On the frond articulation of two large-sized species in the fern genus *Loxogramme*

Fumihiro KONTA**

近田文弘：サジラン属の大型の2種に見られた葉の関節

In the previous papers (KONTA, 1974, 1978), the anatomical features of the frond articulation were reported for four species of *Loxogramme* comparing with those of 10 Polypodiaceous and two Grammitidaceous species. The four species were either medium-sized or small-sized species in this genus. At that time the large-sized species were not available, and I only suspected presence of the frond articulation in large-sized species, because I observed distinctive leaf scars on phyllopodia in *Loxogramme avenia* and *L. involuta* (KONTA, 1974).

In the present paper, it is intended to report the anatomical features of the frond articulation of two large-sized species, *L. avenia* and *L. scolopendrina* which were collected in Malaysia and Thailand in 1982.

**Materials and methods**

After fixed with either 70% ethanol or methanol solution, materials have been reserved in 70% ethanol solution. Voucher specimens are shown in Table 1. Basal stipes being composed of stipe proper and phyllopodium, and rhizomes of both juvenile frond in circinate stage and mature frond with fully developed lamina were vertically sectioned with freezing microtome at the thickness of 15–30 micron. For the juvenile

<table>
<thead>
<tr>
<th>Table 1. Materials observed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
</tr>
<tr>
<td>------------------------------------</td>
</tr>
<tr>
<td><em>Loxogramme avenia</em></td>
</tr>
<tr>
<td><em>L. scolopendrina</em></td>
</tr>
</tbody>
</table>

* Supported by the Grant in Aid of Scientific Research of the Ministry of Education, No. 58043020.

** Faculty of Science, Shizuoka University, 836 Ooya, Shizuoka City
stage, a frond of 7 mm long in *L. avenia* and that of 5 mm in *L. scolopendrina* were sectioned. Phyllododia with leaf scars were also vertically sectioned.

Ferric chloride solution was used to detect the deposition of tannic acid.

**Results**

*Juvenile fronds*: Cells of stipe proper are narrowly oblong and linearly tapered toward both distal ends, and those of phyllodium are oblong or oblong-rhombeoid in

---

Figs. 1–4, 6. Radial section of basal stipe and phyllodium: 1, Mature frond of *Loxogramme avenia* (*×100*); 2, Mature frond of *L. scolopendrina* (*×100*); 3, Juvenile frond of *L. avenia* (*×130*); 4, Juvenile frond of *L. scolopendrina* (*×100*); 6, Mature frond of *L. scolopendrina*, note U-shaped tannic acid free abscission layer (*×3*).

Fig. 5. A row of leaf scars on phyllodia of *L. scolopendrina* (*×1*).
L. avenia. A special cell zone being composed of 3-4 layered small-sized oblong-rhomboid polygonal cells are observed between the cells of the stipe proper and those of the phyllopodium in this species (Fig. 3). In L. scolopendrina, however, the special cell zone is indistinct although many layered round cells are observed between the cells of the stipe proper and those of the phyllopodium (Fig. 4).

Mature fronds: Phyllopodia are 2-3 mm tall and 3-4 mm across at the top in L. avenia, and 4-6 mm tall and 4-7 mm across in L. scolopendrina. They are composed of oblong or oblong-rhomboid polygonal parenchymatous cells in both species. While, stipes are composed of narrowly oblong or oblong parenchymatous cells which are tapered toward both ends in both species. A special cell zone being composed of 5-6 layered small-sized obtuse-polygonal or round parenchymatous cells is observed between the cells of the phyllopodium and those of the stipe in L. avenia. About 2-3 layered cells composing middle part of the special cell zone are free from the deposition of tannic acid in this species (Fig. 1). On the other hand, the special cell zone is not so clearly distinguished between the cells of the stipe and those of the phyllopodium in L. scolopendrina (Fig. 2). In this species, 5-8 layered comparatively small-sized obtuse cells are observed at similar place to that of the special cell zone of L. avenia. These small-sized cells are free from the deposition of the tannic acid and observed as V- or U-shaped narrow white line when sectioned samples are immersed in ferric chloride solution (Fig. 6).

Phyllopodia: The phyllopodia of both species are composed of oblong or oblong-rhomboid polygonal cells only and the deposition of the tannic acid is confirmed at the upper part after fronds have fallen. Ranges of the phyllopodia with a leaf scar on each top are formed (Fig. 5).

Discussions

In the previous papers (Konta, 1974, 1978), I recognized the presence of the frond articulation in middle-sized species, Loxogramme salicifolia and L. saziran, although it had usually been noted that the frond articulation was lacking in this genus (Ching, 1940; Copeland, 1947; Holttum, 1955). The articulation of these species recognized had common anatomical features with those of some polypodoid ferns (Bäsecke, 1903; Mühlendorf, 1925; Philips and White, 1967; Konta, 1974). The features include that (1) a distinct abscission layer composed of several layered obtuse parenchymatous cells is recognized between stipe and phyllopodium in mature frond, (2) the abscission layer is formed during the early stages of development of frond and (3) the defoliation occurs at this layer leaving saucer-shaped leaf scars on phyllopodia and tannic acid was deposited on these scars.

The structure of basal stipe of mature fronds of L. avenia is similar to that of L. saziran, which was observed by myself (Konta, 1974). Between stipe proper and phyllopodium, the special cell zone is also confirmed in L. avenia as in the case of L. saziran. The special cell zone of L. avenia seems to be the abscission layer. Total breadth
of 5–6 layered cells of the cell zone of *L. avenia* is broader than that of 2–3 layered abscission cells of *L. saziran*. This seems to result from the fact that fronds of *L. avenia* are considerably larger than those of *L. saziran*.

