Venuloid Idioblasts in *Pteris* and Their Systematic Implications

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In many ways anatomical characters have been relied upon more in pteridophytes than in spermatophytes in working out taxonomic relationships, especially during the early development of classification at the levels of genus and family. Nevertheless, we are still engaged in seeking new characters that can be exploited in solving controversial problems of relationships and this research continues. In this article I wish to discuss the peculiar "false veins" that are found in the brake ferns, *Pteris*. Such structures have been referred to as "spicular idioblasts," "recurrent veins," "false veins," "Scheinnerven," "sclerites," and other terms. As a name for this phenomenon I propose "venuloid idioblasts." This would cover all structures of various forms and homologies which produce the illusion of tiny veinlets scattered in the interveinal, submarginal, or sinus regions of the lamina. They are not attached to the true veins. Ordinarily, the venuloid idioblasts can be seen with a high-powered hand lens or dissecting microscope with no difficulty, appearing as narrow lines or streaks. In dried herbarium specimens they are often slightly raised. Such veinlet-like structures are widely scattered in the various groups of ferns, but are most familiar in such families and subfamilies as Marattiaceae in Marattiales and Hymenophylloideae and Vittarioideae in the Polypodiales. In some genera (e.g., *Trichomanes, Angiopteris*) they have been used for purposes of species discrimination. The presence of venuloid idioblasts has also been used as a source of evidence for relationships at the higher levels of genus and family.

As part of a general study of venuloid idioblasts in fern leaves, I wish to describe in this paper some of my observations in the genus *Pteris*. This is especially appropriate on this occasion because Professor Motozi Tagawa probably dealt more than any other individual with the species of *Pteris* that display these structures. Indeed he described several of these taxa. I wish here not only to expand the existing descriptions of the venuloid idioblasts of *Pteris*, but also to discuss some of their possible systematic implications.

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Generally speaking the presence of venuloid idioblasts in the brake ferns has gone unnoticed by the majority of authors. Bower (1928) did not mention them in *Pteris*, nor did Copeland (1947) or Ogura (1972). In connection with *Pteris grevilleana Wall.*, Holttum (1954) noticed that "between the veins on both surfaces are irregular short raised lines, commonly two rows between each pair of veins." In his synopsis of the genus *Pteris* in Japan, Ryukyu, and Taiwan, Wang-Cheung Shieh (1966) used what he termed "false-veins in mesophyll" to key out "Subsect. 2. Cadieri." He also adopted the contrast "many false-veins" vs. "few false-veins" as the primary division in his key to the seven taxa in this section, namely *P. yamatoensis* (Tagawa) Tagawa, *P. angustipinna* Tagawa, *P. ryukyuensis* Tagawa, *P. multifida* Poir., *P. kidoi* Kurata, *P. grevilleana* Wall., and *P. cadieri* Christ. A modification of this treatment was also used by Shieh (1975) in the Flora of Taiwan.

**Description.** The following descriptions of the venuloid idioblasts of *Pteris* are based primarily on the species that represent the two extreme types of frond structure, namely *P. multifida* with linear, entire major segments, and *P. grevilleana* with pectinate or deeply lobed major segments. The specimens used are in the University of Michigan Herbarium*. Frond segments were cleared in sodium hydroxide aqueous solution, and stained with tannic acid and ferric chloride.

It became evident early in this study that the idioblasts actually do not occur in the mesophyll, as has been reported; instead they are scattered in the upper and lower epidermis. They are, however, somewhat overlapped by adjacent epidermal cells, as shown in Figure 1. The cross-sectional diameters of the epidermal cells and the idioblasts are smaller by one-half to one-fifth than the true mesophyll cells. There are usually two to four layers of mesophyll parenchyma cells visible in section, and they are rounded and lack projections.

![Fig. 1. Cross-section of a leaf segment of *Pteris grevilleana* showing position of venuloid idioblasts in the upper and lower epidermises.](image)

The idioblasts are narrow, approximately 20-25 microns in diameter, and the secondary walls are extremely thick, the lumen being only 6-9 microns wide. Their lengths vary from 0.1 to 1.2 (rarely more) mm., and most of them are between 0.5 and 1.0 mm. The longest idioblasts tend to be those located approximately midway between the costa and the margin of the segment, and the shortest are found near the costa, and especially along the margin. With few exceptions, they taper at both ends to pointed tips. Fertile segments show the idioblasts running along the adaxial surface and the rolled margin above the sorus, but not in the false indusium itself. The idioblasts have a slightly scalloped appearance as seen under the dissecting microscope and in clearings due to the greater or lesser overlap of the numerous adjacent epidermal cells. The refractive characteristics of the false veins under Nomarski interference contrast illumination are similar to those of the true veins (Fig. 2).

Usually the idioblasts are nearly straight or only slightly curved. Strongly curved or angular ones are most often found close to the costa in the angle of vein departure. Also, along the segment margins many of the idioblasts curve upward toward the apex of the segment. Although there are occasional individuals with more or less knobbed tips, only rarely do the idioblasts branch. On the abaxial surfaces one sometimes finds examples of forking where the tip comes into contact with the auxiliary cells of the stomates.

