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Carl-Johan Widén, Jaakko Sarvela and
Teuvo Ahti: The *Dryopteris spinulosa*
complex in Finland

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THE DRYOPTERIS SPINULOSA
COMPLEX IN FINLAND

BY

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Abstract

A comparative morphological study on *Dryopteris assimilis* S. Walker, *D. dilatata* (Hoffm.) A. Gray, em. S. Walker and *D. spinulosa* Watt was conducted on the basis of Finnish material. Putative hybrids of these species are also reported from nature in Finland. *D. assimilis* is common and widespread in Finland, while *D. dilatata* is rare, being confined to the extreme southwest of the country. *D. spinulosa* is much more widespread in northern Finland than reported earlier, extending to Lapland proper. In many northern localities it is distinctly hemerophilous.

Introduction

In Europe the so-called *Dryopteris spinulosa* complex consists of three allotetraploid ($n = 82$) species, viz. *D. cristata* (L.) A. Gray, *D. spinulosa* Watt (the correct name is possibly *D. carthusiana* (Vill.) H. P. Fuchs; see FUCHS 1959) and *D. dilatata* (Hoffm.) A. Gray s. str., and one diploid species ($n = 41$), *D. assimilis* S. Walker (WALKER 1961), which has not usually been distinguished from *D. dilatata*. *D. assimilis* was first recognized as a cytotype of *D. dilatata* (MANTON 1950; WALKER 1955), although some earlier authors had given varietal rank to some extreme forms of the two species but they were not clearly distinguished from one another. In addition, there is a diploid *D. maderensis* Alston on Madeira and another species, *D. azorica*

(Christ) Alston, on the Azores Islands, which has not been cytologically investigated. According to WALKER (1961) *D. maderensis* is indistinguishable from the eastern North American *D. intermedia* (Muhl.) A. Gray both cytologically and morphologically. For quick identification of the European species, see the keys of CLAPHAM, TUTIN & WARBURG (1962, p. 29) and HEYWOOD (1964, p. 21) and the table of comparison by WIEFFERING, FIKENSCHER & HEGNAUER (1965, p. 741). Other useful recent papers include those by WALKER & JERMY (1964), NANNFELDT (1966) and SIMON & VIDA (1966).

The main purpose of this paper is to compare the morphology of *Dryopteris assimilis*, *D. dilatata* and *D. spinulosa* on the basis of Finnish material and to give an outline of their distribution in Finland. V. SORSA (1958, 1963a, 1963b) reported the chromosome number $n = 41$ for *D. dilatata* s. lat. in specimens from southern and northern Finland. They belong to *D. assimilis*, but the existence of the tetraploid *D. dilatata* s. str. in the country has also been confirmed cytologically (WIDÉN & V. SORSA 1966). However, NANNFELDT (1966) was the first author to report *D. dilatata* s. str. in Finland. V. SORSA (1958) reported the number $n = 82$ for *D. spinulosa* from southern Finland, while in a specimen from Pyhätunturi National Park, Lapponia kemensis, he found the number $n = 41$ (V. SORSA 1963a, 1963b). However, he himself doubted the identification of the plant on which the latter record was based, and one of us (T. Ahti) has confirmed that the voucher specimen is an unusually small *D. assimilis* ('var. *pseudospinulosa*').

D. cristata is obviously different in morphology from the rest of the group and has been clearly recognized and reported from numerous localities in Finland and elsewhere. It is true that it hybridizes with *D. spinulosa*, but it has not been treated more closely in this connection here.

The present study was made in collaboration, but C.-J. Widén is mainly responsible for the morphological descriptions, J. Sarvela for the identification of the herbarium specimens, and T. Ahti for the account on the distribution and ecology of *D. spinulosa*.

Material was examined from the following herbaria: Botanical Museum, University of Helsinki (H), Forest Research Institute, Helsinki (HFR), Department of Silviculture, University of Helsinki (HSI), Department of Botany, University of Oulu (OULU), Naturhistoriska Riksmuseet, Stockholm (S), Botanical Museum, University of Turku (TUR), Biological Institute, Åbo Academy (TURA) and Institutionen för Systematisk Botanik, Uppsala (UPS).

Acknowledgements. We wish to express our gratitude to Dr. Veikko Sorsa for making some chromosome counts and photographs, to Prof. J. A. Nannfeldt, Prof. Max von Schantz, Mr. Tauno Ulvinen, Mr. Tapio Rintanen, and Mr. Unto Laine for information concerning distribution of *Dryopteris* and for other help, and to Miss Kirsti Kaleva and Miss Lahja Vuorinen for technical assistance. We also thank Mr. F. H. Brightman for linguistic revision of our manuscript.

Dryopteris assimilis S. Walker

Rhizome large and sturdy (about $10-25 \times 4-8$ cm), erect or semierect, densely scaly (cf. B. WIDÉN 1944, Abb. 3). Bases of the petioles wide, often densely scaly, more or less flattened, the margins incurved. In cross sections of the rhizome and petioles numerous intercellular spaces with internal hairs may be observed (Fig. 1). The secreting hairs are $60-80 \mu$ long, usually with quite short stalks.

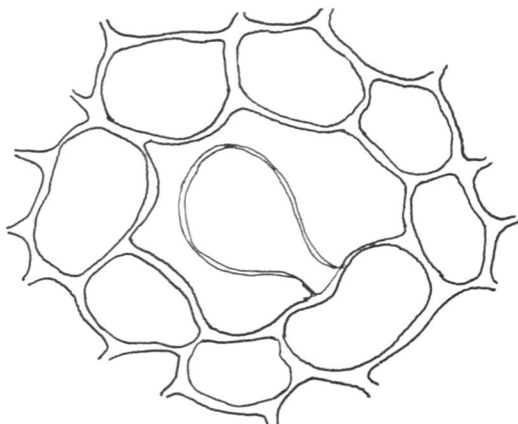


FIG. 1. *Dryopteris assimilis*. Internal hair in an intercellular space of rhizome. 300 x.

Scales (Plates 5, 6) highly variable in shape and size, the larger ones generally 13–18 mm long, 4–7 mm wide, and more or less reddish-brown. As a rule they are fairly long and narrow, with an acuminate apex, but sometimes broadly oval with a mucronate tip. They have a dark central part — at least the most basal ones — which varies in extent and is composed of cells with incrassate walls. This dark stripe rarely extends to the very tip of the scale; often it is present only at the base. It may even be totally lacking, particularly in scales on the upper part of the petiole but sometimes also in those at the base. The margins are commonly fringed with stalked glands, $30-40 \mu$ in length. The number of scales is highly variable. In most cases the petioles are fairly densely scaly but sometimes they are only sparsely so. In a great number of specimens collected above or slightly below the timberline in northern Fennoscandia ('var. *pseudospinulosa*') the colour of the scales is conspicuously reddish-brown and the dark centre absent or poorly developed (cf. NANNFELDT 1966, p. 146).

