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A brief survey of the dromy in fern leaves, with an expanded terminology

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Abstract

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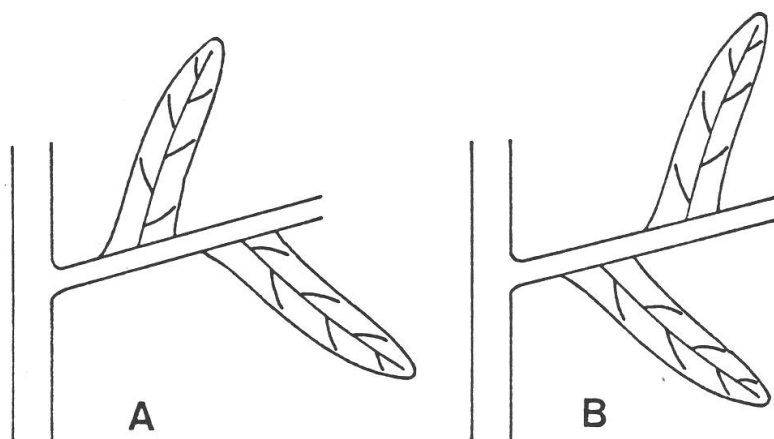
The architecture of compound fern leaves is discussed with regard to the question whether the basal secondary division, or the basal vein of a primary pinna, is on the anterior (“anadromous”) or the posterior (“catadromous”) side; the history of the terminology is briefly reviewed. The terminology is then amplified: the new terms isodromous, heterodromous, pseudoanadromous, and poecilodromous are introduced. The taxonomic importance of the character at family, genus, and species level is discussed.

In most fern leaves that are at least bipinnate, and in many simply pinnate ones, a character can be very readily observed that has proved to be of considerable taxonomic significance, and that often substantially facilitates identification: the anadromous (or anadromic) vs. catadromous (or catadromic) architecture of the lamina. In the majority of bipinnate and more highly compound fern leaves, of which there are very many instances, the character is quite obvious, and in retrospect it is difficult to understand why it has been so long neglected, not to say ignored.

I was first confronted with it when working with Christensen’s monumental “Monograph of the genus *Dryopteris*”. In part II (1919) he drew attention to the usefulness of this character, crediting Mettenius (1858) with its detection and the very appropriate terms coined for it. In the last-named publication, on p. 286, the terms “anadromous” (anadrom) and “catadromous” (catadrom) appear for the first time. There, however, they are employed for the venation rather than for the dissection pattern; but as is quite obvious and is further elaborated below, the two characters are morphologically and taxonomically intimately linked.

In spite of the importance of this phenomenon of the two different basic dromy patterns (I am aware of the awkwardness of this term but do not know an alternative), little or no use was made of it by pteridologists for a long time, even after Christensen (l.c.) again drew attention to it. It has been used to a certain extent, however, by palaeobotanists, e.g. by Appert (1973) and Boureau (1975). There is no evidence that,

