Comparative Anatomy of the Stipe of the Fern Genus *Adiantum* L. (Adiantaceae)

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Abstract

The investigations carried out covering approximately half the species from virtually the entire geographical range of the genus *Adiantum* L. showed that there was a range of shape of the xylem strands proceeding by small steps from the simple (deep-crescent type) to the intricate form (tong-shaped). Eight types of xylem configurations were observed and the genus was subdivided accordingly.

Introduction

The fern genus *Adiantum* comprises about 150-200 species (Abraham *et al.*, 1962; Holttum, 1954; Tryon & Tryon, 1981) and has a nearly cosmopolitan distribution except in regions with extremely dry or cold climates. The genus was subdivided into a number of groups based on its diverse morphological forms by early taxonomists such as Hooker & Baker (1874), Smith (1896), Christ (1897) and Diels (1902). Meanwhile Wylie (1948) investigated the role of leaf epidermis in 18 species of *Adiantum* from America and Bidin (1980, 1984a, 1984b) looked at the cytology, leaf forms and leaf blade anatomy of the genus respectively.

Anatomical and morphological studies of the stipe have also been regarded as useful methods in solving taxonomic problems of ferns. Presl (1847) and Thomas (1886) investigated the structure and arrangement of vascular bundles in the stipes of a wide range of ferns and drew attention to the great variation found. Later authors used these characters in investigating particular taxonomic problems, e.g., Milde (1866) in distinguishing between *Athyrium* and *Asplenium*, whilst Ching (1940) used them in the subdivision of Polypodiaceae s.l. More recently Keating (1968) studied the stipe anatomy of the Dennstaedtioid genera, while Lucansky & White (1974) made comparative studies of the nodal and vascular anatomy of neotropical members of Cyatheaceae. In Taiwan, Lin & DeVol (1977) prepared a multiple choice key based on the study of stipe characters to the species, genera and families of local ferns.

Materials and Methods

Plant material for the study were gathered from various geographical areas by the authors. Live plants were grown at the Moorbank Experimental Garden, Newcastle University, whilst dried specimens were kept at the Herbarium of the Plant Biology Department of the same University.

Segments were cut from three positions along the stipe; i.e., at the base, in the middle region and the upper portion just below the first rachis or pinnule. The segments were each about 1 cm long. Fresh material was fixed in 70% alcohol. Extremely hard stipes and those obtained from the herbarium specimens were

softened by boiling in water for two hours prior to fixation. Various methods of sectioning were employed. In most cases sections were obtained by free hand or by use of the sliding microtome but for hard materials it was necessary to embed in paraffin wax before microtoming. Staining in all cases was in Safranin 0 and Light/Fast Green.

Results and Discussion

The stipe of *Adiantum* is usually dark brown to black, slender and has a polished-glossy appearance. Some species are however sparsely hairy or scaly especially towards the base.

The anatomical structure of the stipe is fundamentally similar to that of the rhizome. It possesses a layer of longitudinally elongated epidermal cells, a cortex, an endodermis and a stele. In all cases the endodermis surrounds each vascular bundle and in certain species the stele is clearly visible in a cross-section even with the unaided eye. The stelar system in the stipe of *Adiantum* consists of one or two traces which are usually arranged in an adaxially curved arc and shows a wide range of variation. The stele in cross-section may have a terete or undulate outline or sometimes an intermediate form. In some species the outlines of the endodermis bear no specific relation to the cross-sectional shape of the stipe (Table 1). The arrangement of strands may change gradually from base to apex, and all the changes however minor should be noted, particularly those affecting the xylem.

Two bundles enter the base of the stipe, and later join upwards to form a four-angled strand. This can be clearly seen in the majority of the species. In some cases the double nature of the bundle is not just confined to the basal region but many extend upward to the middle or even the upper region of the stipe. Observations show that even the double nature of the bundle is not uniform throughout the genus. In the Reniforme and Caudatum groups there is only one bundle present even at the extreme base of the stipe and it persists up the entire length.

Except for the species showing an arc-shaped xylem throughout the entire length of the stipe, all members of *Adiantum* show two Onoclea-type strands in the basal region. Each of these strands contains a hippocampus-shaped xylem mass with hooked or blunt or even sharp ends towards the groove of the stipe. The protoxylem occurs on the inner surface, and a phloem layer surrounds the xylem mass. In some cases the two bundles are more widely separated towards the groove (adaxial) side of the stipe than at the opposite rounded (abaxial) side. Further up the stipe their abaxial ends come in contact and fuse to form a V-shaped, basin-shaped or tongs-shaped bundle with ends which differ in detail from one to another.

