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托叶铁科(苏铁目)羽片脉序和羽片解剖学研究

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摘要: 详细研究了托叶铁科两属的2种代表植物 *Stangeria eriopus* 和 *Bowenia serrulata* 的羽片脉序和羽片解剖学。两个属在气孔器特征与不具副传输组织方面极为相似,而在气孔的分布、羽片脉序式样与叶缘形态、粘液道的有无、海绵组织与栅栏组织的分化、工字形壁组织与表皮细胞垂周壁特征方面则有较大的差异。将这些特征与苏铁科和泽米铁科作了比较,并讨论了这些特征在系统学上的意义。研究结果支持 Stevenson(1992)将该科分为两亚科以及托叶铁科是介于苏铁科与泽米铁科之间的观点。

关键词: 托叶铁科; 羽片羽脉; 羽片解剖学
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Venation and Anatomy of Pinnae in Stangeriacea (Cycadales)

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Abstract: Pinna venation pattern and pinna anatomy of two species, *Stangeria eriopus* and *Bowenia serrulata*, representatives of the two genera in Stangeriaceae were studied in this paper. The two species (genera) are similar in stomatal character and in the absence of accessory transfusion tissue, but they are very different in stomatal distribution, pinna venation pattern and pinna marginal shape, presence or absence of mucilage canal, differentiation of palisade and spongy parenchyma, characteristics of girder parenchyma and epidermal anticlinal wall. Pinna venation and pinna anatomy of Stangeriaceae are compared with those of Cycadaceae and Zamiaceae. Stevenson's classification (1992) with two subfamilies and the treatment of Stangeriaceae as a transitional evolutionary position between Cycadaceae and Zamiaceae is supported by present study.

Key words: Stangeriaceae; Pinna venation; Pinna anatomy

1 Introduction

Johnson[1] separated genus *Stangeria* T. Moore from Zamiaceae and set up family

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Stangeriaceae with one genus, *Stangeria* (with 1 species). *Bowenia* Hooker ex J. D. Hooker (with 2 species) was included in Zamieae, one of the three tribes of Zamiaceae in his classification. Subsequently, based on the parallel-veined pinnae in *Bowenia* Hooker ex J. D. Hooker, Stenvenson[2] had ever removed *Bowenia* from Zamiaceae and established a new family, Boweniaceae, and, *Stangeria* was included in this family. However, in his new classification[3, 4], Boweniaceae was reduced to subfamily level within Stangeriaceae. Both Crane[5] and Stevenson[4] put the monogeneric Cycadaceae as the sister taxon of all other extant cycads, and believed that *Stangeria* and *Bowenia* formed a clade that was a sister taxon of Zamiaceae. Although near thirty characters were used by Stevenson in his cladistic analysis[3], many characters of vegetative organ anatomy, which probably had important systematic significance, such as the pinna venation pattern and anatomical features, were neglected in his work.

Hitherto, the vegetative organs, wholly or in part, of Stangeriaceae have been studied anatomically[6-10], however comprehensive investigation on venation pattern and anatomical feature of the two genera in Stangeriaceae is still limited. In this paper, pinna venation pattern and pinna anatomy of two species representing two genera of Stangeriaceae are described and their systematic significances are discussed.

2 Materials and methods

Materials of *Stangeria eriopus* and *Bowenia serrulata* were obtained from living plants cultivated in South China Botanical Garden (SCBG). Pinnae from the middle part of frond were fixed in FAA and sectioned with sliding microtome. Cross sections of 15–30 μm thickness were taken and duplicate slides were stained with Ehrlich hematoxylin, dehydrated with alcohol series and cleared by xylene, and finally mounted in neutral balsam. All sections were examined and photographed under Leitz Ortholux II.

3 Results

Anatomical characteristics of pinnae of Stangeriaceae are shown in Table 1 and detailed pinna anatomy is described as below.

