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Vessel anatomy studies in orchids (Orchidaceae)

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Abstract: Members of the Orchidaceae family have significant flower morphology problems. There are many morphological studies as well as anatomical researches in the solution of these problems. In these anatomical studies, very useful results have been obtained in terms of plant taxonomy. Another important parameter in terms of phylogeny and anatomical separation is vessel anatomy. However, in terms of vessel anomaly, only a few studies have been conducted on epifitic and tropical orchids (Apostasioideae, Spiranthoideae subfamilies and some epiphytic epidendroideae taxa). Noteworthy results in these studies were obtained; but the orchid subfamilies, also found in Turkey, (terrestrial Orchidoideae, Epidendroideae) such studies have not been studied in detail. Therefore, it is aimed to summarize the studies of vessel anatomy performed in orchids up to now.

Keywords: Orchidaceae, Orchid, Xylem, Vessel anatomy.

Introduction

The Orchidaceae family is the second largest family of plant life, and it is estimated that with approximately 25,000 taxa on Earth; this number can quickly reach 30,000 with new species discovered every year (Bateman et al., 2003; Govaerts, 2010). The Orchidoideae subfamily contains 101 genera. Part of the orchids that spread in Turkey and in the triangle of Europe and West Asia, belong to Orchideae tribus and Orchidinae subtribus from this subfamily. When Orchideae tribe has 62 genera, Orchidinae subtribe contains more than 1700 taxa (Pridgeon et al., 2001). Orchidinae subtribus is the biggest group in Europe with the largest taxon of the family (Bateman et al., 2003). Generally these orchids are spread in the northern temperate hemisphere and a few in the tropical regions of the old and new worlds (Inda et al., 2012). Epidendroideae subfamily is the largest subfamily of family with 140 genera (Pridgeon et al., 2014) and usually spread in the northern hemisphere (Dressler, 1993).

A review on orchids vessels

Frost (1930a, 1930b) provided for the origin and specialization of vessel members in the secondary xylem of dicotyledons. According to Cheadle (1942, 1943a, 1943b), and Stem et al. (1993), evolutionary origin and specialization of vessel members arised from in the primary xylem of monocotyledons. Briefly, Cheadle (1942, 1943a, 1943b) proposed that vessels first appeared in the roots; they evolved and subsequently moved acropetally and specialized in the same direction. Contrastly, Cheadle and Kosakai (1982) argued in their initial own work on the orchids that any there was not been any difference between terrestrial and epiphytic orchids in terms of vessel structure. However; terrestrial orchids in the Cranichideae tribe of subfamily Spiranthoideae have been successfully compared with epiphytic taxa in the Epidendroideae subfamily in terms of vessel perforation table characteristics, trachea and tracheid diameters and phylogenetic relationships (Thorsch and Stern, 1997). Stern et al. (1993) reported that in their research, there was a simple or scalariform style perforation table in orchids and that the character of the perforation table could be used in phylogenetic relationships. In addition, although there are obvious variations in the perforation table in the family, it is generally claimed that they are in a scalariform style. In the same way, Cheadle (1942) also stated that vessel properties in orchids were of various types.

Other similar studies have emphasized that although the scalariform perforation plate is generally found in the