Observations on the juvenile fronds show that the abscission layer of both species is formed during the early stages of development of frond. Observation on the structure of phyllopodium with leaf scar in both species also shows that the defoliation occurs at the abscission layer leaving saucer- or cup-shaped leaf scar and the tannic acid is deposited on the upper part of it.

On the other hand, distinct special cell zone is not observed in *L. scolopendrina*. In this species, 5–8 layered comparatively small-sized obtuse cells are observed at similar place to that of the abscission layer of *L. avenia*. Although structurally indistinct, the V- or U-shaped zone of the small-sized cells of this species seems to be the abscission layer, because the cells in this zone are free from the deposition of the tannic acid and it is evident that the defoliation occurs at this cell zone leaving cup-shaped leaf scar. Judging from the structure of the basal stipe of juvenile frond of this species, it seems that the cells of the abscission layer are not formed after frond has fully developed but formed during young stages of development of frond as *L. saziran* and other polypodiaceous ferns. Many layered (5–8 layers) cells of the abscission tissue seems to result from the fact that this species is none of the largest ferns in this genus.

In addition to the results of observations reported in the previous papers (Konta, 1974, 1978), the present observation on the frond articulation of two large-sized species seems to support the suggestion of Tagawa (1943) who suspected the presence of the frond articulation in *Loxogramme*.

**Acknowledgements**

I am greatly indebted to Prof. T. Shimizu of Shinshu University, Dr. T. Smitinand and Mr. T. Wongprasert of Royal Forest Department of Thailand for their kind help. I am also indebted to Prof. K. Iwatsuki of Tokyo University for his valuable suggestions.

**References**


摘要 サジラ属のシダは東南アジアの熱帯を中心に約40種近く知られている。この属の分類学的定位について異なる様々な考えがなされてきた。その原因のひとつに、この属の葉が根茎と関節するか否かの評価に相違があることが挙げられる。Copeland (1947) や Holttum (1955) 等は、サジラ属の葉は根茎と関節しないと考えた。一方田川先生 (1943) は、関節の存在を示唆された。これらの主張は、いずれも野外での観察または葉柄標本による外部形態にもとづくもので、Bäcke (1908) や Phillips と White (1967) 等のように、葉柄の内部構造やその発生にまで立入った観察にもとづくものではなかったようであった。

そこで筆者 (1974) は、サジラ属のサジラ、イワナギシダ、ヒメサジラ、Loxogramme lankokensis に、葉が根茎と関節するといわれるウラボシ科と、サジラ属との類縁が問題とされるヒメウラボシ科の数種を加えて、葉柄の内部構造を詳細に観察した。そして、サジラやイワナギシダの葉は、ウラボシ科に見られるものと同様に、根茎と関節するという結果を得た。この時筆者は、サジラよりはるかに大型の葉を持つ種では葉の関節はどのようなものであろうかという疑問を持った。

1982年、筆者はタイとマレーシアに於ける植物調査の一環として、これらの国に分布する大型のサジラ属の葉の関節を調べる資料を得ることに努めた。そして、Loxogramme aveni と L. scolopendrina の資料を今回観察することができた。観察の要点は、成熟した葉の葉柄基部の構造、極端に小型の葉を伴う種の葉柄基部の構造、葉を落とした後の根茎の構造の3点である。

L. aveni の成熟葉では、葉柄基部における葉足は直径が3-4 mm、高さ約3 mm であった。葉足とその上の葉柄の径はほぼ同じで、葉足は表面に密な鱗片をつけるという点で葉柄から区別される。放射断面では、葉柄の長方形または長楕円状菱形の細胞群と葉足の短軸形の細胞群の間に、4〜5層から成る小型の短軸形の細胞群が見られた（図1,3）。このような葉柄基部の構造は極端に小型の葉を伴う種のものであった。さらに、葉が落ちた後の葉足では、この小型の細胞群の所で葉足が起ったことが示され、葉足上部にタニンの沈着が見られた。これらの観察は、サジラやウラボシ科の葉柄と良好一致するもののであった。

一方、より大型の葉を持つ L. scolopendrina では葉柄が長いが、この種の成熟した葉では、葉足は直径が4〜7 mm、高さが4〜6 mm であった。葉柄と葉足の境界に、L. aveni に見られるような明瞭な小型の細胞群は認められず、葉柄の細胞と葉足の細胞の中間的な形のやや小型の、6〜8層の細胞群が観察された。この細胞群の部位は、顕微鏡を用いずに見ると、タニンを含まない白いUまたはV字状の筋として良く判別される。そして、落葉はこの部分で起きているようである。

L. aveni の葉柄と葉足の間に見られる小型の細胞群は、サジラの観察で述べたと同じく、Phillips と White (1967) のいう離層であって、これは葉の極端に小型化した場合を存在し、この離層の所で落葉が起こるのである。L. scolopendrina では、離層として明瞭に他と区別出来る細胞群はないと考えられていた。しかし、これとは、いわゆる離層が存在しないのではなく、L. aveni のそれよりも、はるかに多層の細胞層から成っていて、葉柄の細胞と葉足の細胞の中間の形をしているものと考えた方が良いようにと思われた。L. scolopendrina の葉柄基部の構造は、この種が特に大型の葉を持つことと関係があるようである。

結論として、ヒメサジラや L. lankokensis のような極端に小型の種は別として、サジラ属の大部分の種の葉は根茎と関節するといえるであろう。