesophyll (palisade cells + spongy cells). Scale bar = 10 µm. The cross sections have been prepared, stained by toluidine blue (0, 2%), examined using Electronic Microscope (Axioskop 2 plus, Carl Seiss Technika Kft, Hungary) and photographed using Scop-Photo software by Neama Abdalla

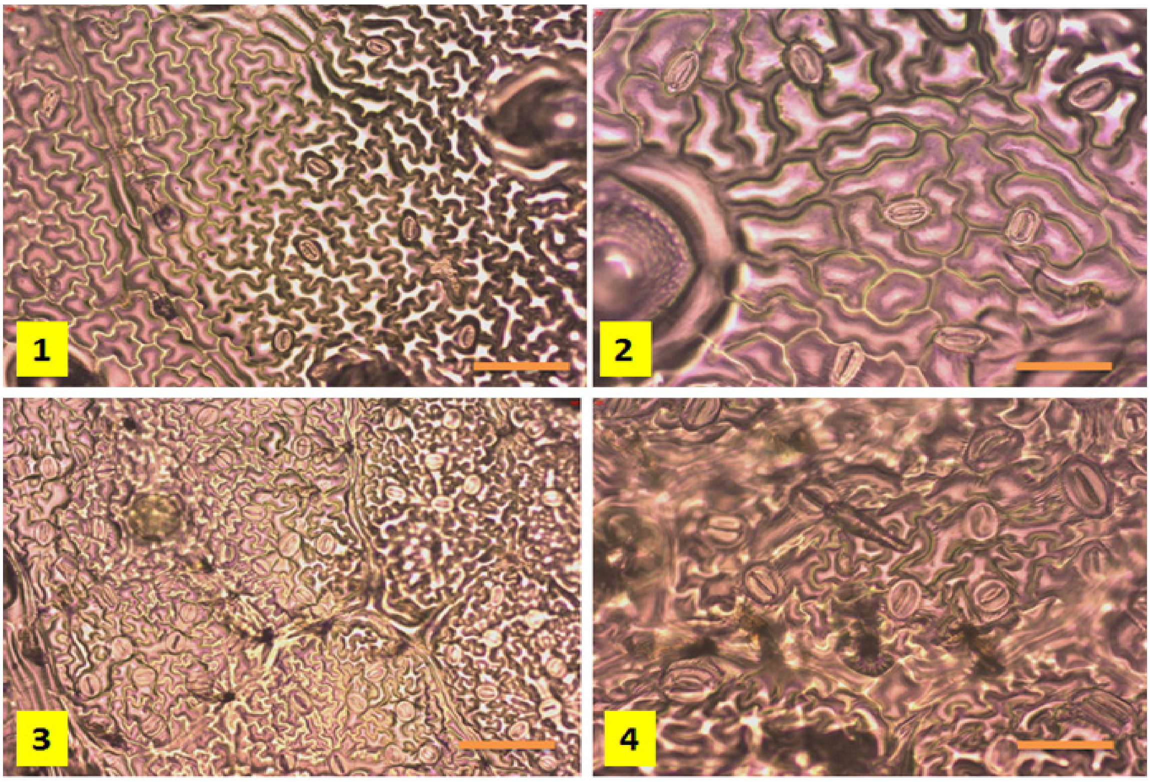

Fig. 5. Stomata of Jerusalem artichoke. Photos (1, 2) and (3, 4) represent stomata of upper and lower surface of the leaf, respectively. Scale bar = 10 µm for photos (1, 3) and 5 µm for photos (2, 4). Slides of stomata were prepared and examined using Electronic Microscope (Axioskop 2 plus, Carl Seiss Technika Kft, Hungary) and photographed using Scop-Photo software by Neama Abdalla

