Volume 59(2):103-08, 2015
Acta Biologica Szegediensis
http://www2.sci.u-szeged.hu/ABS

ARTICLE

New report on anatomy of lenticel development in *Fraxinus* (Oleaceae) species from Iran

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ABSTRACT The adaptive abilities of plants allow them to survive in wide ranges of physical conditions. These adaptations appeared to be associated with lenticels. Lenticels are essential to the plants, since they control gas exchange in the absence or losing the function of stomas. *Fraxinus* is a morphologically variable genus and this is regarded as individual adaptations to environmental conditions. Plant adaptations to different environmental conditions can also influence their anatomical structures. In present study, the anatomical features of leaf petioles and fruits were examined in two *Fraxinus* species from Iran. Samples of young to mature petiole and fruit samples were collected from the trees. The anatomical observations revealed different origins of lenticel development which are recorded for the first time. Lenticels on the petioles have epidermal origin however lenticels on the fruits are originated from stomas.
Acta Biol Szeged 59(2):103-108 (2015)

KEY WORDS
anatomy
Fraxinus angustifolia
Fraxinus excelsior
Iran
lenticel

Introduction

A number of plant species are known to grow in dry to permanently saturated or inundated soil conditions. The high flooding tolerance of certain species of forest trees has been attributed to one or more adaptive mechanism. The adaptive abilities of plants allow them to survive in a broad range of physical conditions that they can be found growing in upland, dry conditions, and also physiological or morphological adaptations allow them to survive in wetlands. Anatomical structures of plants affect their adaptation to different environmental conditions. Some anatomical features of plant organs such as leaves and fruits may change when exposed to the extremes of environmental factors. Lenticels are macroscopic openings occurring on the surface of organs and are responsible for gas exchange and transpiration (Rymbai et al. 2012). Lenticels can be found on the surface of stems, old roots and on several fruit types. The ongoing increase of the thickness in stems and roots make them bordered outside by a periderm, a protective tissue of secondary growth origin. Lenticels are circumscribed parts of the periderm in which the phellogen is more active and periodically produces a tissue with numerous intercellular spaces. Because of this relatively open arrangement of cells and the continuity of the intercellular spaces with those in the interior parts of the stems, the lenticels are supposed to provide pathways for the gas exchange needed for photosynthesis, respiration and transpiration especially in the absence of stomata (Bezuidenhout 2005). Dietz et al. (1988) proposed that lenticels in mango (*Mangifera indica*) fruits may originate in one or two ways from preformed stomata or from shearing of the fruit epidermis as a result of rapid fruit growth. In fact one origin is development from changing stomata into the lenticels and another origin is not from existing stomata but from resin ducts developing too close to the surface of that part of plant (Bezuidenhout 2005).

Fraxinus L. is one of 24 genera of family Oleaceae (Hinsinger 2010; Taylor 1945). It is a variable genus supported by the great variability in the leaf morphology (shape, texture, number of leaflets, leaflet margin, petiole length, indumentum, epidermal papillae, rachis wings etc.), which can be regarded as a sign of individual adaptation towards environmental demands (Wallander 2008). Two *Fraxinus* species (*Fraxinus angustifolia* Vahl. and *Fraxinus excelsior* L.) have been recorded for the flora of Iran (Azadi 2005a, 2005b; Kaveh et al. 2014). The aim of this paper is to investigate the anatomy and origin of development of lenticels in leaf petioles and fruits of *Fraxinus* species from Iran.