Leaves (Plates 1, 2) usually 50–150 cm long and 20–50 cm broad but in alpine areas much smaller, about $10-20 \times 5-10$ cm. Petiole stout, usually about as long as the blade. Blade tripinnatifid, sometimes almost quadripinnate, thin, usually pale green, with plane or rarely slightly convex tertiary segments. The length of the basal pinnule on the lower side of the lowest pinna is usually more than half the total length of the pinna; more rarely it is shorter. The under side of the blade is more or less densely beset with glandular hairs, $80-100 \mu$ in length, and narrow, band-like, scales 1–2 mm long; rarely it is quite without any hairs. The blades generally die in autumn but individuals which seem to

have regularly some overwintered fertile or sterile green leaves are found, at least in southern Finland. The blades of 'var. *pseudospinulosa*' are tripinnate at the base, but bipinnate toward the apex, thus resembling *D. spinulosa*. Even the lowest pinnae usually produce sporangia. The sori are often very small, 0.5–1 mm in diam., arranged in one or two rows on the tertiary segments or scattered without any distinct order. The indusium is reniform and fringed with stalked glands (ca. 60 μ in length) or sometimes quite glabrous.

Spores rather large, but variable in size, ca. 48–60 \times 32–40 μ (perine included). Perine pale and thin, sparsely folded and with rather widely spaced acute spinules. The spinules are usually less than 1 μ long. In a few specimens the spinules were observed to be somewhat denser and up to 2 μ long (cf. CRANE 1955; WALKER & JERMY 1964; P. SORSA 1964, s.n. *D. dilatata*).

Discussion

The present species is fairly variable in southern Finland but even more so in the north, where besides some 'southern forms' a form group that has been referred to as *D. dilatata* var. *pseudospinulosa* Rosend. (ROSENDAHL 1916) is present. Some authors have at first sight regarded the latter type as *D. spinulosa* (see e.g. SAMUELSSON 1919; V. SORSA 1963a). According to NANNFELDT (1966), var. *pseudospinulosa* consists of northern low-growing and pale green modifications of *D. assimilis*. One of us (C.-J. WIDÉN 1967) has found that chromatograms run from the rhizomes of var. *pseudospinulosa* show about the same variation in phloroglucinol compounds as those made from South Finnish *D. assimilis*. This supports the idea that var. *pseudospinulosa* is of no taxonomic importance. However, cultivation experiments are required for a final solution of the problem.

Three individuals of *D. assimilis* (Sarvela nos. 1, 8, 9) growing in Helsinki with overwintered green leaves (some fertile) in the spring of 1966 were studied by thin-layer chromatography. There proved to be some chemical differences between the specimens (which is common in *D. assimilis*), as well as some differences in habit, so that the ability to overwinter does not seem to indicate any significant taxonomic heterogeneity in this case.

On the other hand, some specimens of *D. assimilis* collected by C.-J. Widén at Parikkala, Karelia ladogensis, S.E. Finland, are more noteworthy. They yielded very unusual chromatograms (C.-J. WIDÉN 1967) and they deviate morphologically in having more widely spaced secondary segments in the leaves.

Distribution

In general, the Finnish literature records of *D. dilatata* and *D. austriaca* may be regarded as belonging to *D. assimilis*. In the southern half of Finland *D. assimilis* is more or less common. *D. spinulosa* is, however, much

commoner, and in some parts of southern Finland even *D. filix-mas* is more frequent. In northern Finland *D. assimilis* is less common but in Lapland proper it is still the most frequent species of *Dryopteris*. In the extreme northern tips of Finland, Enontekiö and Utsjoki, it becomes commoner again with the increasing oceanic influence of the Norwegian coast, where the species is quite common.

In Eurasia *D. assimilis* extends from Ireland and France at least as far as Western Siberia (cf. HULTÉN 1958; SIMON & VIDA 1966). The status of this species in North America is still an open question, although it is probable that the diploid 'western *D. dilatata*' (WALKER 1961) is not specifically different from *D. assimilis* (LÖVE & LÖVE 1966; BRITTON 1967). In coastal northeastern North America the prevalent type is the closely related tetraploid species *D. campyloptera* Clarkson. Another diploid, so far only poorly known, belonging to this complex, is also present in the Lake Superior area (WAGNER & HAGENAH 1962; BRITTON & SOPER 1966), but according to BRITTON (1967) it is the same as the 'western *D. dilatata*' and thus probably conspecific with *D. assimilis*. He was also unable to find any simple way to distinguish between the 'Lake Superior *D. dilatata*' and *D. campyloptera*. In any case, *D. assimilis* is apparently more closely related to *D. campyloptera* than to *D. dilatata* s. str.

Dryopteris dilatata (Hoffm.) A. Gray, em. S. Walker

Rhizome large and sturdy (10–15 cm long, 3–6 cm wide), erect or semierect, densely scaly. Bases of the petioles wide, more or less flattened, the margins incurved and densely scaly. Internal hairs and intercellular spaces in rhizome and petiole bases are rather sparse. The hairs are quite short-stalked, but they are 90–100 μ long and thus larger than in *D. assimilis*.

Scales (Plate 5) very similar to those of *D. assimilis* though less variable in colour and shape. The bigger ones are 16–20 mm long and 4–5 mm wide at base on an average. The marginal parts are light brown while in the middle there is a distinct dark-brown fairly broad stripe (very rarely lacking) of cells with incrassate walls.¹ The stripe usually extends to the very tip of the scale, even in the upper smaller scales on the petiole — unlike in *D. assimilis*. The scale margins are often beset with stalked glands 60–80 μ long. The petiole is generally strongly scaly, not only at base but also fairly high up.

Leaves (Plate 3) 20–85 cm long and 15–20 cm wide. Petiole stout, frequently shorter than the tripinnatifid, dark green and comparatively thick leaf blade, often about 1/3 of the blade. When seen above the tertiary segments are usually convex and in pressed material parts of the margins are bent down. The length of the basal pinnule on the lower side of the lowest pinna was less than half (usually about one third) the total length of the pinna in all the specimens that were measured. The lower side of the blade, the petiole, and usually the rhachis are rather heavily hairy, having glands 90–110 μ long and flat

¹ In 1967 a specimen was found in the Gullö stand, Ekenäs, with most of the scales without conspicuous stripes.

band-like hairs 1–2 mm long. Some glands are present also on the upper side of the blade. The leaves overwinter. Even the lowest pinnae bear sori, which are about 1 mm in diam. and arranged in two rows along each side of the middle nerve of the tertiary blade segments. The indusium is reniform and beset with glandular hairs 60–80 μ long.