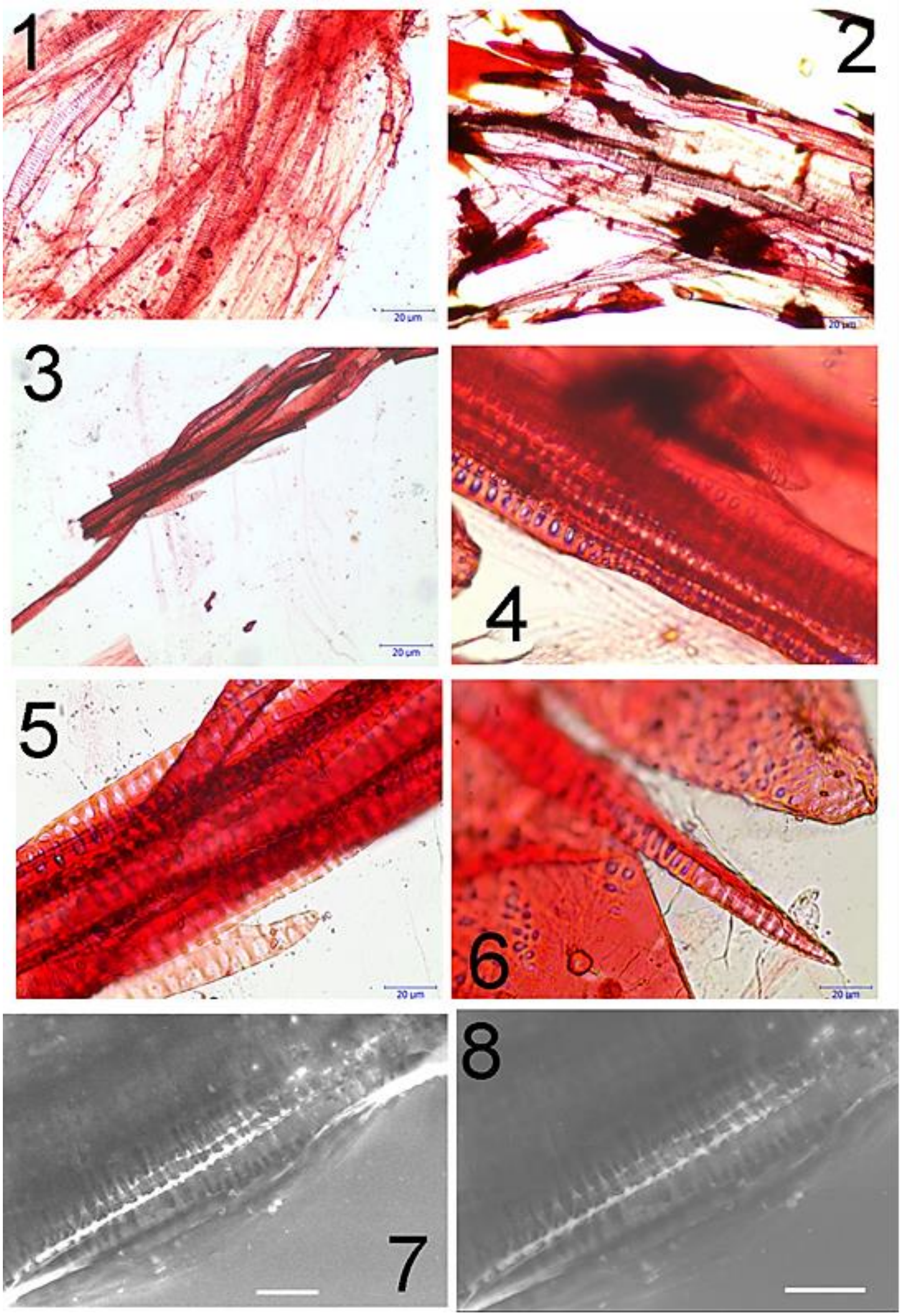

Figure 1-8. Stem longitudinal section, several vessel elements in Orchidoideae and Epidendroidea subfamilies after maceration liquid preparation (Aybeke, unpublished results). **1-2.** *Orchis mascula* subsp. *mascula*, Orchidoideae subfamily, **3-6.** Epidendroideae subfamily, *Limodorum abortivum*, (please note that the vessel elements are different in both groups), **7-8.** SEM preperetaions of **Fig. 1-2.** Scale bars, **7-8.** 5 µ.