In most plants, some epidermal cells elongate outward and become trichomes, also called hairs. Trichomes make it difficult for an animal to land on, walk on, or chew into a leaf. Trichomes can also create a layer of immobile air next to a leaf surface, which allows water molecules that diffuse out of a stoma to bounce back in rather than be swept away by air currents.Trichomes exist in hundreds of sizes and shapes; many are unicellular, multicellular and branched. Most trichomes die shortly after maturity, and their cell walls provide protection for plant; but others remain alive and act as small secretory glands. Some secrete excess salt; others produce antiherbivore compounds, and those in carnivorous plants secrete digestive enzymes onto trapped insects. The poisonous, irritating compounds of stinging nettle (*Urtica dioica* L.) plant are held in trichomes.Where it has many hollow stinging trichomes on the leaves and stems, which act like hypodermic needles, injecting histamine and other chemicals that produce a stinging sensation upon contact (contact urticarial) both by mechanical irritation to skin *via* spicules or by biochemical irritants; histamine, serotonin, and acetylcholine (Mauseth, 2017).

Trichomes are multicellular extensions or unicellular of the epidermis found on stems and leaves of many angiosperms, ferns and gymnosperms and called pubescence when they found in abundance. Trichomes could be divided into two main types, glandular and non-glandular and several plant species have both types of trichomes on the same leaf surface (Crang et al. 2018). Concerning plant glandular trichomes, they are epidermal secretory structures having the ability to produce different specialized metabolites. These metabolites may support the plant adaptation to its environment and a lot of them have remarkable properties exploited by flavor, fragrance and pharmaceutical industries.The role of plant trichomes have recently documented in many reports including its absorption the foliar applied Zn compared to stomata (Li et al. 2018, 2019), glandular trichomes as a barrier against atmospheric oxidative stress (Li et al. 2018), water use efficiency (Galdon-Armero et al. 2018), and its secretaries (Chwil and Kostryco, 2020). Recently, some reports confirmed the potential of trichomes for plant supporting and adaptation to stresses such as salinity (Zhou et al. 2018), UV radiation and cold stresses (Tang et al. 2020), oxidative stress (Li et al. 2018; Paulino et al. 2020), and copper toxicity (Zehra et al. 2020a, b).

Regarding the trichomes, they are specialized structures on aboveground surfaces of the JA plants, which project and originate from epidermal cells. Depending on the location, it could be found different types of trichomes on the same plant with common variations in their shape, size and its density. The trichomes of JA (Fig. 6) and other plants of the sunflower family often have a very abrasive surface texture, which may act partially as a component of the plant defense system against the herbivores and other stresses. The JA has at least four types of trichomes, which vary in its size, locationand density (Kays and Nottingham, 2008).

Concerning the young stem of JA, their surface is covered with very long acuminate trichomes. The growth of trichomes may directly outward from the stem and often about 2.6 mm in length. These trichomes also vary among clones in its number per unit surface area, though none were devoid of these trichomes. The tip of the stem has more trichomes compared to the base especially the upper 30 cm. With time, many trichomes may be lost due to their breakage and the stem might increase in radial diameter (Kays and Nottingham, 2008).

Moreover, the blade and petiole of JA leaves have abundant trichomes. The trichomes could be found in three forms including multicellular moniliform, curved multicellular falcate and single-celled glandular trichomes, which vary between the abaxial and adaxial surfaces based on their structure, size, and density (Kays and Nottingham, 2008).

Conclusions

Jerusalem artichoke is a promising multi-beneficial and non-food energy crop for human and animal health due to its content of bioactive compounds (e.g., phenolic acids, flavonoids, terpenoids and amino acids) and functional ingredients in their tubers and aerial part. It has a wide ecological adaptability, great ecological resiliency, high tolerance to different abiotic stresses, high photosynthetic efficiency, little demand for fertilizer requirements and high commercial value. This crop can grow well in saline-alkali soils and other stressful conditions due to its physiological and biochemical properties, which support this plant under these harsher conditions. The anatomical properties of some grown plants under stress have been reported in many studies but not yet for JA. Recently, an increase concern about the histochemical studies of cultivated plants under stress has been noticed including the anatomical parameters such as leaf trichomes, stomatal density and upper epidermal thickness, the lignification, suberization and thickening of the endodermis. Further studies are needed to highlight the behavior of JA under stress through measurement the antomical parameters. The role of leaf trichomes also still needs moer investigations particulrly under stressful conditions.