Spores about $48-56 \times 36-40 \mu$ (perine included), perine dark brown, thick, densely beset with rather coarse spinules up to 2μ in length, less folded than in *D. spinulosa* (cf. CRANE 1955; WALKER & JERMY 1964; NANNFELDT 1966).

Discussion

The great morphological variability of the present species is emphasized by several European authors (e.g. CLAPHAM, TUTIN & WARBURG 1962; WALKER & JERMY 1964; NANNFELDT 1966). In the light of the rather sparse Finnish material it is evident that even in Finland it is variable, but quite easily distinguished from the related species. Only one herbarium specimen, collected in Korpo (Korppoo) (see the list below), has caused real difficulties. It consists of the upper part of an overwintered blade only. The glandular hairs on the lower side of the blade are longer and scarcer than usual in

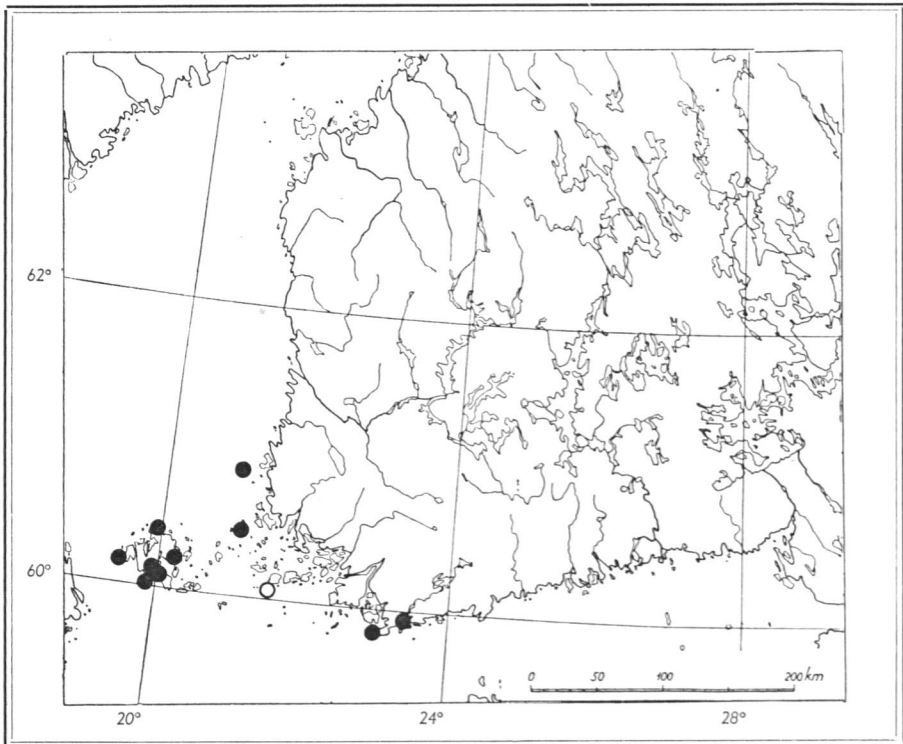


FIG. 2. Distribution of *Dryopteris dilatata* in Finland. The open circle represents an uncertain record.

D. dilatata and the blade segments are flat. If it is not *D. dilatata*, it may be the hybrid *D. dilatata* × *spinulosa*, although another Finnish specimen of this hybrid looks different.

Distribution (Fig. 2)

Alandia. Brändö: Åfva, 1923 A. Palmgren (H). — Eckerö: Tolding, 1900 A. Sternberg (H). — Geta: near the cavern »Djupviks kyrka», 1889 Ch. E. Boldt (H). — Jomala: Möckelö, moist spruce forest, 1925 H. Buch (H); spruce forest by Rosenquist's shipyard, 1925 H. Buch (H); grass-herb forest, 1930 L. E. Kari (TUR). A few kilometers from Mariehamn, 1925 A. Palmgren (H). — Lemland: Lemböte, 1923 E. Vainio (TUR). Kobbaklintar, 1931 Ulla Bärlund (H). — Sund: Bomarsund, 1928 Hj. Möller (S).

Regio aboënsis. [Korpo: Stora Hästö, 1963 O. Niemi (TUR), uncertain]. — Uusi-kaupunki rural parish: on a lake in the interior of Vekara Island, 1961 I. Kause (TUR).

Nylandia. Hangö: Stora Kolaviken, ditch in forest, 1931 H. Buch (UPS). — Ekenäs rural parish: Gullö, 1966 C.-J. Widén & V. Sorsa (H).

In Finland *D. dilatata* is distinctly an oceanic species. As far as is known all localities are situated within less than 2 km from the sea shore and some of them are on small islets in archipelago. Even in S.W. Finland it is much less frequent than *D. assimilis*. In the light of the data given by NANNFELDT (1966) on its distribution in Sweden, Norway, and Denmark it is obvious that *D. dilatata* belongs to HULTÉN's (1950, pp. 61–63) distribution group 'subatlantic plants' in N.W. Europe. NANNFELDT (1966) also suspected that the species will prove to be restricted in western and central parts of Europe. Notes by other authors (e.g. SIMON & VIDA 1966) and our examination of herbarium specimens support this idea.² In any case, *D. assimilis* is much more widespread than *D. dilatata*.

Dryopteris spinulosa Watt

Rhizome long and narrow (about 6–10 × 2–3 cm), nearly horizontal, not or sparsely scaly (cf. B. WIDÉN 1944, Abb. 2). Bases of the petioles narrow, somewhat flattened with incurved margins, scaly, but not very densely so. Internal secreting hairs and intercellular spaces are few. The hairs are usually long-stalked, more or less conical and 80–100 (140) μ long.

Scales (Plate 6) rather short, broadly oval, usually ca. 5–8 mm long, 3–4 mm wide, pale to slightly reddish brown and mucronate. They are often fringed with some glandular hairs, 40–45 μ in length.

Leaves (Plate 2) generally 15–60 cm long and 5–25 cm broad. Petiole approximately as long as the bipinnatifid (to tripinnate at base) leaf-blade. The pinnules and their divisions are flat and dark to pale green. The pinnae are usually somewhat upwardly directed and the two basal pairs are rather distant. The length of the basal pinnule on the lower side of the

² In S there is a specimen of *D. dilatata* from Leningrad District, U.S.S.R. (Isthmus karelicus: Sakkola, in palude, 23.VIII.1897, G. Lång; ex herb. Selim Birger), bearing the name '*Polystichum cristatum* × *spinulosum*'. However, since other specimens (H, HSI) of this hybrid collected by Lång in the same locality are correctly identified, it is probable that a change of labels has taken place.

lowest pinna is less than half the total length of the pinna. Glands are absent, or the lower side of the blade is sparsely beset with very thin stalked glands usually 100–140 μ in length. Also the rhachis may be glandular (see the discussion below). The sterile blades mostly overwinter, and more rarely the fertile ones overwinter as well. In general the basal pinnae are without sori. A few individuals with sori-bearing lower pinnae have been observed, however. Sori are 0.5–1 mm in diam. and arranged in one or two rows along each side of the middle nerve of the pinnules or the tertiary segments. The indusium is reniform, fairly thin, not glandular.