Submitted Dec 25, 2014; Accepted May 6, 2015
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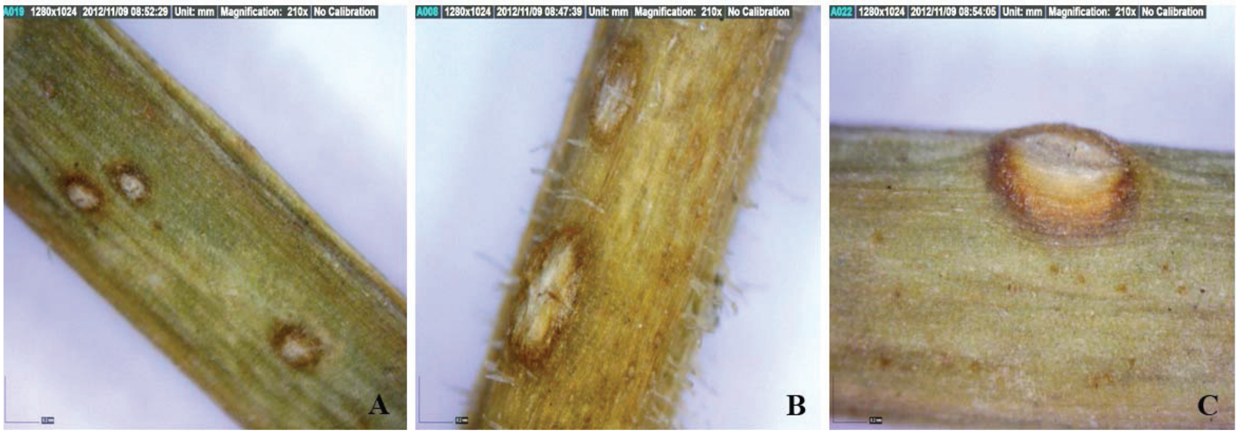

Figure 1. Lenticels on the petiole of *Fraxinus excelsior* (Unit: mm / Magnification: 210x).