Dedicated to Prof. T. Reichstein on the occasion of his 90th birthday



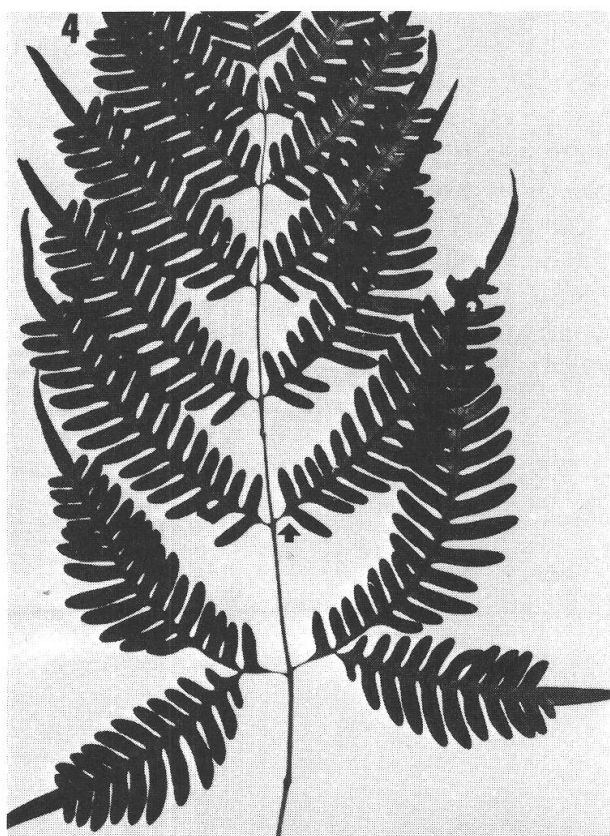
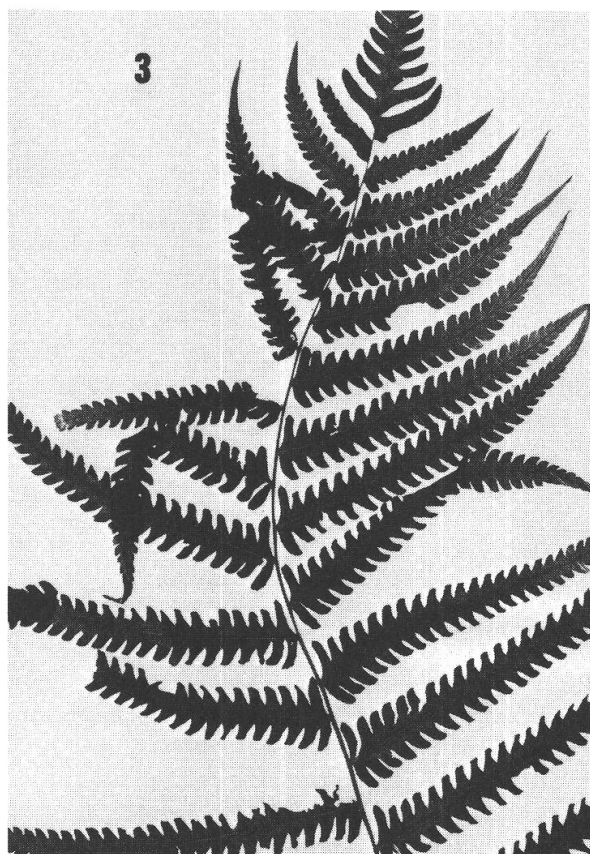
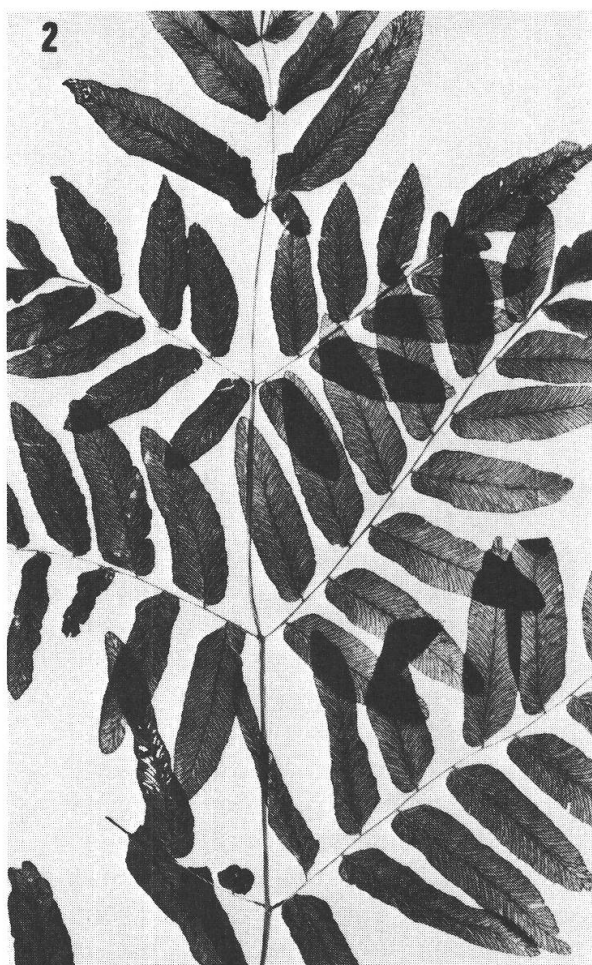
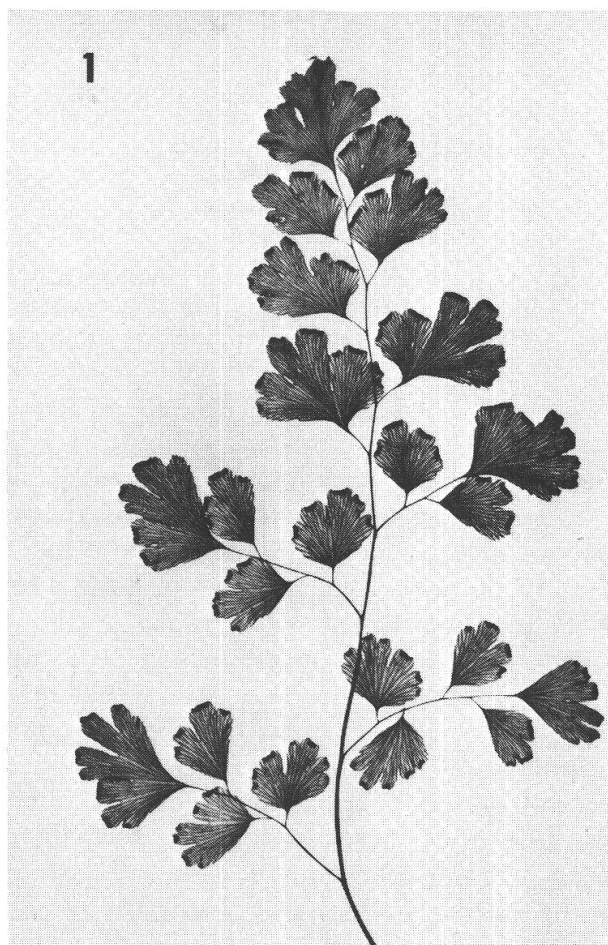
A: anadromous dissection and venation. B: catadromous dissection and venation. (From Appert, Schweiz. paläontol. Abh. 94: fig. 3, 1973).