subfamily of Apostasioideae, this subfamily has a more primitive and ancestral characteristic because of the simple perforated traches in its genera such as, *Apostasia* Blume and *Neuwiedia* Blume (Cheadle and Kosakai 1982; Stern et al., 1993; Thorsch and Stern, 1997). Furthermore distribution of tracheids and vessel members in terrestrial orchids in tribe Cranichideae, subfamily Spiranthoideae, and from tribes of subfamily Epidendroideae were compared with those in epiphytic orchids in tribes of subfamily Epidendroideae to determine the evolutionary status of these groups (Thorsch and Stern, 1997). In these subfamilies, perforation plate values of vessel members were assessed and the dimensions of tracheids and vessel members were considered to indicate the phylogenetic position of these taxa. Consequently, Thorsch and Stern (1997) stated that vessel elements in the roots of epiphytic orchids all possessed scalariform perforation plates. Also narrow tracheids in epiphytic epidendroids living under stressful conditions of seasonal drought compared with wider tracheids in terrestrial spiranthoids that exist in mesic conditions are potentially attributable to conditions of safety. Vessel members are distributed throughout the plant, i.e., in roots, stems, and leaves, in epiphytic and terrestrial epidendroids, but they occur only in the roots of spiranthoids. Because vessels evolved first in the roots of monocotyledons and subsequently appeared in stems, leaves, and inflorescence axes, and they conclude that terrestrial spiranthoids represent the ancestral condition (Thorsch and Stern, 1997). According to Robinson and Bums-Balogh (1982), they suggested that the velamen is primitive and its loss among some terrestrial species is derived.

Spiranthoideae subfamily, vessel members have scalariform perforation plates in the roots. Also, the scalariform perforation plates are usually very long and have numerous complete bars in *Ponthieva tuerkheimii* (Thorsch and Stern, 1997). Tracheids occur in the leaves of *Zeuxine strateumatica* and *Spiranthes vernalis*. However, stems and leaves of terrestrial spiranthoids lack vessel members (Thorsch and Stern, 1997).

Considering the terrestrial epidendroids, some species have vessels and others lack them. Vessel members with scalariform perforation plates from roots found in *Pogonia ophioglossoides*, *Cleistes divaricata*, and *Bletia purpurea* (Thorsch and Stern, 1997). Also it was determined that vessel members are wide and often have long scalariform perforation plates. In a leaf of *Calopogon pallidus*, vessel member with a scalariform perforation plate appeared (Thorsch and Stern, 1997).

Considering the epiphytic epidendroids, they have vessel members with scalariform perforation plates in their roots. As for *Arpophyllum giganteum,* it shows a large vessel member with a scalariform perforation plate from the root (Thorsch and Stern, 1997). A much narrower vessel member with a scalariform perforation plate is from the root of *Maxillaria tenuifolia*. But in *Stanhopea oculata* and *Huntleya heteroclita,* leaves have vessel members with scalariform perforation plates (Thorsch and Stern, 1997). Thorsch and Stern (1997) suggested that in generally vessel members are wider than tracheids and when comparing the diameters of tracheids in the roots, stems, and leaves of epiphytic epidendroids, terrestrial epidendroids, and terrestrial spiranthoids, they find tracheids emerge as narrower in epiphytic and terrestrial epidendroids than in terrestrial spiranthoids. Also they propose that the persistence of narrower tracheids in epiphytic orchids results from selective pressures that maintain this condition to accommodate the stressful environments under which many epiphytes live (Thorsch and Stern, 1997). This condition could be interpreted as a derived condition in terrestrial spiranthoids (Thorsch and Stern, 1997). In fact, in strict stressfull conditions, cavitation occurs in tracheary cells. It is reasonable to assume, then, that periodically formed embolisms would be features of cells from plants growing in a droughty environment. It has been suggested that the formation of embolisms occurs at lower xylem tensions in wider cells (Ewers, 1985; Tyree and Sperry, 1989; Benzing, 1990; Hargrave et al., 1994; Kramer and Boyer 1995; Thorsch and Stern, 1997).