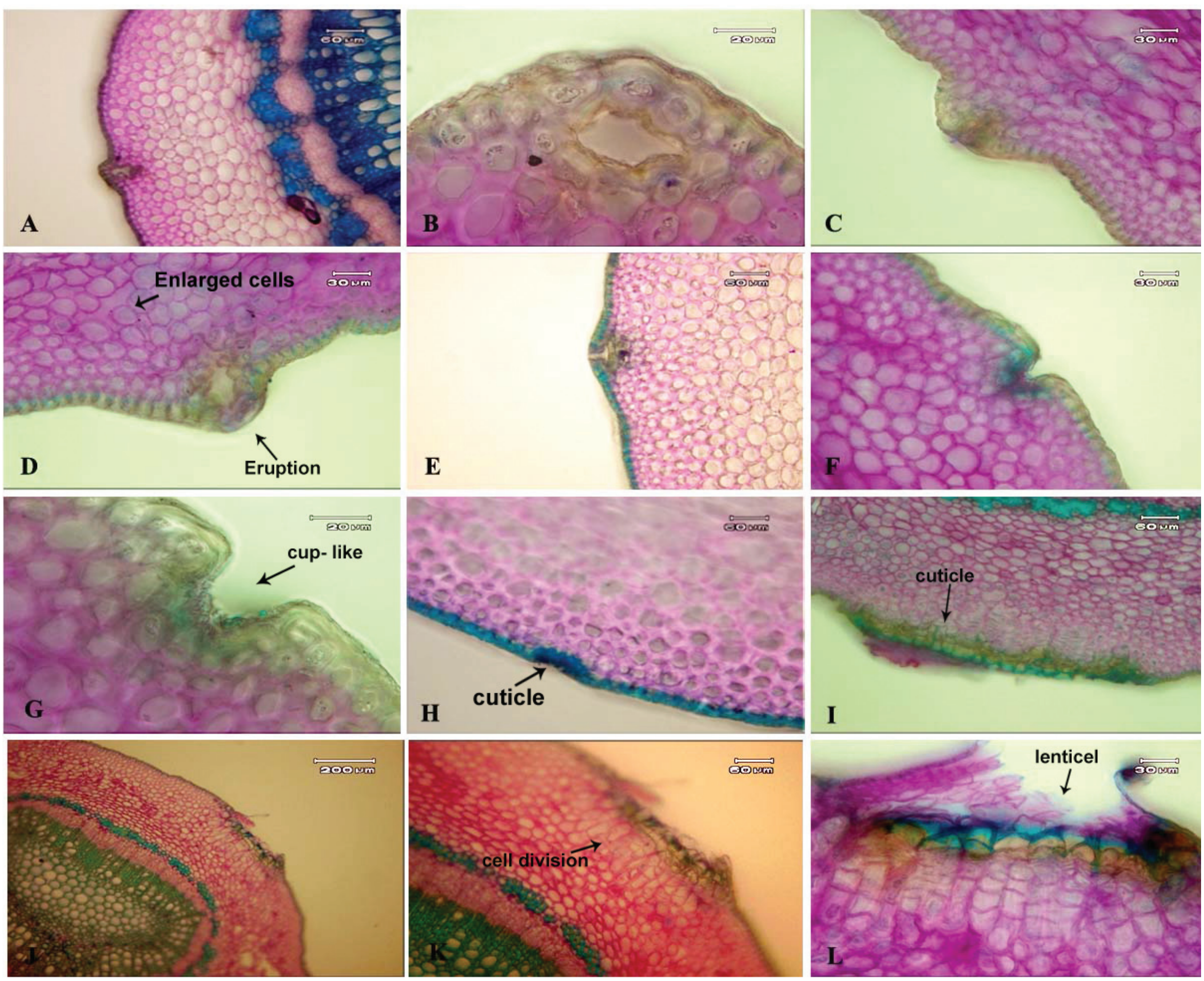

Figure 2. Successive stages of lenticel development in petioles of *Fraxinus angustifolia*. A: enlargement of the petiole cells led to increased tension on the cells above these cells; B-E: epidermis and accompanying cells above them caused to the rupture; F, G: the lenticels opened up and formed a neat, cup-like lenticels; H: cuticle covering the lenticel cavity; I, J: anticlinal cell division of epidermal cells is visible; K, L: its resulting in volcanic-like protuberances on the petiole surface.