e.g., W. J. Hooker, the eminent pteridologist of the 19th century, was at all aware of its existence; nor even his contemporary John Smith who distinguished himself favourably from Hooker by his keen eye for, and astute use of, “vegetative” characters in the classification of ferns. Even in much of the newer literature the character is not often mentioned, with favourable exceptions. The dromy is a useful and very easily observed field character; yet even field manuals often do completely without it (e.g., Lellinger 1985). One of the few papers that go into the character in detail, albeit in a limited fern group, is by Serizawa (1974).

When editing or preparing the treatments of the fern groups for the series “The Families and Genera of Vascular Plants” (Kramer et al., in prep.), I was faced with the fact that for the great majority of genera this character had not, or only very incompletely, been recorded. I was forced to remedy this as far as possible, by direct observation of living plants and of the material in the herbarium of the Institute of Systematic Botany at the University of Zürich, as well as in some other herbaria visited in the course of the preparation of the treatments. Beside the many gaps in the observations to be filled, I noted that the terms “anadromous” and “catadromous” were not quite sufficient for covering the situation observed in certain ferns. Consequently, a number of new terms derived from them is coined below, with explanations and examples. This is accompanied by some observations on the relations between the various character states. I hope that not too many of the generalizations implicit in my statements need to be modified; the limited amount of material (and time) available, and particularly and lamentably, the fragmentary nature of so many fern collections found in herbaria, may in some cases have misled me as to the general applicability of certain observations.

The original terms “anadromous” and “catadromous” require no explanation; for the sake of completeness they are illustrated in the text figure; see also figs. 1–3. It must

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- Fig. 1. Anadromous lamina of *Adiantum capillus-veneris* (A. Kaiser 822, Sinai).
 Fig. 2. Catadromous lamina and venation of *Osmunda japonica* (Kramer et al. 8280, Hong Kong).
 Fig. 3. Catadromous lamina of *Thelypteris* (*Christella*) *parasitica* (Zogg & Gassner 4005, Taiwan).
 Fig. 4. *Pteris* aff. *quadriaurita*. Lamina heterodromous: basal pinnae anadromous, second pinna (arrow) and higher ones catadromous (Mokry 9, Seychelles).



be stated explicitly that they apply to both dissection, from pinnate + lobed to higher degrees, and to venation.

The only author known to me who attempted an investigation into the character in a broader context, including its expression in flowering plants, is Heidenhain. In his book “Die Spaltungsgesetze der Blätter” (1932) he devoted about one chapter to the dromy, but he expressed it in an awkward way, stating whether the basal division of a twice compound leaf was on the right (“dextrans”) or on the left (“sinistrans”), thus coining a relative terminology rather than an absolute frame of reference. Heidenhain was apparently unaware of the significance of the character for fern taxonomy; his unfortunate terminology has luckily not been followed by any pteridologist known to me.

In some cases a clear recognition of anadromy or catadromy is hardly possible, namely, when the basal divisions or veins spring essentially from the same point. In this case we may speak of an isodromous architecture, or *isodromy*, called “opposite” by Serizawa (l.c.). This is not truly comparable to anadromy or catadromy in most cases, as it is clearly a borderline condition; nearly always it occurs in genera where most other species (or even individuals) are either catadromous or anadromous, and the basal symmetry of the dissection or venation is a marginal case. The emphasis is here on basal; in many instances the next higher segments and/or veins are staggered, and careful observation will tell us whether the architecture or venation is essentially catadromous or anadromous (fig. 9, 10). It is rare to find isodromy prevailing throughout a genus (as is common in dicotyledons); a well-known example is *Histiopteris*, and even here the venation is catadromous. But there are species that are consistently isodromous, e.g., some species of *Pellaea* (see below). In my opinion isodromy is but rarely part of the “Bauplan” but most often a borderline condition. Thus, it is “marginal” to anadromy in, e.g., *Mohria*, *Acystopteris* (fig. 10), and *Woodsia*, and to catadromy in, e.g., *Histiopteris* and some Blechnaceae (fig. 9).