Spores rather large, ca. $44-56 \times 32-36 \mu$ (perine included). Perine dark brown, densely beset with spinules up to 2 μ long, and characteristically folded (cf. P. SORSA 1964), but more so than in *D. dilatata*.

Discussion

Eglandularity is regarded as one of the key characters of *D. spinulosa*. Recently this was emphasized by NANNFELDT (1966, p. 146) on the basis of Swedish material. In Finland, e.g. in the vicinity of Helsinki, one may often search in vain for fully eglandular individuals, because at least in the upper part of the rhachis there are some glands quite normally present. Also in some herbarium specimens collected in various parts of the country there are glands, which has sometimes been noted on the labels. For instance, good examples of plants with glands have been collected by Mr. Tauno Ulvinen in Rautio, Ostrobothnia media, in 1964 (H, OULU). One distinctly glandulose individual (J. Sarvela no. 12) from Ruskeasu, Helsinki, was stated to be tetraploid ($n = 82$) by Dr. V. Sorsa.

In herbaria some difficult specimens were detected. A few South Finnish specimens approach *D. assimilis* in habit, e.g. in having fairly broad leaf-blades. Some authors have referred them to *D. dilatata* s. lat. (incl. *D. assimilis*), particularly when the rhachis has been distinctly glandulose. However, the basal scales are without a dark central stripe and the spores are dark brown as in typical *D. spinulosa*. The density of epidermal cells, counted according to the method of WIEFFERING, FIKENSCHER & HEGNAUER (1965, p. 746), supported the assumption that the specimens were tetraploid.

Distribution (Fig. 3)

Most of the earlier data on the range of *D. spinulosa* in northern Europe are rather confusing and misleading. The map in HULTÉN's (1950) atlas looks unfinished (JALAS 1950, p. 140; TUOMIKOSKI 1951); the northern limit is placed too far south, apparently because it was difficult to distinguish the reliable literature records from the unreliable ones. Another map by HULTÉN (1958, Map 174) has been supplemented by a few new dots in North Sweden.

HJELT's (1888, p. 51) records of *D. spinulosa* s.str. throughout N. Finland are mostly erroneous (based on *D. assimilis*). LINDBERG (1917) revised the herbarium material and found that the northernmost station was at Kemi.

However, in recent decades *D. spinulosa* has generally been accurately recognized in Finland. According to HYLANDER (1953) the species only reaches as far as Rovaniemi and Kuusamo but HITONEN & POIJÄRVI (1955) reported it from all Finnish provinces except Lapponia inarensis. TUOMIKOSKI (1958) pointed out that there is an isolated station on the fjeld Ounastunturi in Enontekiö Lapland, where it was first reported by MONTELL (1921).

KUJALA (1964, p. 29 and Map 17) gave the best description of the distribution of *D. spinulosa* in Finland, although the material at his disposal was not fully reliable in detail. According to him a front of abundant occurrence reaches the line Raahe—Kuhmo, with a northward extension along the hill

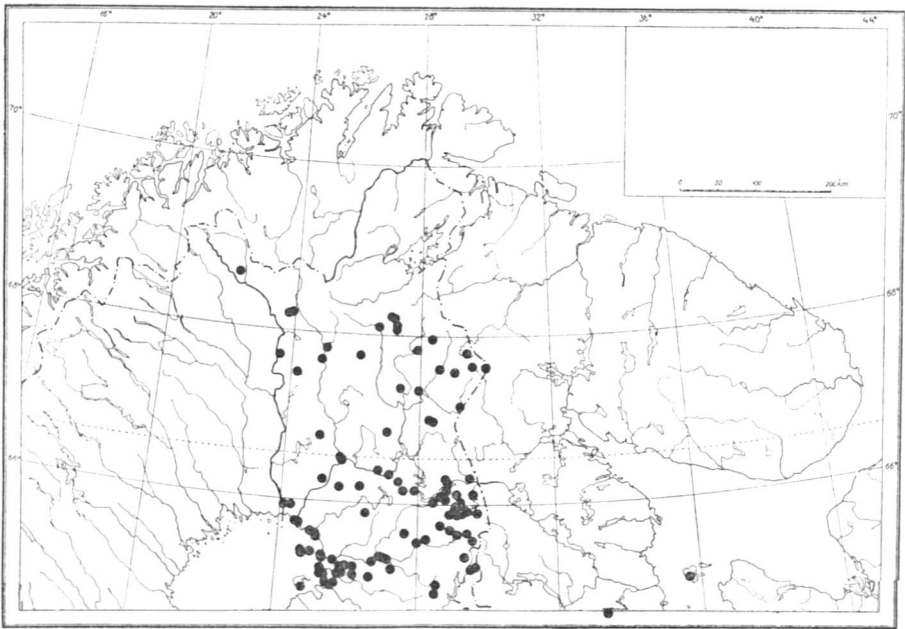


FIG. 3. Distribution of *Dryopteris spinulosa* in northern Finland (north of 65°N) and adjacent U.S.S.R.

range north of the lake Oulujärvi (op. c., Map 17), while more or less continuous distribution seems to cease only at the line Ylitornio—Kemijärvi—Suomussalmi, although a few localities were recorded north of it, up to Enontekiö.

From a revision of herbarium specimens supplemented by field notes made over a period of several years by one of us (T. Ahti), by Mr. Tauno Ulvinen, and Mr. Tapio Rintanen it has become clear that *D. spinulosa* is widespread in northern Finland. On the coast of the Gulf of Bothnia it seems to be quite common, though somewhat less frequent than further south, but through

most of the area it is only scattered. In Lapland proper it is very rare, however, and perhaps in most of North Finland it is less frequent than *D. as-similis*.

Fig. 3 and the following list of localities in North Finland — approximately north of lat. 65° N. — are mainly based on herbarium specimens or sight records. Some recent literature records were included, but e.g. those marked on KUJALA'S (1964) map have not been taken into account. Abbreviations of collectors' names: P.J. = Paavo S. Jokela, T.A. = Teuvo Ahti, T.R. = Tapio Rintanen, T.U. = Tauno Ulvinen. In cases of sight records no herbarium symbols are given.

Ostrobottnia kajanensis. Puolanka: Suolijärvi, Siikavaara, Nuottivaara, 1953 P. Havas (OULU). Pyssykulju, 1952 P. Havas (H). Äylönvaara, 1952 P. Havas (H). — Suomussalmi: Piispajärvi, Moilala, 1937 O. Kyyhkyinen (H). Murtovaara, 1955 L. Heikkinen (H). Juntusranta, 1963 L. Heikkinen (OULU).