3.1 Characteristics of venation

Pinna venation is of dichotomous parallel vein in both *Stangeria eriopus* and *Bowenia serrulata*, but midrib with four parallel vascular bundles exists only in *Stangeria eriopus* (Plate I: 1). Dichotomous veinlet endings connect each other, or end at the margin of pinna or at serratures in *Stangeria eriopus* (Plate I: 1, 6), while those run straight to the serrature tip (Plate I: 11) in *Bowenia serrulata*.

3.2 Anatomical description

Epidermal cells The epidermis of pinna is heavily cutinized in the two species

examined, and both of the upper and lower epidermis consist of one layer of epidermal cells (Plate I: 2, 3, 7, 8). Some of the epidermal cells contain druses.

Epidermal cells are irregularly polygonal in shape, 90 μm × 70 μm to 250 μm × 20 μm in size, and anticlinal wall is undulate in *Stangeria eriopus*; while in *Bowenia serrulata* epidermal cells are irregularly rectangular in shape, about 260 μm × 15 μm in size, and anticlinal wall is straight (Plate I: 9).

Stomata Stomata are restricted to lower epidermis and cyclocytic with a T-shaped thickening at the pole region in *Stangeria eriopus* (Plate I: 4). Accessory cells are about 5–6 in number and irregular in shape. The size of stomata is about 80 μm ×80 μm in diameter (Plate I: 5). Encircling cells overlapping the stomata are raised to form a flat rim, which appears at the same level as other epidermal cells.

In *Bowenia serrulata*, stomata are actinocytic with arch-shaped thickening at the pole region. Accessory cells are irregular in shape and about 4–6 in number. Stomata are densely distributed on lower epidermis, while sparsely on upper epidermis and are restricted to the bases of the pinnae. The encircling cell rims are flat and are located at the same level as other epidermal cells. Stomata are about 100 μm × 60 μm in size (Plate I: 7, 8).

Hypodermal sclerenchyma cells In pinna margin, hypodermal sclerenchyma appears as 2–3 layers of cells in thickness beneath upper and lower epidermis in *Stangeria eriopus* (Plate I: 2), while those as 1 layer in *Bowenia serrulata* (Plate I: 8). In midrib region of *Stangeria eriopus*, as described by Alice Lamb[8], 1–3 layers of sclerenchyma cells occur beneath upper and lower epidermis, and are scattered in groups through the narrow regions internal to the upper and lower epidermis, and singly through the rest of the midrib (Plate I: 1).

Mesophyll In *Bowenia serrulata*, both palisade and sponge tissues are not differentiated in mesophyll, and some idioblastic cells are sparsely distributed among parenchyma cells (Plate I: 7). Whereas in *Stangeria eriopus*, palisade cells are differentiated and slightly elongated, often closely arranged in two layers beneath upper epidermis; spongy cells are irregularly arranged and elongated with apparently intercellular space (Plate I: 3).

Vascular bundles Vascular bundles are collateral. Phloem is regular in *Stangeria eriopus*, but irregular in *Bowenia serrulata*. Fibre cells form abaxial and adaxial "caps" which connect with both abaxial and adaxial epidermis and termed as girder parenchyma in *Stangeria eriopus* (Plate I: 2). However, girders are absent in *Bowenia serrulata* (Plate I: 7, 8). Accessory transfusion tissue is absent in both species/genera.

Mucilage cannals Mucilage canals and sclerenchymatous cells are present in midrib region (Plate I: 1) in *Stangeria eriopus*, and absent in *Bowenia serrulata*.

Sclerenchyma cells at pinna margin Sclerenchymatous cells are arranged in 2–3 layers within pinna margin in *Stangeria eriopus*, but in one layer in *Bowenia serrulata*.