A more detailed examination of a large number of taxa (50) reveals that it is not only basin-shaped or V-shaped xylem strands which can be found in Onoclea-type meristeles in the upper region o the stipe (Plate 1). The shape develops gradually from a simple crescent configuration in the Caudatum and Reniforme groups (Fig. 1) to a more complex one in the shape of tongs as in *A. lucidum* and *A. tetraphyllum* (Fig. 8). The first sign of change is that the crescent-shaped strand begins to show a weak constriction in the middle which finally divides the strand into two halves. The tips of the halves curve downwards and are blunt with no hooks present (Fig. 3). This is a transitional shape between the simple crescent-like and the more complex, tongs-like configuration and is found in *A. lunulatum.*

Fig. 1: Deep crescent

Fig. 2: Light crescent

Fig. 3: Bird-shaped

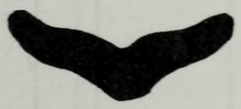

Fig. 4: Slightly curved-upward

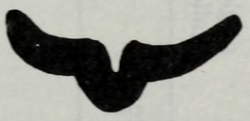

Fig. 5: Saucer-shaped

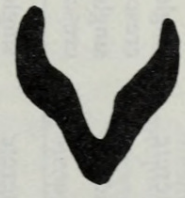

Fig. 6: V-shaped

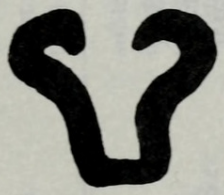

Fig. 7: Basin-shaped

Fig. 8: Tongs-shaped

Plate 1. Shape of xylem strands in the stipe of *Adiantum*. The types are arranged in order of increasing complexity, which is believed to coincide with the direction of evolutionary change. The numbers in this figure correspond to the number of the groups in Table 1 of the types of stipe in *Adiantum*.

Table 1. Stipe Types of *Adiantum* L.

	Species	Shape of T.S. of stipe	Strand	Xylem (base of stipe)	Xylem (middle & upper stipe)
1.	*A. reniforme* L.	subterete at the base, terete above	terete	single stranded, deep crescent	single stranded, deep crescent
	A. reniforme L. ssp. *asarifolium* Willd.	subterete at the base, terete above	terete	single stranded, deep crescent	single stranded, deep crescent
2.	*A. caudatum* L.	terete	terete	single stranded, shallow crescent	single stranded, shallow crescent
	A. incisum Forsk.	terete	terete	single stranded, shallow crescent	single stranded, shallow crescent
	A. malesianum Ghatak	terete	terete	single stranded, shallow crescent	single stranded, shallow crescent
	A. zollingeri Mett. ex Kuhn	terete	terete	single stranded, shallow crescent	single stranded, shallow crescent
	A. rhizophorum Sw.	terete	terete	single stranded, shallow crescent	single stranded, shallow crescent
3.	*A. lunulatum* Houtt.	subsulcate	subsulcate	2-stranded	slightly curved downward, bird-shaped
4.	*A. formosum* R. Br.	subterete at the base, terete above	terete	2-stranded	slightly curved upwards
	A. diaphanum Bl.	subterete at the base, terete above	terete	2-stranded	slightly curved upwards
	A. deltoideum Sw.	terete	sulcate	2-stranded	slightly curved upwards
	A. capillus-veneris L.	terete	sulcate	2-stranded	slightly curved upwards
	A. tenerum Sw.	terete	sulcate	2-stranded	slightly curved upwards
	A. concinnum Willd.	terete	sulcate	2-stranded	slightly curved upwards
	A. aethiopicum L.	terete	sulcate	2-stranded	slightly curved upwards
	A. raddianum Presl.	terete	sulcate	2-stranded	slightly curved upwards
	A. fragile Sw.	terete	sulcate	2-stranded	slightly curved upwards
	A. venustum Den.	terete	sulcate	2-stranded	slightly curved upwards
	A. henslovianum Hook.	terete	sulcate	2-stranded	slightly curved upwards
5.	*A. patens* Willd.	terete	sulcate	2-stranded	saucer-shaped
6.	*A. hispidulum* Sw.	subterete	sulcate	2-stranded	V-shaped
	A. cunninghamii Hk.	terete	sulcate	2-stranded	V-shaped
	A. affine Hk.	subterete	sulcate	2-stranded	V-shaped
	A. silvaticum Tindale	terete	subsulcate	2-stranded	V-shaped