Ostrobottnia borealis. Alatornio: Liakka, Petäjämäa, 1956 M. J. Kotilainen (H). Yli-vojjakkala, 1963 Teija Pelttari (OULU). — Hailuoto: Syökari, 1952 V. Törnroos (OULU). Scattered (LUTHER 1948). — Haukipudas: Kello, 1930 O. Seppänen (OULU); Nurmeslehto, 1962 T.U. Häyryseniemi, Villenniemi, 1962 T.U. Niemeläntörmä, 1957 P.J. (OULU), 1960 T.U. (OULU). Virpiniemi, 1961 T.R. — Ii: 1933 A. Ahmavaara (OULU). Alaranta, Pirttikari, 1954 Maiju Malvari (OULU, TUR). Asemakylä, 1954 Maiju Malvari (OULU, TUR). Maakrunni, 1947 Terttu Vartiainen (OULU). Ulkokrunni, 1962 R. Väisänen (OULU); fairly common on this island according to ROIVAINEN (1954). Pohjankari, 1957 Terttu Vartiainen (OULU). — Kemi: 1915 A. Rantaniemi (OULU). Saarenkrunni, 1864 M. Brenner (H; LINDBERG 1917). — Kiiminki: Kiiminki, 1958 P.J. (OULU). Kotajärvi, 1965 P.J. (OULU). Hannusperä, Rukavaara, 1966 T.U. Vasikkasuo, on Kuusamo highway 24 km from Oulu, 1963 T.U. — Kemijärvi: Javarus, between Karhupalo and Jäkälätunturi, 1966 T.R.; west of Karhupalo, 1966 T.R.; between Varsatunturi and Varsanhäntä, 1966 T.R. — Oulu: leg. W. Nylander (H), 1911 Y. Hellman (OULU). Hietasaari, 1929 Vappu and Anna-Liisa Niinimäki (OULU). Karjasilta, 1950 T. Mankila (OULU). Oulujoki, 1936 Vappu Niinimäki (H). On the river Oulujoki, 1899, I. Leiviskä (H). Oulujoki church, 1963 T.U. Myllyoja, 1961 T.R. 1963 T.U. Niilesjärvi, Sarvikangas, 1963 T.U. Sanginjoki, Isonsuonräme, 1961 T.R. — Pudasjärvi: Kollaja, Naisjärvi, Peukalo, 1963 P.J. (OULU). Hetekylä, Viinivaara road, Jyrkänalanne, 1963 P.J. (OULU). Hilturanta, 1957 Liisa Hiltula (OULU). Kurenalus, 1965 T.A. On the river Iijoki 6 km E of Kurenalus, 1963 T.U. Jonku, SW end of Jongunjärvi, 1963 T.U. Naamanka, W slope of Iso-Syöte, 1963 T.U. (OULU). — Ranua: Ranua church, 1959 T.A. 1480 (H). Ylimaa, Saukkojärvi, Raappana, 1955 and 1964 T.A. — Rovaniemi rural parish: Pisavaara, near Pitkäraeme, 1946 L. Teivainen (HFR); Isolomanoja—Linnunoja, 1956 L. TEIVAINEN (HFR); according to TEIVAINEN (1949) fairly common in Pisa Nature Park. Viirinkylä, Kaihuanvaara, 1956 V. Kujala (HFR). Sonka, Typpyrännummi, 1955 M. J. Kotilainen (H). Autti, by mouth of Pirttijoki, 1959 P. Havas (OULU). — Rovaniemi town: Korkalovaara, dumping place, 1954 T.A. Pappilan metsä, 1962 K. Uino (OULU). — Simo: Kumurainen, 1921 Laina Kivekäs (TUR). Onkalo, Simojokisuu, 1962 T.U. Simo church, Pappila, 1962 T.U. — Tervola: Vähäjoki, Lintupirtti, 1950 V. Kujala (HFR). — Yli-Ii: Jakkukylä, Ritola, 1965 P.J. (OULU). — Ylikiiminki: Somero-vaara road, 1963 P.J. (OULU). Joloskylä, Ylä-Jolosjärvi, 1963 P.J. (OULU).

Kuusamo. Kuusamo: Kuusamo church, Kitronin puisto (Pappilan vesakko), 1951 Raija-Leena Hämet (OULU); from the same place reported by TUOMIKOSKI (1951); Säynäjäperä, Toranginaho, Kuusela, Nilonkangas, and Petäjälampi, several localities, 1962 —66 T.A. 11283, 11284, 11285 (H) and sight records. Irni, Heikkiseniva, 1966 T.A. Kero, Karvonen, 1966 T.A. Kurvisenvaara, 1966 T.A. Murtovaara, 1957 Y. Vasari (H), 1966 T.A. Penttilänvaara, 1966 T.A. Kuoliovaara, 1966 T.A. Oijusluoma road, 1966 T.A. Vantaja, SW of Sänkikangas and Kaihlaniemi, 1966 T.A. Kantoniemi, 1966 T.A. Koskenkylä, Koski, 1966 T.A. & Leena Hämet-Ahti 22203 (H), Lehto and Jämsä, 1966 T.A. Jyrkänkoski, 1966 T.A. Haataja, Soidinkumpu, 1964 T.A. Vasaraperä, Puromäki, 1964

T.A. Rukatunturi, Talvijärvi, 1963 Leena Hämet-Ahti (H); Yli-Pessarini lampi, 1963 Marjatta Kainuhaarju (OULU). Alakitka, several localities on highway between Kilkilön-salmi and Patoniemi, 1964—66 T.A. East shore of Ylikitka, between Keräsniemi and Taivallahti, 1963 T.U. Käylä (KOTILAINEN 1951, p. 90; not mapped). Liikasenvaara, Oulankajoki, E side of Peuraperänvaara, 1957 Y. Vasari (H). — Posio: Akanlahti, Livo log-floating flume, 1966 T.A. Ahola, as an ornamental plant in a home garden, 1966 T.A. (not mapped). Peräposio, several localities, 1954, 1955, 1964 T.A. On highway 13 km from Pernu towards Rovaniemi, 1964 T.A. Korouoma, below Alaköngäs on Kurttajoki, 1964 T.U. — Salla: Ahvenselkä, on highway by the bridge over Koutelajoki, 1961 T.R. (H). Ahvenvittikko, Tapuliselkä, 1965 T.R. (H). Naruska, Siekaköngäs, 1961 T.R. (H, OULU). Ylä-Tuntsa, on the river Peurahaara 1.5 km above the Peurahaara camp, 1961 T.R. (H, OULU); on Peurahaara on N side of Peuratunturi, 1961 T.R. (H). Värriötunturi, 1957 P. Kallio (TUR). — Taivalkoski: between Taivalkoski and Sorsavaara, Sorsaoja, 1955 Y. Vasari (H). Parish centre, 1962 T.A. 11114 (H); highway bridge over Kostonjoki, 1963 T.A. Jurmu, by bridge over Iijoki, 1966 T.U.