Table 1 Anatomical comparison of pinna characteristics between *Stangeria eriopus* and *Bowenia serrulata*

	Stangeria eriopus	*Bowenia serrulata*
Midrib	present	absent
Epidermal anticlinal wall	undulate	straight
Distribution of stomata	lower epidermis	lower and upper epidermis
Stomata	cyclocitic	cyclocitic
Encircling cell rim (encircling cells)	flat (5–6)	flat (4-6)
Abaxial hypodermal sclerenchyma cells	1–3 in midrib	absent
Adaxial hypodermal sclerenchyma cells	1–3 in midrib	absent
Sclerenchyma cells at pinna margin	2–3	1
Palisade and sponge tissues	differentiated	undifferentiated
Girder	present	absent
Accessory transfusion tissue	absent	absent
Mucilage canals in midrib	present	absent
Pinna margin	round	beak-like

4 Discussion

Stangeria eriopus and *Bowenia serrulata* are very similar in stomata. Moreover, accessory transfusion tissue is absent in these two species/genera. However, they are quite different in pinna venation pattern, marginal shape, differentiation of palisade and spongy tissues, characteristics of epidermal anticlinal wall and the absence or presence of girder parenchyma and mucilage canals in midrib (Table 1). These evidences strongly support Stevenson's classification of Stangeraceae with two subfamilies[4].

Epidermal anticlinal wall is undulate in *Stangeria*[9], but is nearly straight in *Bowenia*, and straight in family Cycadaceae as well. Genus *Bowenia*, on the other hand, shares some characteristics with some species of Zamiaceae, such as *Mcrozamia moorei*, with stomata distribution on both adaxial and abaxial epidermis (Tang, Liu, Xie, Wu and Liao, unpublished).

According to our studies, the evolution of mucilage canals in midrib in Zamiaceae have a tendency from numerous to a few, and that of sclerenchyma cells from unobvious to obvious. Present investigation shows that both mucilage canals and sclerenchyma cells are present in midrib in *Stangeria*, but absent in *Bowenia*. It is interesting that mucilage canals are also observed in some species of Zamiaceae[12]. Based on these features, it is likely to be reasonable to assume that *Stangeria* has a close relationship with some taxa of Zamiaceae.

The venation pattern is characteristic and constant for each taxon of Cycadales, and has been considered to be a diagnostic feature at the family level[10]. In comparison with the known pinna venation patterns of Cycadaceae and Zamiaceae, an interesting result can be found, i.e. venation patterns of the two genera of Stangeriaceae are apparently transitional features between Cycadaceae and Zamiaceae. For example, the venation of *Bowenia* is more similar to that of most species of Zamiaceae (except *Chigua*) because they have no midrib, while that of *Stangeria* is more similar to that of Cycadaceae which has midrib. In addition, midrib in *Stangeria* consists of 4 parallel vascular bundles, which is also regarded as a transitional feature by present authors,

because there is one main vascular bundle in midrib of Cycadaceae, but Zamiaceae has parallel veins.

In our latest unpublished studies, as well as previous investigation[11], it is not difficult to find out that the accessory transfusion tissue is well developed in Cycadaceae but it is absent in Zamiaceae [12]. Accessory transfusion tissue of Stangeriaceae is also absent absolutely. This difference seems to implicate that the accessory transfusion tissue has an evolutionary tendency from present to absent in these three families. Therefore, according to present investigation on pinna venation and anatomy, the characters concerned more strongly support the treatment of Stangeriaceae as a transitional evolutionary position between Cycadaceae and Zamiaceae [4].

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Explanations of plate

Plate I

1-6: *Stangeria eriopus*; 7-11: *Bowenia serrulata*. Upper side is adaxial surface of pinnae in plate I: 1, 2, 3 and 7. 1: A part of pinnae through midrib in transverse section, showing vascular bundles (white arrow) and the mucilage cannals (black arrow) in the midrib, ×32; 2, 3: Parts of pinnae in transverse section, × 84; 4: Upper epidermis in surface view, × 340; 5: Lower epidermis in surface view, showing stomata, × 340; 6: Pinna venation, × 2.8; 7: Part of pinnae in transverse section, × 130; 8: Part of pinnae in transverse section, × 64; 9: Upper epidermis in surface view, showing stomata, × 340; 10: Lower epidermis in surface view, showing stomatal apparatus, × 340; 11: Pinna venation, × 2.8.