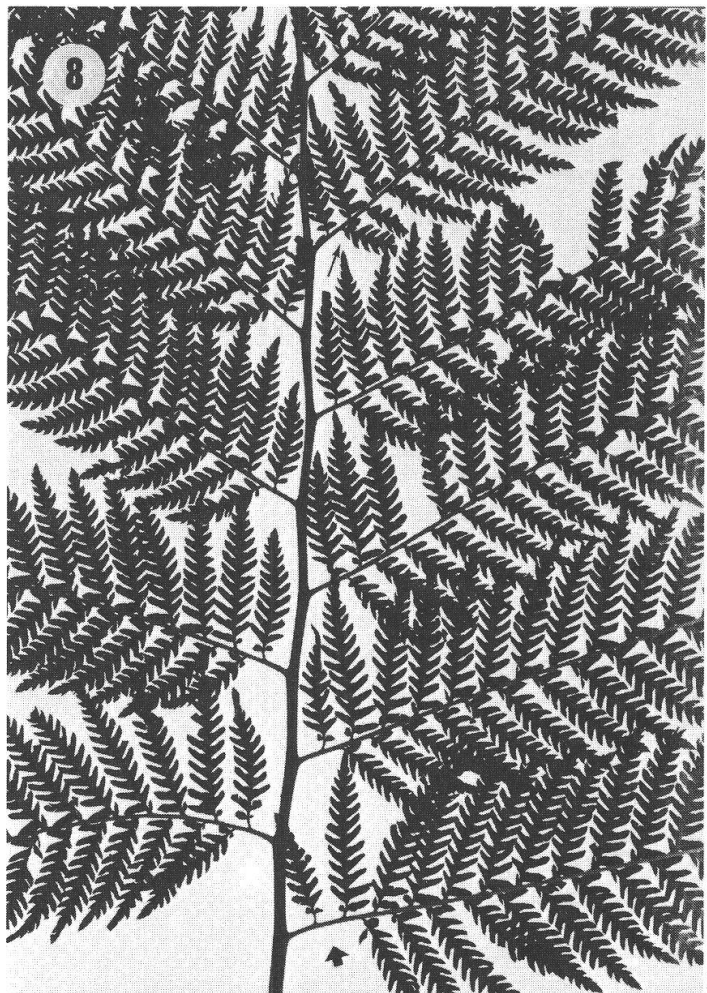
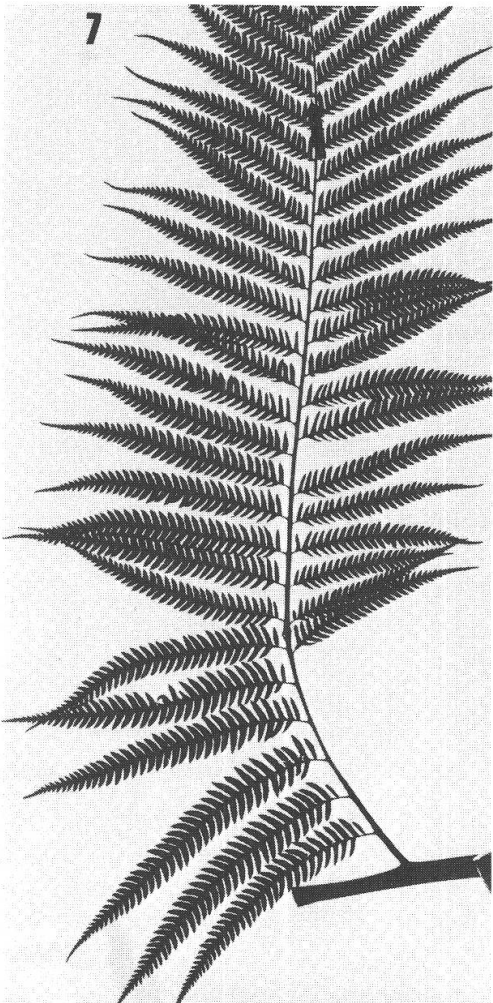
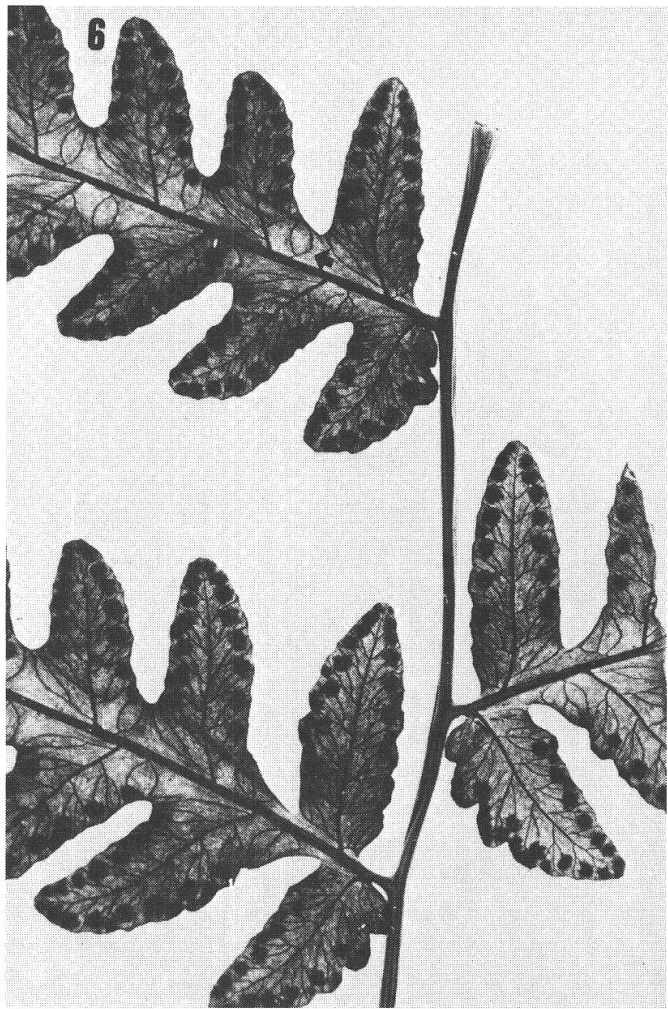
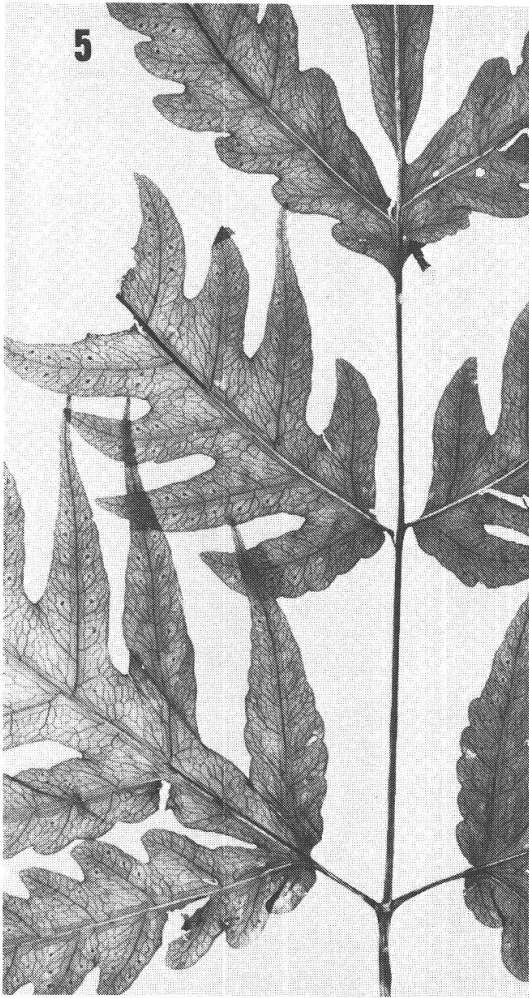
An unusual and quite rare character is what I call *pseudoanadromy*. In the basal pinnae (and pinnules) of otherwise catadromously dissected and veined leaves, one or several basal posterior divisions are apparently suppressed, making these pinnae/pinnules appear anadromous; the dissection of the other, especially smaller, divisions, their venation, and the situation in related species shows that the architecture in the taxon is essentially catadromous, with only the pinna/pinnule bases not conforming. Mostly this is very obvious through the fact that more than one place for a basal posterior pinna is open (fig. 7) which I regard as conclusive evidence for the suppression of some divisions. The few examples known to me are in the genera *Cibotium* and, less conclusive, *Woodwardia*. In *Lophosoria* (fig. 8) the ultimate divisions are catadromously pinnatifid, but the divisions of lower order, at least the major ones, are anadromous.