Laponia kemensis. Kittilä: Sirkka, on the river Loukinen 3.5 km from Äijänoja towards Sotkajoki, 1961 K. Laaksonen (H). Kittilä church, 2 km W of Riikonoja, 1960 Eija Välitalo (OULU). Between Kaukonen and Alakylä, 1967 K. Alho & U. Laine (TUR; not mapped). — Kolari: Taapajärvi, 1967 K. Alho & U. Laine (TUR; not mapped). Ylläs-järvi, on the creek Sulaoja, 1964 T.U. (H, OULU). — Muonio: Eskelinen, 1922 J. Montell (TURA); MONTELL 1945. — Pelkosenniemi: Hietajoki, near Lavamännikkö, 1966 T.R. — Savukoski: Ylikemi, Leukkuhamara, on the creek Vahtioja, 1961 T.U. (H, OULU, TUR). Nuortijoki region, Ainijärvi, 1961 T.U. (H, OULU). Between Kivitunturi and Vasatunturi, 1962 T.R. (OULU). Värriöjoki, near mouth of the tributary Puukkohaara, 1966 T.R. — Sodankylä: Korvanen, the river Parakainen, by Aulekkuetuore, 1958 T.U. Mutenia, Sompiojärvi, Kotaoja, 1958 T.U.; on Mutenianjoki 1959 T.U. (H), T.U. & J. Poijärvi (H). Lokka, W side of Vuoltistunturi, 1959 K. Laaksonen (H). Ylikitinen, on the river Kitinen 2 km NW of Rovaniemi, 1959 R. Ruuhijärvi (H), S. Eurola (H). Pomokaira, Hirvilauttanen, 1963 T.R. & S. Vuokko (H). Vuotso N, Tankavaara, E end of the Varpupää road, 1959 T.R. (H), Vuomaselkä, near the Inari boundary on highway, 1965 T.R. (H).

Laponia enontekiensis. Enontekiö: Pallas—Ounastunturi National Park, Ounastunturi, 'regio subalpina', 1917 J. Montell (TURA), 'in palude alpino ad Pahakuru', 1917 J. Montell (H, TURA; MONTELL 1921); SE of Ruototunturi, 1953 S. Eurola (HFR). North of Kelottijärvi, Saitsijoki, Saitsikursu, 400 m s.m., 1948 H. Roivainen (H).

The distribution of *D. spinulosa* also seems to be poorly known in northern Sweden. In the eastern part of that area it has been collected near the coast as far as the end of the Gulf of Bothnia (e.g. HULTÉN 1958, Map 155; JULIN & PEKKARI 1960) but in the west the northernmost certain locality appears to be at Arvidsjaur, Pite Lappmark (cf. WISTRAND 1962; HYLANDER 1965, p. 397). The earlier record for Lule Lappmark (SELANDER 1950, p. 28; HYLANDER 1953) is incorrect (HYLANDER 1965, p. 397; NANNFELDT 1966, p. 137). Oddly enough, it is not known from North Norway at all.

POYARKOVA (1953, Karta 5) reported *D. spinulosa* from a number of localities throughout the Kola Peninsula. According to TIKHOMIROV (1959, p. 599) it has been found, though rarely, even in a few places in the arctic between Kanin Peninsula and the Ural Mts. The reported distribution on the Kola Peninsula, in particular, looks strange in the light of the data from Finland and Scandinavia. HULTÉN (1958, p. 174) suspected that the majority of POYARKOVA's records were based on *D. dilatata* s. lat. This suspicion is supported by the fact that she reported the hybrid '*D. austriaca* × *spinulosa*' to be fairly common in Kola (11 dots on the map), which is very unlikely in

our opinion. In addition, even the illustration of *D. spinulosa*, particularly its rhizome, in her treatment (POYARKOVA 1953, p. 35, Tabl. V) looks very much like *D. assimilis*. In H there are no specimens of *D. spinulosa* from the Murmansk District and the northernmost specimens from N.W. Russia are from Solovetzk Is. and Ushkova (Uskela); see our Fig. 3.

Ecology

D. spinulosa has a wide ecological range, but it is particularly characteristic of moist to wet forests. However, unlike *D. assimilis*, it is able to grow in fairly dry and open habitats as well, but it avoids highly calcareous places (e.g. TUOMIKOSKI 1958).

In northern Finland the species is conspicuously hemerophilous. This was already noted by TUOMIKOSKI (1951), who regarded it as questionable whether it was quite indigenous in a locality at Kuusamo, where he found it as new to the province. MONTELL (1945) also considered the species to be adventive at the only locality where the species has been recorded in Muonio, Kemi Lapland. From the observations of one of us (T. Ahti) it is quite clear that it is effectively being spread by human activities, particularly along highways, in northern Finland, although a great number of undoubtedly native occurrences are also known. It is noteworthy that the majority of the finds have been made during the last ten years. Several localities are represented by very small stands, even by single tufts, which are commonly on roadside ditches or at edges of fields and meadows. Whether this indicates a northward extension in connexion with the climatically favourable period in the 1920's and 1930's is questionable, because the species has certainly been much overlooked by earlier collectors, and road construction and traffic have increased greatly during the last two decades. However, ERKAMO (1956, p. 181–83) regarded it as possible that the pteridophytes *Thelypteris palustris* (*Lastrea thelypteris*) and *Lycopodium inundatum*, spread northwards considerably during the warmer period. When a locality on the highway by Raappana farm at Ranua, where *D. spinulosa* was growing very sparsely in 1955, was revisited by one of us (T. Ahti) in 1964 it was found that the stand had become much enlarged in the course of nine years. This observation supports the idea that a recent extension of range in northern Finland has taken place, for some reason or another. On the other hand, the specimen from Ounastunturi was collected 1917, and in general the native occurrences seem to be quite old.

Hybrids

The following hybrids between *D. dilatata*, *D. assimilis* and *D. spinulosa* are known: *D. dilatata* × *spinulosa*, tetraploid (MANTON 1950), *D. assimilis* ×

dilatata, triploid (DÖPP & GÄTZI 1964), and *D. assimilis* × *spinulosa*, triploid (WALKER 1955). The last one has not been reported from nature but was produced synthetically.

The present authors have examined numerous mixed stands of the above mentioned species in Finland in order to find hybrids, with some success, as described below.