Pteris grevilleana (Fig. 2) displays the most striking development of spicular cells, and these are immediately evident to the eye, even with a low powered hand lens. They are very numerous and crowded, and a typical interveinal area including both laminar surfaces totals roughly between 20 and 40 idioblasts (Fig. 2). They occur throughout the interveinal areas and there is no special tendency to cluster along the true veins. Numerous examples of joined pairs or triplets of idioblasts can be found. They are
joined in various ways. Although they may sometimes be contiguous for nearly or quite their full length, they are commonly attached near their tips. Careful examination often is needed to establish that what appears to be a single unusually long idioblast is in reality two or three connected along their tips.

*Pteris multifida* (Fig. 3, 4) differs in having only relatively few idioblasts, usually 0–5, rarely more, per interveinal area. These tend to cluster along the true veins, and this may make it possible to overlook them in a casual examination. Joined idioblasts are rare in *P. multifida*, except along the midrib, and curved examples are also not so common as in *P. grevilleana*. However, short individuals, as in the latter, do tend to occur mainly along the costa and along the margin. *P. ryukyuensis* (Fig. 5) has the fewest idioblasts of any of the taxa I studied.

Plants of the general description of *P. cadieri*, i.e., those with more or less dimorphous fronds that show irregular combinations of the characters of *P. grevilleana* and *P. multifida*,

Fig. 3. Distribution of venuloid idioblasts in *Pteris multifida* showing their tendency to cluster around the true veins.

Fig. 4. Detail of venuloid idioblasts in *Pteris multifida* showing their relation to the veins and to the sorus.
appear to have intermediate expressions of the idioblasts (Fig. 6). They occur in numbers ranging from 10–30 in the interveinal areas. However some specimens resembling *P. cadieri* (e.g., Amano 6738 from Okinawa, which appears to be a hybrid of *P. semipinnata* L. with *P. multifida*) have fewer idioblasts per interveinal area.

**Discussion.** It is intriguing to speculate on the origin of the venuloid idioblasts of *Pteris*. They are apparently very rare in the genus as a whole, being known in only a few taxa of the western Pacific and southeastern Asia. One hypothesis might be that these structures arose entirely *de novo* from ordinary epidermal cells. Another hypothesis, and the one which I would favor, is that they had their origins in the more or less elongate epidermal cells above and below the true veins. These cells tend to have somewhat straighter walls and to have greater length than the majority of adjacent epidermal cells in the interveinal regions. According to this hypothesis these epidermal cells located over the veins provided some sort of mechanical strengthening and they became exaggerated to the present form of short sclerenchymatous fibers. Subsequent evolution would call for the progressive diffusion of such cells into the epidermises of the interveinal regions until they had an essentially uniform distribution.

Both extremes described above are found: In *P. multifida* we see the condition of few idioblasts, these tending to cluster closely along the true veins. In *P. grevilleana*, in contrast, we see numerous idioblasts, and these are thoroughly spread throughout the interveinal areas. If this hypothesis is true, then, *P. multifida* displays the primitive condition, and *P. grevilleana* the most specialized. Other taxa, such as *P. cadieri*, are intermediate.

I do not doubt that *P. grevilleana* and *P. multifida* are related, in spite of the seemingly radical differences in their frond structure. The Sino-Japanese area has been cited by WALKER (1962) as one of the centers of speciation in the genus *Pteris*. We are familiar with several cases of hybridization between species with linear, unlobed pinnae and with
deeply lobed pinnae. In Hawaii occur obvious intermediates between *P. cretica* L. and *P. irregularis* Kaulf. known as *P. × hillebrandii* Copel. which not only appear to be hybrids but which have become established as an apogamous species (Wagner, 1974). In the case of *P. multifurca* AG. and *P. quadriaurita* Retz., T. Walker (1958) was able to demonstrate an almost complete hybrid series between them. In their hybrid swarm sexual reproduction prevails and there is no loss of ability for the chromosomes to pair. The plant known as *P. otaria* Bedd. is an especially common hybrid form. The striking point about these and other known or suspected hybrids in *Pteris* that involve sharp differences in leaf blade structure is that the compromise between parental extremes is strongly irregular (cf. Wagner, 1962; Walker, 1962, fig. 2; Wagner, 1974, Fig. 6).

I would like to suggest that *P. cadieri* is analogous to *P. × hillebrandii* and *P. × otaria* in that it arose by hybridization and that it displays irregular frond structure. Shieh (1975) describes *P. cadieri* as having “fronds dimorphous, sterile fronds... with one or two pairs of lateral pinnae, pinnae pectinate, pinnatifid, or irregularly producing segments, in the simplest form the terminal pinna simple and linear.” The development of venuloid idioblasts in *P. cadieri* is intermediate between that of *P. grevilleana* and *P. multifida* (Fig. 6). According to the cytotaxonomical compilation of Löve, Löve, and Pichi Sermolli (1977) both *P. grevilleana* and *P. multifida* are tetraploids with 2n=116. Mitui (1975) also reports *P. cadieri* as being n=87 apogamous, and *P. ryukyuensis* as n=58. Further work is desirable before we can evaluate the significance of these observations.