Fig. 5. *Tectaria camerooniana*. Catadromous upper part of heterodromous lamina. Basal secondary vein of uppermost pinna springing from rachis, not from costa (arrow) (“hypercatadromous”) (Geerling & Bokdam 1807, Ivory Coast).

Fig. 6. *Tectaria paradoxa*. Catadromous upper pinnae. Lowermost (posterior) basal vein of costule springing from costa, not from costule (e.g., arrow) (“hypercatadromy”) (Faden & Faden 76/511, Ceylon).

Fig. 7. *Cibotium taiwanense*. Lower primary pinna; apex of lamina at left. Basal basisopic pinnules and basal posterior segments of lower pinnules wanting, but the segments present in the upper pinnules (arrow) (pseudoanadromy) (Zogg & Gassner 6155, Taiwan).

Fig. 8. *Lophosoria quadripinnata*. Basal posterior pinnules wanting (thick arrow), but basal posterior segments of pinnules mostly present (e.g., thin arrow) (primary dissection probably also pseudoanadromous) (Nee & Taylor 29362, Mexico).



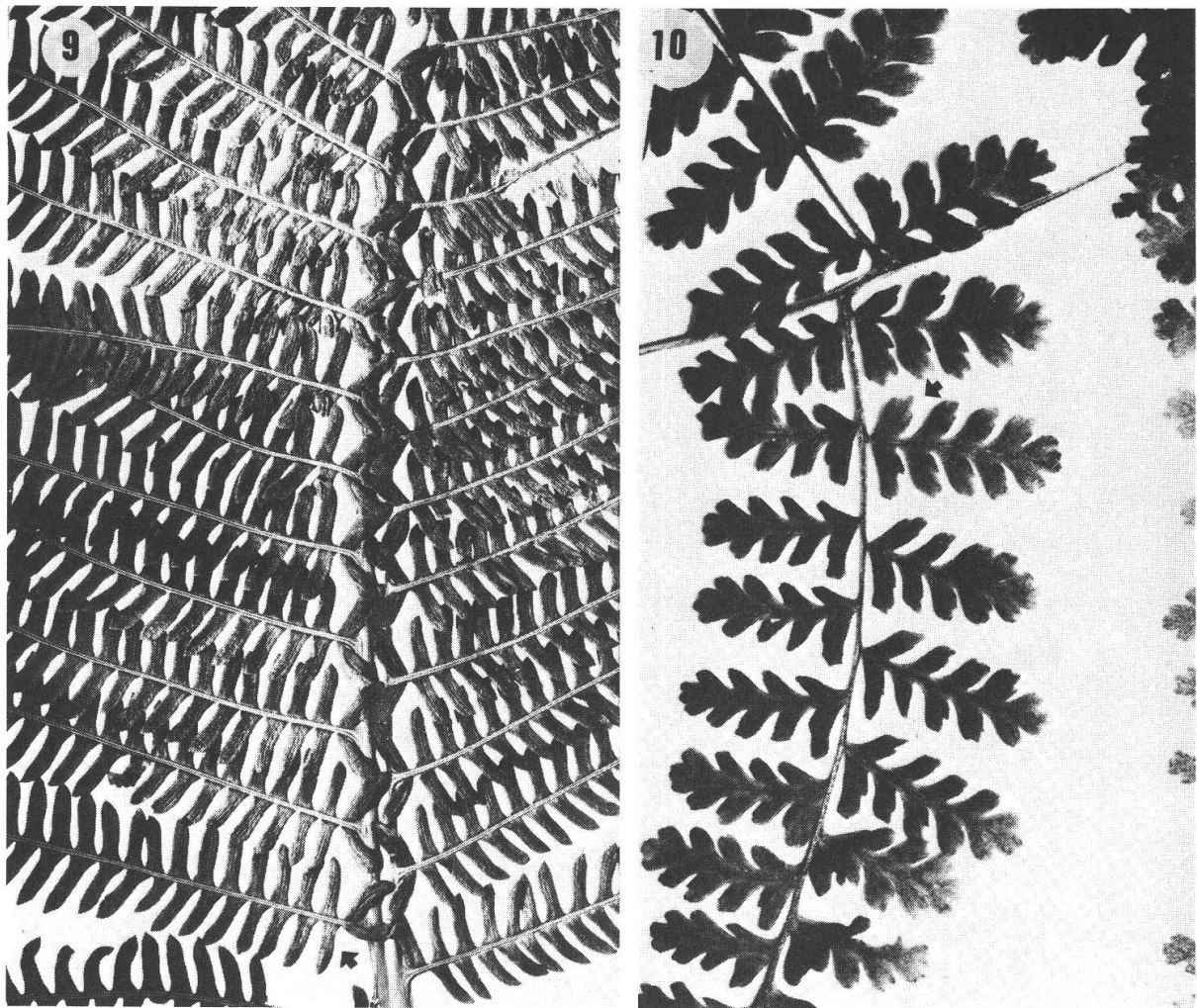


Fig. 9. *Sadleria cyatheoides*. Basal pinnules opposite (isodromous), but second pair already distinctly catadromous (e.g., arrow) (Hochreutiner 3657, Hawaii).

Fig. 10. *Acystopteris japonica*. Apex of lamina at left. First pair of pinnules opposite (isodromous) or weakly catadromous, second pair distinctly anadromous (e.g., arrow) (Kramer et al. 7736, Taiwan).

The material at my disposal is too fragmentary for a definite conclusion; but I believe that here, too, a pseudoanadromous condition prevails.

Only one genus is known to me where the dromy seems to fluctuate freely, without much regularity, namely, *Pteridium*. If desired, this condition may be called "poecilodromy", which might be expanded to refer to genera where the dromy fluctuates between the species; but this would result in a certain amount of ambiguity. It remains to be seen whether the character, when observed for the infraspecific taxa of *Pteridium* recognized by R. Tryon (1941), does not prove to be more consistent for each one by itself. Again, the material I was able to examine did not permit a conclusion.