Dryopteris dilatata × *spinulosa*

A close examination of a mixed stand of *D. dilatata* and *D. spinulosa* at Gullö, Ekenäs (prov. Nylandia), made in 1966, revealed two morphologically intermediate tufts. They proved to have aborted spores and sporangia (WIDÉN & V. SORSA 1966). These putative hybrids resemble *D. dilatata* but differ in having lighter green leaves and flat leaf segments (Plate 4). In addition, there are only few glandular hairs (70–100 μ long) on the lower sides of the blades. The petioles are thinner and less scaly than in *D. dilatata*. The scales, which possess the dark central stripe of *D. dilatata*, decrease strongly in number and size towards the upper parts of the petioles. The scales are generally 8–11 mm long and 2–3 mm wide and fringed with some stalked glands, which are ca. 40 μ long (smaller than in typical *D. dilatata*). The indusia are densely fringed with 60–80 μ long glandular hairs as in *D. dilatata*. The rhizome is semierect, and densely covered with dark scales.

In chromatograms made from the plants characteristic chemical components of both *D. dilatata* and *D. spinulosa* were discovered, which strongly supports their hybrid origin, although this has not yet been proved cytologically (WIDÉN & V. SORSA 1966).

Dryopteris assimilis × *dilatata*

In the same stand at Gullö where the hybrid *D. dilatata* × *spinulosa* was found there were some tufts (perhaps one clone) that appeared to be intermediate between *D. dilatata* and *D. assimilis*. Their spores were poorly developed in otherwise normal sori, and the sporangia contained a brown powdery mass, which according to DÖPP & GÄTZI (1964, p. 46) and WAGNER & CHEN (1965) is a good indication of hybrid origin. The plants were conspicuously large and stout, which is also characteristic of hybrids (MANTON 1950). In 1967 single tufts of the other parent, *D. assimilis*, were recognized in the same stand.

The specimens in question differ from *D. dilatata* in having lighter green leaves, only slightly convex leaf segments and a basal lower pinnule in the lowermost pinna, which is long compared with the other pinnules (Plate 4). The length of this pinnule was about 42 per cent of that of the whole pinna. The blades of all the intermediate leaves were densely covered with glandular hairs 80–100 μ long, particularly on the lower side. However, according to DÖPP & GÄTZI (1964), who studied cytologically controlled material, the present hybrid is less glandular than the parents but also their material was small. The petioles are particularly densely covered with both scales and glands in our specimens.

As was expected, the majority of the scales have a wide dark central stripe. In some of them the stripe does not extend into the upper half, as is often the case in *D. assimilis*. The scales (Plate 5) are 19–20 mm long and 3–6 mm wide and rather densely fringed with 50–60 μ long glandular hairs. Thus the size of the larger ones approaches *D. dilatata*. This is also true of the indusia, which are fringed with glandular hairs 80–90 μ in length. The rhizome is erect, stout and densely covered with dark scales.

A chromatogram of this supposed hybrid resembled that of typical *D. dilatata*, although distinct quantitative deviations in some phloroglucinol derivatives were observed. The cytological and chromatographical data will be published by V. SORSA & C.-J. WIDÉN (1968).

Dryopteris assimilis × *spinulosa*

In a mixed stand of *D. assimilis* and *D. spinulosa* one of us (J. Sarvela) found a clone (5 to 6 tufts within less than one sq.m) of strongly intermediate specimens with abortive spores (Nylandia. Espoo: Luukki, NE of lake Väärälampi, 1966 J. Sarvela no. 19; H). The contents of the sporangia formed an amorphous mass.

The blades of the specimens are bipinnatifid to tripinnate as in *D. spinulosa* (Plate 4). Only the lowest pinnules are clearly pinnate while the rest are only more or less pinnatifid. The lowest pinnae are comparatively short and distinctly triangular in shape with fairly long basal lower pinnules (their length about 45 per cent of that of the whole pinna). The blades are densely glandular particularly on the lower side as in *D. assimilis*. The glands are very long, 100–130 μ on an average. The rhachis is also beset with glands, in addition to blades. The basal pinnae are without sori. The leaves do not overwinter.

The scales (about 8–11 × 5–6 mm) are much like those of *D. spinulosa* in shape being thin, broad, mucronate and light brown (Plate 6). However, a relationship with *D. assimilis* is indicated by a narrow dark central stripe, which is clearly distinct only in the scales at the extreme base. There are no glands on the scales, but the indusia are sparsely fringed with glandular hairs 80 μ long. The rhizome grows almost horizontally as in *D. spinulosa* but is densely covered with dark scales as in *D. assimilis*.

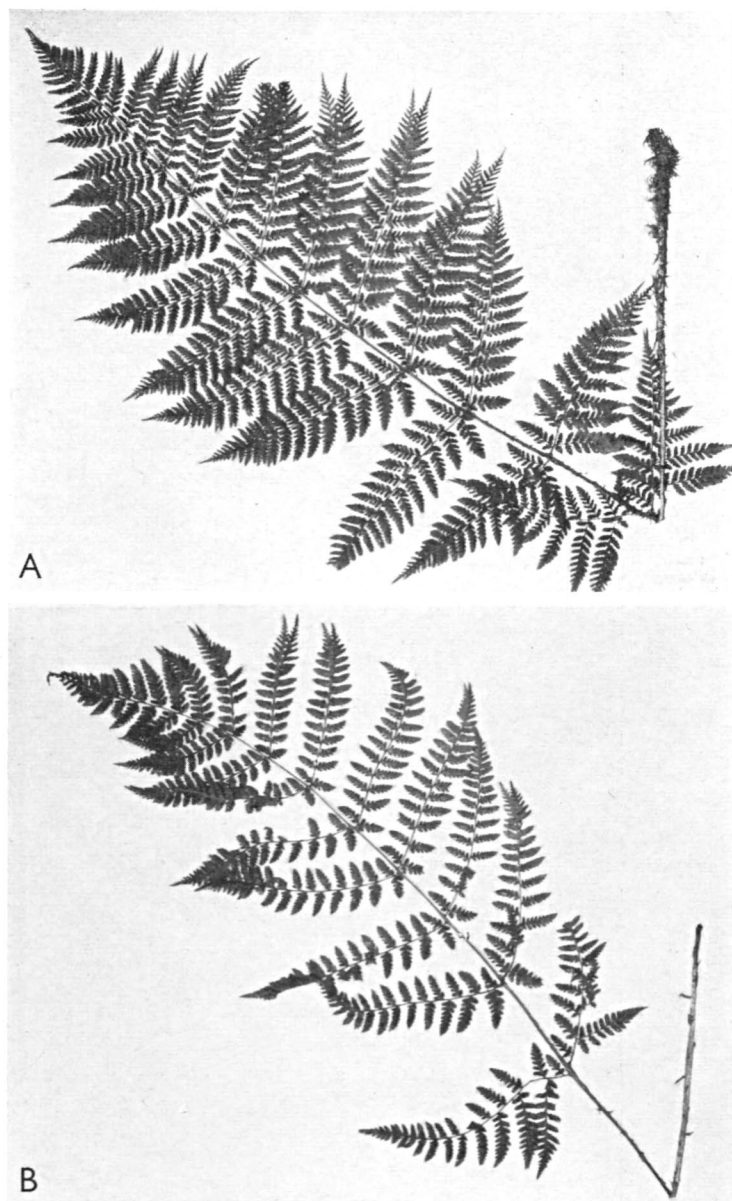
A chromatogram of the phloroglucinol derivatives run from the present material showed a great similarity to *D. spinulosa*. The cytological and chromatographical data will be published by V. SORSA & C.-J. WIDÉN (1968).