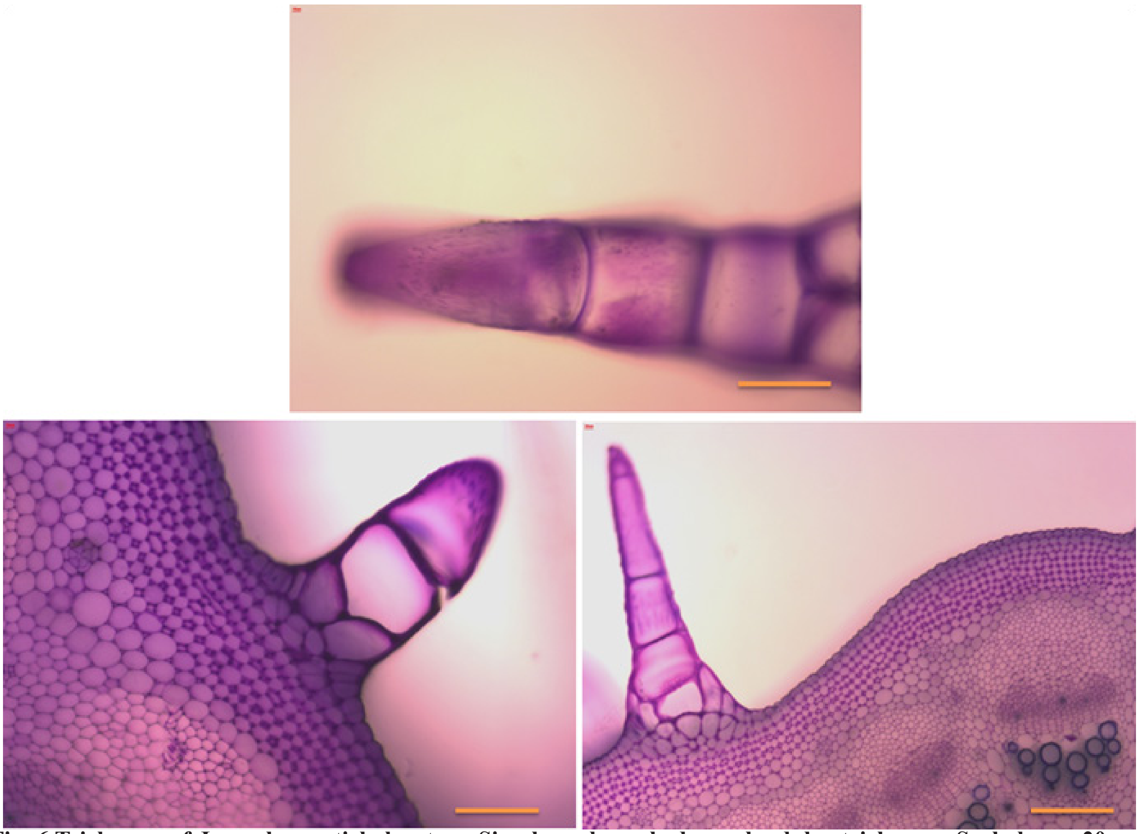

Fig. 6.Trichomes of Jerusalem artichoke stem. Simple, unbranched nonglandular trichomes. Scale bar = 20 µm Photos of trichomes have been taken using Scop-Photo software by Neama Abdalla

Author Contributions

This work was designed, implemented and written by Dr. Neama Abdalla under supervision of Prof. Dr Mohamed Ragab, Prof. Dr Salah El-Miniawy, Prof. Dr Hussein Taha and Dr. Nermeen Arafa. Hungarian authors kindly provided us with the needed chemicals and instruments for anatomy. The anatomy of JA was completely performed by Neama Abdalla under supervision of Dr. Szilvia Kovács and with kind help and great advices of Ibolya Tóth. The original draft was written by Prof. Dr Hassan El-Ramady, revised and edited as well. All authors have read and agreed to publish the final version of the manuscript.

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Conflicts of Interest

The authors declare that there is no conflict of interest.

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