Another character state, less common than anadromy or catadromy but not particularly rare, is what I should like to call *heterodromy*. Here the basal and apical parts of one and the same lamina differ as to their dromy. Good examples are the genera *Salpichlaena*, *Steenisioblechnum*, and *Stenochlaena* of the Blechnaceae; some species of *Anemia* (Schizaeaceae); *Metaxya* (Metaxyaceae); a considerable number of genera of

Dryopteridaceae: *Peranema*, *Stenolepia*, *Nothoperanema*, *Tectaria*, *Heterogonium*, *Pleocnemia*, *Aenigmopteris*, *Dryopolystichum*, *Dictyodroma*, and *Diplaziopsis*; and some species of *Dryopteris*, *Dryopsis*, *Lastreopsis*, *Athyrium*, and *Diplazium*; furthermore the great majority of the species of *Pteris* (except for subgenus *Pteris* = the group of *Pt. longifolia*) (fig. 4), and all species of its relatives *Acrostichum* and *Neurocallis*. In all these cases the lamina is anadromous (rarely isodromous) in the basal pinnae, changing abruptly or more gradually to catadromous architecture in the more distal part. There is no connection between the dromy and the shape of the pinnae, as very many species of *Pteris*, and of *Tectaria* and its relatives, have strongly basitonically produced basal pinnae; but these are anadromous, at least in their primary dissection pattern. In most of these cases the dissection of the pinnae at higher order (if any) and the venation are quite catadromous. I do not know of any instance of a lamina that is catadromous at base and anadromous distally.

In the upper pinnae of many catadromous or heterodromous taxa the pinnae are \pm strongly decurrent, or even wing-connected with their neighbours. Here the catadromy of the venation is often expressed in a special way: the basal, basispic veinlet springs, not from the costa of the pinna but from the axis of next lower order: the rachis, and is contained, so to speak, in the decurrent wing (fig. 5). A homologous situation sometimes prevails in the venation of the pinna segments (if any), or in the veinlets borne by the strongly differentiated secondary veins. In such cases the basal veinlet does not branch off from the (posterior side of the) secondary vein, but its base is shifted to the costa of the pinna (fig. 6). Holttum (e.g., 1983) recognized this as an important feature that characterizes the genus *Tectaria*. This might be called "hypercatadromy", if a special term is required; but I think we should guard against too strong a proliferation of terms relating to the dromy.

Dromy as a family character. Few of the larger fern families are entirely consistent as to their dromy; the only example known to me is Aspleniaceae which are entirely anadromous. Anadromy prevails, but is by no means universal, in Davalliaceae (exception: *Davallodes*), Dennstaedtiaceae, Hymenophyllaceae, and Pteridaceae. Entirely catadromous families are Cyatheaceae, Marattiaceae, and Thelypteridaceae. Blechnaceae are preponderantly catadromous, but heterodromy also occurs. The inclusion of *Stenochlaena* in Blechnaceae is corroborated by, i.a., its heterodromy.

The question may be raised whether catadromy or anadromy is the "primitive" condition in ferns. It is arguable whether such a question is truly meaningful. But it can hardly be dismissed as fortuitous that a majority of fern families generally regarded as primitive are entirely or very predominantly catadromous; Gleicheniaceae (exception: *Stromatopteris*), Marattiaceae (as far as can be observed), Matoniaceae, Ophioglossaceae (*Botrychium*, most species), Plagiogyriaceae, Schizaeaceae (*Lygodium* and mostly *Anemia*). Primitive anadromous families exist, too, but in smaller number: Cheiroleuriaceae, Dipteridaceae (both monogeneric), Hymenophyllaceae except for *Trichomanes* sensu Iwatsuki (1984) and for representatives where no dromy can be observed. Loxomataceae and Dicksoniaceae are about equally divided between anadromy and catadromy.

Families and genera with simple or with dichotomous lamina cannot of course be judged as to their dromy: Vittariaceae – *Rheopteris*, if rightly placed here, seems to be anadromous; many Grammitidaceae – those with non-simple lamina are anadromous; *Ophioglossum*; *Schizaea*; etc.

The Polypodiaceae seem to represent a special case. The dromy is often not observable, even when the lamina is not entire; secondary veins are not clearly differentiated

in the complicated reticulation of the tertiary venation; or the dromy is only weakly and/or inconsistently expressed. It is my impression that its taxonomic significance is small or none in this family. This lends some support to the authors who believe that the primitive condition in this family is a simple lamina, and that dissection, where present, has been secondarily developed. In terms of dromy this would mean that the character was lost when the lamina was simple and that it did not reappear in the "Bauplan" when dissection, often notoriously fickle in the family, secondarily reappeared.