I suspect that hybridization has taken place between *P. grevilleana* and *P. multifida* (and) or other species with linear pinnae to produce plants of the description of *P. cadieri*. Several different species may be involved, thus making a complex picture. To Nakaike’s (1970) list of hybrid *Pteris* in Japan we may have to add others not heretofore suspected of having had hybrid origin, not only *P. cadieri* but *P. kidoi*, *P. ryukyuensis*, and possibly others.
The major significance of the unusual anatomical character discussed in this paper involves the systematic relationships of the genus *Pteris*—a long undecided question. For many years it was a tradition to associate the brakes with the worldwide bracken fern genus, *Pteridium*, mainly because of the gross appearance of the cutting of the fronds and the marginal coenosori. However, in recent years there has been a tendency to question this, and indeed to separate the genus *Pteris* and its allies wholly from *Pteridium*, placing the former with the adiantoid-cheilanthoid ferns, and the latter with the dennstaedtioid-cyatheid ferns. One major impetus for this change came from the discovery by cytologists that the *Pteris* complex is characterized by the base chromosome number of \(x=29\), like typical adiantoid-cheilanthoid ferns with \(x=29\) or 30, whereas *Pteridium* has a base number of \(x=26\). 

Mickel has written (1973) that “The genus *Pteris* presents a problem that is not easy to solve. I would place it with the Adiantaceae on the basis of its reflexed marginal false indusium, chromosome number of \(n=29\), and commonly pedate architecture. On the other hand it does have in some species polycyclic steles as in *Dennstaedtia*, and epipetiolar branches, but the branches are entirely abaxial rather than lateral on the petiole.”

I submit that the presence of epidermal idioblasts of the type described here, albeit rare in the genus as a whole, may have a systematic bearing on the classification of *Pteris* at the familial level. It is well known that similar structures are found in the genus *Adiantum*, although again in a minority of the species. Also, those epiphytic ferns presumably derived from ancestral adiantoid-cheilanthoid ferns, the Vittarioideae, have similar idioblasts in the majority of genera and species. In my survey of venuloid idioblasts in ferns in general I have found no other group beside the adiantoids, pteroids, and vittarioids where venuloids of this description occur.

All other venuloid idioblasts in ferns have strikingly different structure, and appear to be examples of convergent rather than parallel evolution. Those of the filmy ferns, Hymenophyllioideae, for example, apparently involve changes and detachments of whole veins, and those of the giant ferns, Marattiaceae, modifications of the true mesophyll. Both are multicellular false veins, and neither can be homologized with the isolated epidermal idioblasts described here. On the other hand, the false veinlets of the adiantoid and vittarioid ferns are so much alike that they are certainly homologous. This is not to say that they are necessarily directly derived from one another. They more probably represent parallel evolution in three separate lines. Thus it is the predisposition to the evolution of such structures that betrays systematic affinity.

**Literature Cited**


摘要 シダ植物の分類形質としていろいろの形態学的形質が採用されてきたが、新しい形質を求める努力も続けられている。この論文では、イノモトソウ属の偽脈について論じるが、この種の構造はこれまで様々な呼び名で呼ばれていおり、脈以外のこの種の構造をひっくり返して「脈状異型細胞 venuloid idioblasts」と呼ぶことを提唱したい。脈状異型細胞はシダ植物のいろいろの群にみられるが、リュウビンタイ科、コケシノブ亜科、シンラン亜科に普通のものである。

イノモトソウ属のもとでは、脈状異型細胞はよく記載されているように業内の組織のうちにあるのではなく、上下の表皮組織内に散在している。異型細胞は幅狭く、径20～25ミクロンで厚い。長さは0.1～1.2 mmで、多くのものは0.5～1.0 mmの範囲である。通常両端は狭くなり、先端は尖る。表面観では異型細胞は直線的で、曲ったり枝分かれしたりするのは特殊な場合などだけである。

アシガタシダにはこの種の異型細胞が多く、容易に観察される。イノモトソウでは異型細胞が少なく、脈の近くに集まる傾向があるので見落しやすい。リュウキュウイノモトソウでは、筆者が調べたもののうちで、異型細胞は最も少なかった。カワリパアマクサシダではこの形質にも大きな変異が認められた。

イノモトソウ属の脈状異型細胞はアジア東部の種にだけみられるものであり、その起源についてもいくつかの仮説が立てられるが、筆者は表皮細胞から変形してきたものではないかと考えたい。また、この属の類縁について、同じような異型細胞をもつホライシダ属やシンラン亜科との類似にも注目したい。ホライシダ群・イノモトソウ群・シンラン群以外のものの脈状異型細胞は構造上異ったもので、相似の形質である。上記3群のもつ形質は相互に由来し合ったというよりは同じように形成されてきたものだろうが、この形質を指摘にしてこれら3群の関係を考えることは強力無理とはいえないだろう。