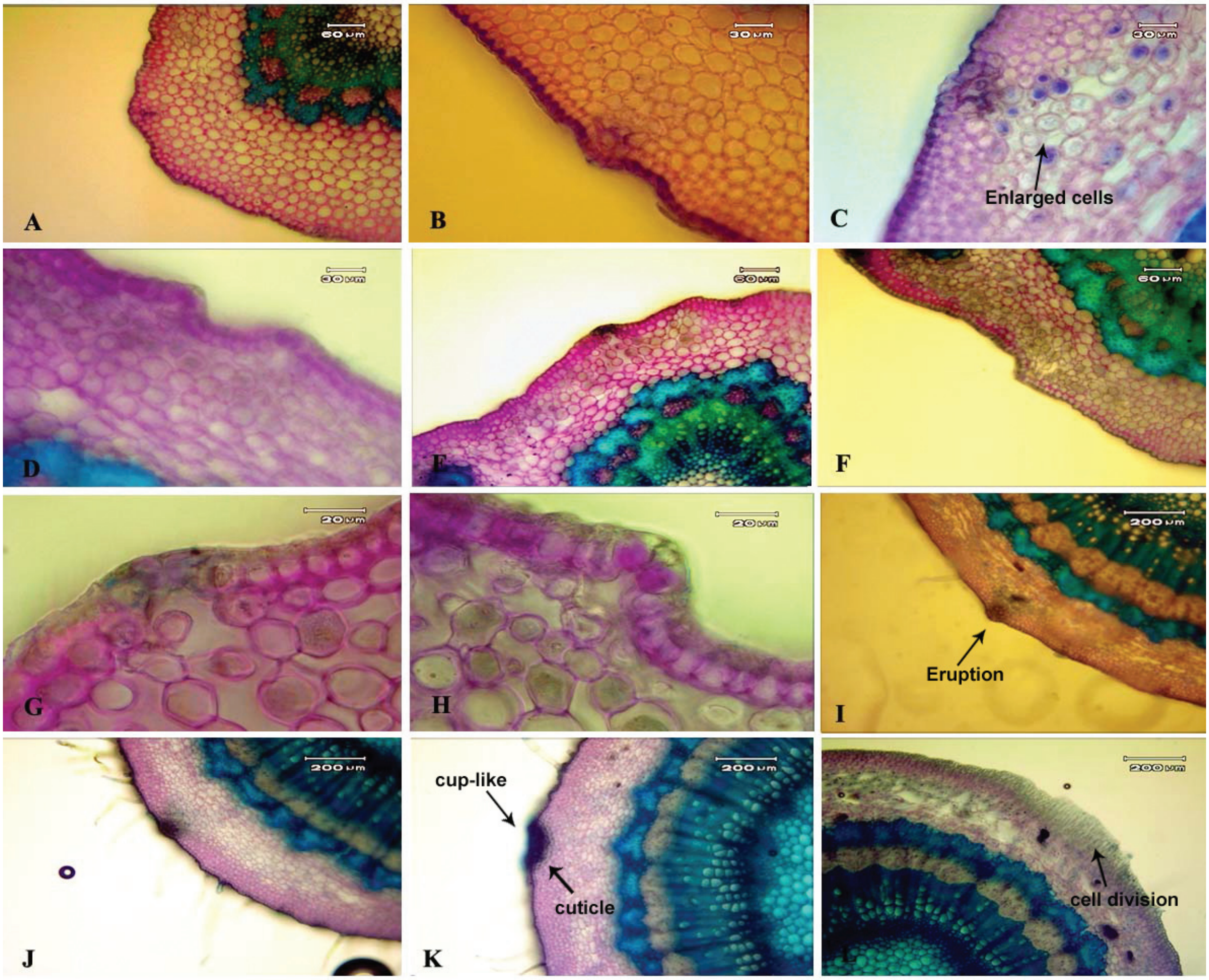

Figure 3. Successive stages of lenticel development in petioles of *Fraxinus excelsior*; A-E: enlargement of the petiole cells led to increased tension on the cells above these cells; F-I: epidermis and accompanying cells above them caused to the rupture; J: the lenticels opened up and formed a neat, cup-like lenticels; K: cuticle covering the lenticel cavity; L: anticlinal cell division of epidermal cells is visible and its resulting in volcanic-like protuberances on the petiole surface.

Materials and Methods

Representative young to mature petiole and fruit samples were collected from fruit bearing trees of two *Fraxinus* species (*F. angustifolia* and *F. excelsior*) cultivated at the National Botanical Garden Tehran, Iran (35° 41' N, 51° 57.19' E). About 10-12 samplings were repeated during two growing seasons. We also used the fresh herbarium specimens from TARI (Herbarium of Research Institute of Forests and Rangelands, Tehran, Iran) and FUMH (Herbarium of Ferdowsi University of Mashhad, Mashhad, Iran) herbaria. Materials were fixed in equal proportion of glycerin-70% alcohol. Free-hand cross sections of petioles and exocarp of the fruits (wings of samara) were prepared for anatomical study. Sections were not embedded in paraffin. The sections were stained using methyl green and carmine (Tamjinda et al. 1992) fixed on glass slides and examined by the light microscope model Olympus Bx51.

Results and Discussion

The anatomical observations revealed different stages of the lenticel development. From the structural analyses we suggest a developmental process taking place in the lenticels which is similar in two studied *Fraxinus* species.

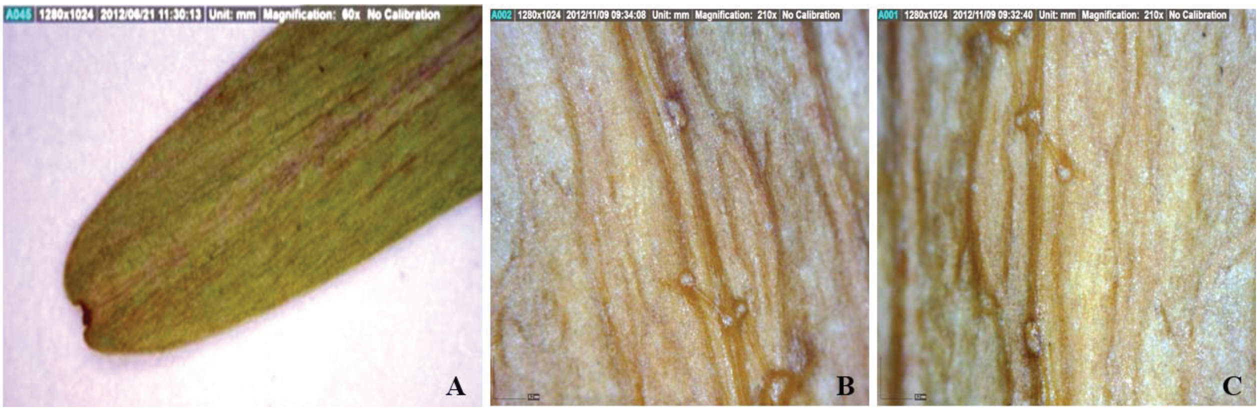

Figure 4. Lenticels on the fruit of *Fraxinus excelsior* (A: Unit: mm / Magnification: 60x; B-C: Unit: mm / Magnification: 210x).