Dromy as a genus character. All by itself the character state expressed by the dromy is insufficient for separating genera. In some instances it is, however, a convenient diagnostic feature, one of several, but often the most evident for separating related genera. A few examples may be given.

The related genera *Culcita* and *Calochlaena** of the Dicksoniaceae are separable at first glance by being catadromous versus anadromous; there are several more, strongly correlated characters.

Dryopteris is very often catadromous or heterodromous. A few, only once pinnate species like *D. scottii* and *D. sieboldii* are anadromous or heterodromous; but the highly dissected species are not, and this is a very helpful character for distinguishing *Dryopteris* from the closely related and often very similar genus *Arachniodes* which is mostly highly compound and pronouncedly anadromous; see also Serizawa (l.c.).

The separation of *Steenisioblechnum* from *Pteridoblechnum* (Hennipman 1984) is corroborated by the former being heterodromous, the latter catadromous.

The redefinition of *Trichomanes* as circumscribed by Iwatsuki (1984) is very well confirmed by its catadromy, in contrast to the other genera where the pattern is anadromous, or where no dromy can be observed, including several genera formerly united with *Trichomanes* on soral characters.

Dromy as a species character. I did not come across a large number of instances where the dromy is inconstant for a genus but can be used for discriminating between species. Some good examples that have come to my attention are the following.

Botrychium (Ophioglossaceae): *B. virginianum* (subgenus *Osmundopteris*) is anadromous in contrast to most (all?) other species of the genus.

Hypolepis (Dennstaedtiaceae): anadromous and catadromous species occur side by side, e.g.: *H. hostilis*, *H. muelleri*, *H. nigrescens* versus *H. neocaledonica*, *H. rugosula*, *H. sparsisora*. Further investigation is required.

Paesia (Dennstaedtiaceae): anadromous except for *P. anfractuosa*.

Monachosorum (Monachosoraceae): *M. flagellare* and *M.* ("Ptilopteris") *maximowiczii* are anadromous, *M. subdigitatum* is catadromous in its primary divisions.

Pellaea (Pteridaceae): the genus (as delimited by Tryon & Tryon 1982) is preponderantly anadromous, but consistently isodromous species also occur. A number of species are, however, catadromous, which to my knowledge has been overlooked so far: *P. calomelanos*; and a group of closely related species from the New World: *P. ovata*, *P. intermedia*, *P. sagittata*; see the excellent illustrations in A. Tryon (1957).

Pityrogramma (Pteridaceae): the entire genus is distinctly anadromous (isodromous in one or two species), except for *P. triangularis*, in which large leaves are often catadromous. This may be another example of a poecilodromous species, but *P. triangularis*

* *Calochlaena* (a section of *Culcita*) is not yet validly raised to the rank of genus as this paper goes to the press.

is perhaps an aggregate species. Its inclusion in the genus is very possibly wrong (see, e.g., Tryon & Tryon 1982); it seems to me that it is much nearer to *Cheilanthes* s. lat.

Polystichum (Dryopteridaceae): *P. braunii* can easily be distinguished from similar species by having at least some distinctly catadromous pinnae, a rare character in the genus very rarely mentioned in floras.

Pteris (Pteridaceae): the great majority of the species are heterodromous, as are the allied genera *Acrostichum* and *Neurocallis*. But the small group of species related to *Pt. longifolia*, which make up subgenus *Pteris*, are entirely catadromous.

The relation between dromy in dissection and in venation. Not surprisingly, the dromy of the dissection and that of the venation are intimately connected; there are only very few ferns, like a few Hymenophyllaceae, where the incision/dissection of the lamina or its segments is independent of its venation; incisions of any size are, of course, between the (major) veins, if any. But in heterodromous leaves, when they are more than once pinnate, the basal or lower pinnae are anadromous and the higher ones catadromous; yet the venation is usually (always?) catadromous throughout, including the basal pinnae. When the pinnules of the latter are divided again, their dissection pattern is, logically, also catadromous.

Dromy in Selaginella. The species of *Selaginella* with a fern-leaf-like architecture in the upper, branched part of their erect stems have a very regular branching pattern, and I tried to observe whether a regular pattern of dromy could be traced. As far as I could ascertain, the most basally inserted leaf on a branch is always the lateral (lower plane) leaf on the posterior side, making these (and many other, less or not fern-like) species catadromous. The pattern is, of course, not quite comparable to that of ferns as selaginellas have so-called axillary leaves at each branching (bifurcation). The extent of applicability of this character requires further study.

Another point that requires, and deserves, further study is the expression of dromy during the blastogeny of a fern plant.

I hope that this concise exposé will convince pteridologists that the character of the dromy deserves more attention than it has received so far.

The author is indebted to Mr. A. Zuppiger, Zürich, for skilfully preparing the photographs.

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