In addition, it has been reported that scalariform perforated trachea were found in the genera *Calopogon* R.Br., *Stanhopea* J. Frost ex Hook., *Huntleya* Bateman ex Lindl., *Epidendrum* L. ve *Scaphyglottis* Poepp. and Endl. from the Epidendroideae subfamily (Thorsch and Stern, 1997; Cheadle, 1942). In another study with the same subfamily, researchers argued that the results were not productive due to the variable nature of the trachea and perforation table, which was mainly due to the limited number of taxa in the study. For this reason, researchers have indicated that the study would be more beneficial by expanding the study to include more taxa of Orchidoideae and Epiderndroideae (Stern et al., 1993; Stern, 2014). As a result; it is emphasized that all of the epifitic orchids have a scalariform perforation table as well as narrower tracheids under severe arid conditions, and wider tracheids in terrestrial taxa in temperate climatic conditions, and that terrestrial Spiranthoid orchids have more ancestral characteristics (Thorsch and Stern, 1997). Carlquist and Schneider (2006), have shown that the details in the trache walls give important clues in terms of environmental conditions, developmental stages, and even evolutionary development. According to this; on 13 taxa from 4 different subfamilies, trache, tracheid and intermediate form vessel elements were examined in root, stem and scapula (Carlquist and Schneider, 2006). In conclusion, it has been found that the pits in the root trachea end walls are "nonporose", especially in Cypripedioideae and Vanilloideae subfamilies, while in Orchidoideae and Epidendroideae they are in different types from "porose" to "reticulate" (Carlquist and Schneider, 2006).

According to Carlquist and Schneider (2006), xylem of the orchids indicates how conductive tissue evolves in monocotyledons. End walls of tracheary elements are porose to reticulate in roots of all species, but nonporose in stems of Cypripedioideae and Vanilloideae, and porose to reticulate in stems of Orchidoideae and Epidendroideae. According to these researchers (Carlquist and Schneider (2006), the position of Cypripedioideae and Vanilloideae are as outgroups to Orchidoideae and Epidendroideae. Based on their observations, intact pit membranes occur in tracheary element end walls of *Vanilla.* Considering current molecular phylogenies and their opinions (Carlquist and Schneider, 2006), vessel elements differ from tracheids by means of several characteristics, which may have evolved independently (Carlquist and Schneider, 2002). Also tracheary elements the pseudobulbs of *Cymbidium* and *Odontoglossum* have more prominent porose end walls compared to *Epidendrum* and *Sobralia* pseudobulbs. According to Carlquist (1975), because the succulent organ is less permeable, naturally succulence of pseudobulbs will decrease the degree of porosities in end walls, so less rapid conductive rates per unit time will be occurred.

In short; it is understood that tracheal studies in orchids are performed on some subfamilies and genera, and that taxonomic and phylogenetic results are obtained in part from them. Therefore, it is seen that there is a big gap in trachea anatomy especially in Orchidaceae and Epidendroideae subfamilies. In the present situation, the ancestral habitat of Orchidaceae, the well-demonstrated application of tracheary element evolution might serve to define the status of terrestrial Orchidoideae and Epidendroidea, as denotd by (Thorsch and Stern, 1997).

Conclusion

Scientific and technological contributions of trachea anatomy; tracheal anatomy is not only a taxonomic parameter but also an important character that can be safely used in various physiological, agronomic and ecological studies. The consequences of this can be regarded as important data in any work to be done in these areas. Determination of each types of pit membranes in tracheary element and end walls of many terrestrial Orchidaceae and Epidendroideae taxa will be contribute to both orchid phylogeny and indicate steps in evolution of conduction under different habitat conditions. In our preliminary studies, differences were found in tracheal structures in both subfamilies. For example, the Orchids and Limodorum taxa differ in terms of tracheal structures. It is believed that more detailed results will be obtained by using detailed SEM methods in addition to light microscopy studies, as described our preliminary studies. Studies in this direction in the terrestrial orchids belonging to the Orchidaceae and Epidendroidea families are very rare. Therefore, it is thought that it will contribute considerably to orchid taxonomy and phylogeny with this sort of studies in this direction.

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