Table 1. *Contd.*

Species	Shape of T.S. of stipe	Strand	Xylem (base of stipe)	Xylem (middle & upper stipe)
(6.) *A. pedatum* L.	subterete at the base, terete above	sulcate	2-stranded	V-shaped
7. *A. macrophyllum* Sw.	subterete at the base, terete above	sulcate	2-stranded	basin-shaped
A. serrato-cristatum Willd.	subculcate at the base, sulcate above	sulcate	2-stranded	basin-shaped
8. *A. tetraphyllum* Willd.	subterete at the base, terete above	sulcate	2-stranded	tongs-shaped
A. lucidum Willd.	subterete at the base, terete above	sulcate	2-stranded	tongs-shaped
A. villosolucidum Jermy & T.G. Walker	subterete at the base, terete above	sulcate	2-stranded	tongs-shaped
A. trapeziforme L.	terete	sulcate	2-stranded	tongs-shaped
A. polyphyllum Willd.	terete	terete	2-stranded	tongs-shaped
A. pulverulentum L.	sulcate	sulcate	2-stranded	tongs-shaped
A. petiolatum Desv.	subterete at the base, terete	sulcate	2-stranded	tongs-shaped
A. villosum L.	subterete at the base, terete above	sulcate	2-stranded	tongs-shaped
A. serratodentatum Willd.	subterete at the base, terete above	sulcate	2-stranded	tongs-shaped
A. cristatum L.	terete	sulcate	2-stranded	tongs-shaped
A. obliquum Willd.	sulcate	sulcate	2-stranded	tongs-shaped
A. kendalii Jenm.	subterete	sulcate	2-stranded	tongs-shaped
A. cristatum × *A. pulverulentum*	terete	sulcate	2-stranded	tongs-shaped
A. terminatum Kunze ex Miquel	terete	sulcate	2-stranded	tongs-shaped
A. malanoleucum Willd.	terete at the base, sulcate above	sulcate	2-stranded	tongs-shaped
A. latifolium Lam.	terete	sulcate	2-stranded	tongs-shaped
A. peruvianum Kl.	terete	subsulcate	2-stranded	tongs-shaped
A. pulverulentum L. *var. caudatum* Jenm.	sulcate	sulcate	2-stranded	tongs-shaped
A. aneitense Carr.	terete	sulcate	2-stranded	tongs-shaped

The next type of xylem strand is still simple in form but in this case the tips of the two halves point upwards and are blunt and not hooked (Fig. 4). This shape is found in *A. formosum* and all members of the Capillus-Veneris group. The strands in *A. patens* is a modification of this; here the tips of the two halves are sharp and curve upwards, whilst the centre of the strand makes a shallow curve downwards forming a saucer-shaped strand (Fig. 5). A further development may be seen in *A. hispidulum, A. cunninghamii, A. affine, A. whitianum, A. silvaticum* and *A. pedatum.* In these examples the xylem strand has a very characteristic V-shaped configuration and the tips of the two halves are sharp and a little curved (Fig. 6).

In some species such as *A. macrophyllum* and *A. serratocristatum* where the fluting of the stipe is very deep the abaxial arms of xylem join to form a basin-shaped strand with a nearly flat base. The arms are very slender and well separated from each other in the central region (Fig. 7). In other cases the metaxylem portions although fusing with each other fail to develop fully in the central region of the abaxial part of the strand resulting in a shape similar to a pair of tongs with long curving handles (Fig. 8). This type is found in almost all members of the Polysorus group.

Conclusion

From the observations, it will be seen that there is a sequence of shapes of the xylem strands ranging by small steps from the deep-crescent type seen in *A. reniforme* to the rather intricate tongs-shaped type seen in *A. tetraphyllum.* This sequence is illustrated in Plate 1. Part of the sequence was described by Ogura (1972) but with important gaps present.

Lin & De Vol (1977) in their investigation of the ferns of Taiwan stated in the key to the identification of genera that *Adiantum* had a V-shaped type of xylem configuration. There is no indication of whether or not more than one species was examined and indeed no direct indication of what species it was. However Tsai (1972 and 1973) lists 53 ferns of Taiwan which he has cytologically examined and the only species figuring in the list is *A. capillus-veneris.* This species has indeed a shallowly V-shaped xylem configuration. It is evident that a key of this nature based on inadequate samplings would not necessarily work in other regions and such information may be misleading if indiscriminately applied.

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