Development of lenticels in petioles

The lenticels in petioles of two species (Fig. 1) show an epidermal origin in their development stages (Fig. 2 and 3). These cells developed from petiole surface. Enlargement of the petiole cells led to increased tension on the cells above these cells and therefore caused the epidermis and accompanying cells above them to the rupture, which left an opening in the petiole surface (Fig. 2 A-C and Fig. 3 A-C). The lenticels opened up and formed a neat, cup-like lenticels with a cuticle already covering the lenticel cavity (Fig. 2 F-H and Fig. 3 D-I). First sign of cells arranged in rows, anticlinal to adjacent surface, was becoming visible (Fig. 2 I, J and Fig. 3 J, K) continued anticlinal cell division of epidermal cells resulted in the petiole surface take on an undulating, resulting in volcanic-like protuberances on the petiole surface. This is the first stage of the development of a phellogen (in this instance, a wound cambium due to the rupture in the epidermis) (Fig. 2 K, L and Fig. 3 L). Phelloderm, consisting of rays of cells, is now clearly visible around the lenticels cavity. In fact development of lenticel occurs in the stage between development of stomata as an epidermal structure and lenticel, that with gradually lignification process develop into lenticel. These processes are visible in petioles of two species (Fig. 2 and Fig. 3).

The developmental stages for lenticels of *Fraxinus* may be similar in two species in the genus. Lenticels on petiole originate from shearing of the epidermis as a result of rapid growth and lenticel on *Fraxinus* fruit originate from stomata, appear and intensify gradually with the growth and maturity of fruit.

Development of lenticels in fruit

Some fruit lenticels may develop from pre-existing stomata (Fig. 4). Like in other fruit, the peel of *Fraxinus* protects the fruit from several external factors. Lenticels after their appearance on fruit peel gradually intensify in color with fruit maturity. Rymbai and co-workers (2012) showed stomata are prominent on young fruit but gradually degenerate in older fruit, which leads to the formation of lenticels. Lenticels in this way differentiate from existing stomata (Fig. 5 A) that lose their function and protrude above the fruit surface (Fig. 5 B-D) as a result of rapid anticlinal cell division in the epidermis of exocarp. Dietz et al. (1988) showed the sequence of events during the information of lenticels from pre-existing stomata in fruit are: death of guard cells, loss of cuticular membrane in substomatal chambers, suberization of the cells lining the substomatal camber and empty cavity of the lenticels chamber due to the absence of cork cambium. The sublenticellular cells were also smaller in diameter than surrounding parenchymatous cells. The epidermis consisted of single layer of approximately isodiametric cells undergoing active anticlinal cell division. Epidermal cells of fruit appeared tangentially flattened radially elongated and covered by the waxy cuticle, staining green with methyl green (Fig. 5 H). Stomatal guard cells were probably still functional at this stage, with well developed guard cells and a substomatal cavity. Continued anticlinal cell division of epidermal cells resulted in the fruit surface take on an undulating appearance and stomata become elevated above the fruit surface. Stomatal guard cells did not return to their original position. The stomata possibly lost their function due to the erupting of stomatal opening. This led to a permanent opening in the epidermis, apparently a vulnerable area that needs to be closed from the environment. Fruit has adapted to this phenomenon by producing cuticular cutin enters the stomatal cavity, permitting gas exchange and forming a typical lenticel. These lenticels lack cork cambia, but due to this adaptation, have the ability to limit fungal penetration and prevent excess moisture loss from fruit during fruit growth and development. Furthermore, cells directly under the lenticels had thinner cell

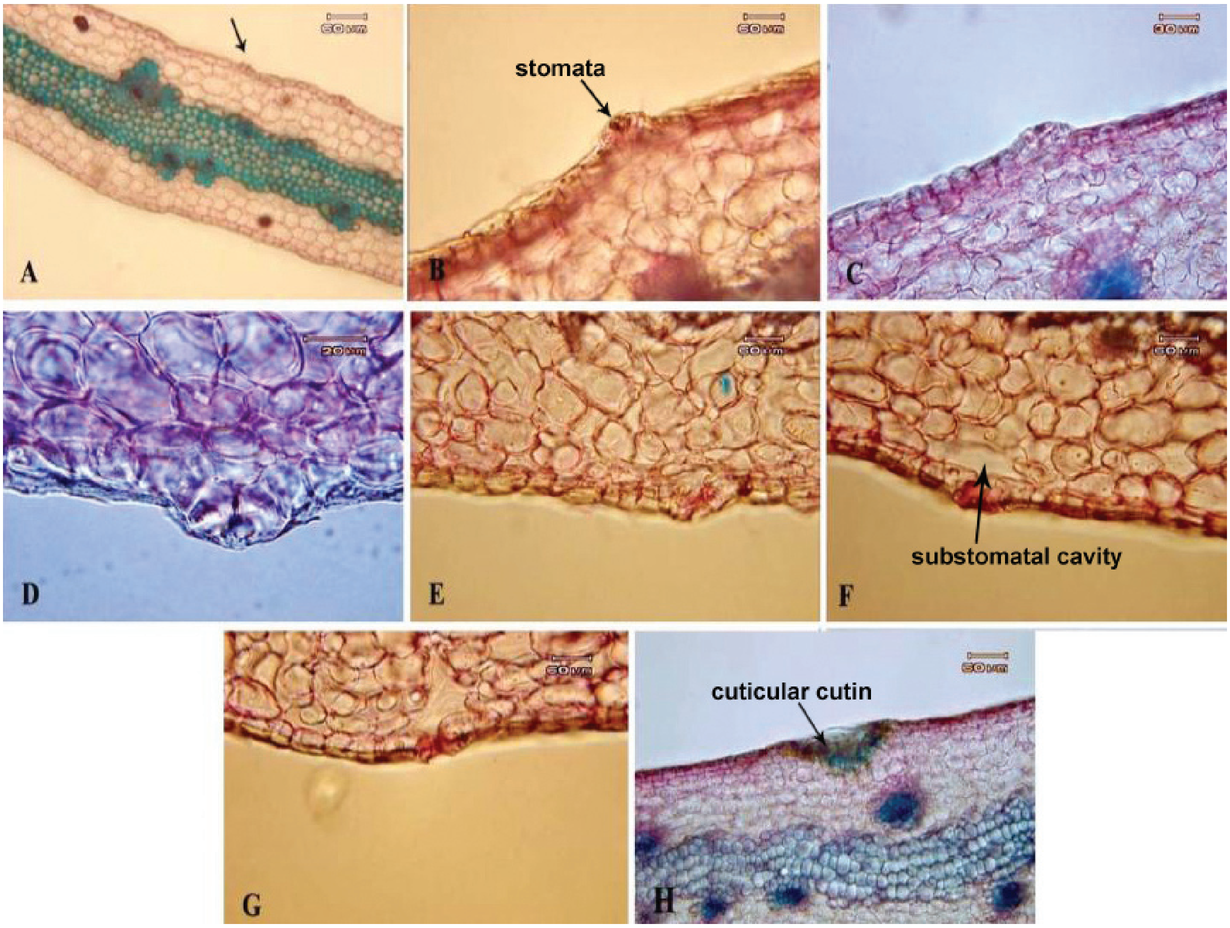

Figure 5. Successive stages of lenticel development in fruits of *Fraxinus* species.A: lenticel appears on fruit peel; B-D: stomata are prominent on young fruit as a result of rapid anticlinal cell division in the epidermis of exocarp; E-G: stomatal guard cells lost their function due to the rupture of stomatal opening and developed a substomatal cavity; H: fruit has adapted to this phenomenon by producing cuticular cutin enters the stomatal cavity.

walls and larger intercellular spaces than surrounding tissue, enabling gaseous exchange and transpiration. Bezuidenhout (2005) showed lenticels cavity is only partially covered with cutin, making it more susceptible for penetration of foreign objects.

Acknowledgment

The authors appreciate the assistance and advice received in making this study to dear masters, Mr. Mohammad Reza Joharchi, Dr. Maneezheh Pakravan Fard and Dr. Nooshin Toghraie. Special thanks to the National Botanical Garden of Iran (Tehran) and Herbarium of the Ferdowsi University of Mashhad (FUMH) for supporting and preparing of the plant materials.

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