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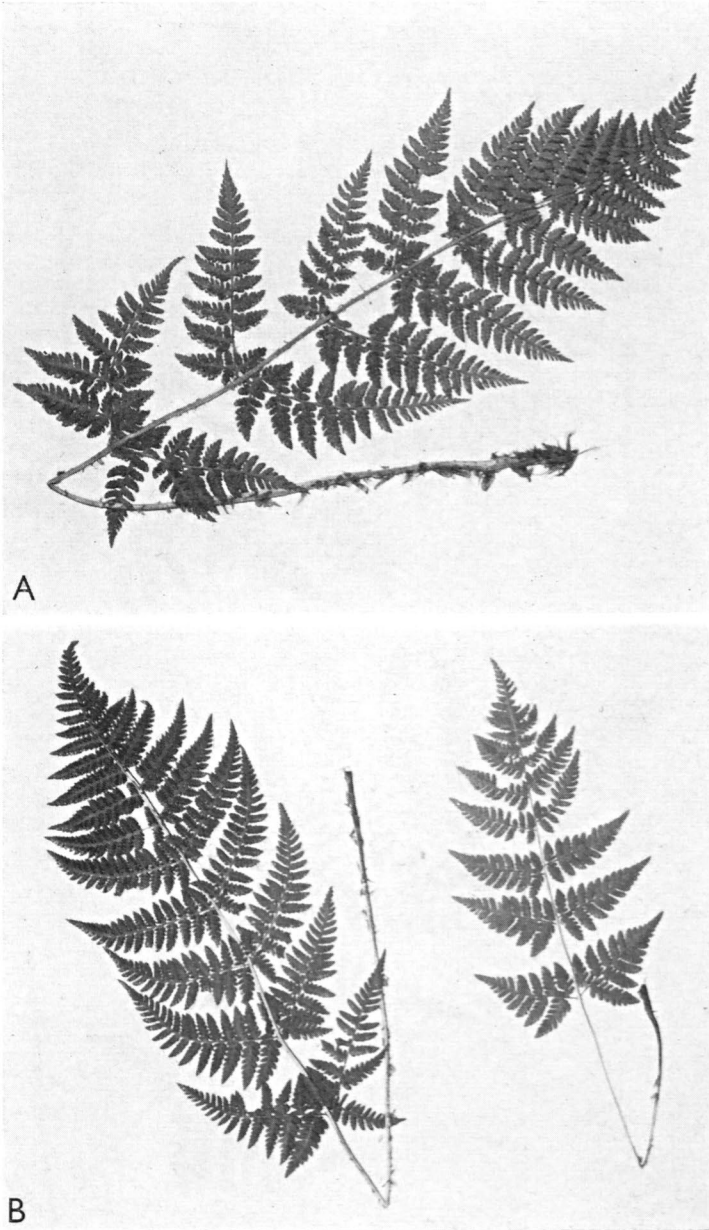
Dryopteris assimilis.

A. Borgå parish, Hasselö, 18.IX.1966, C.-J. Widén (H).

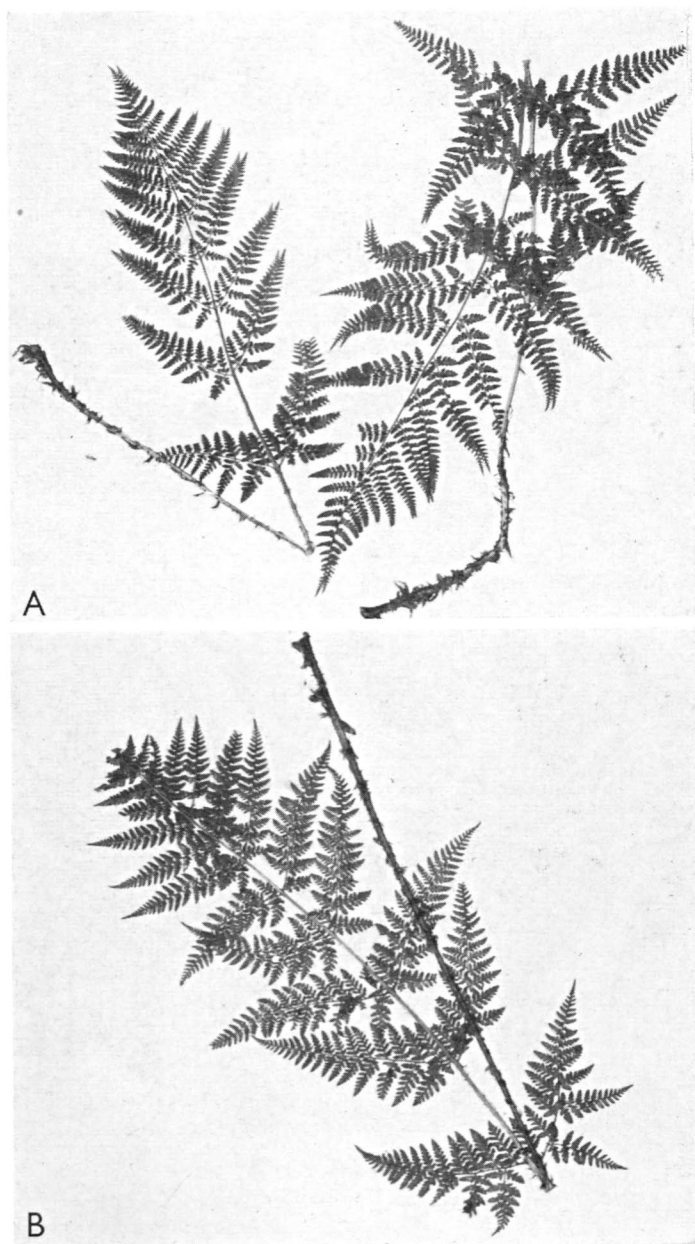
B. Parikkala, Surumäki, 9.IX.1966, C.-J. Widén (H).

$\frac{1}{5}$ of natural size (photo V. Sorsa).

PLATE 2

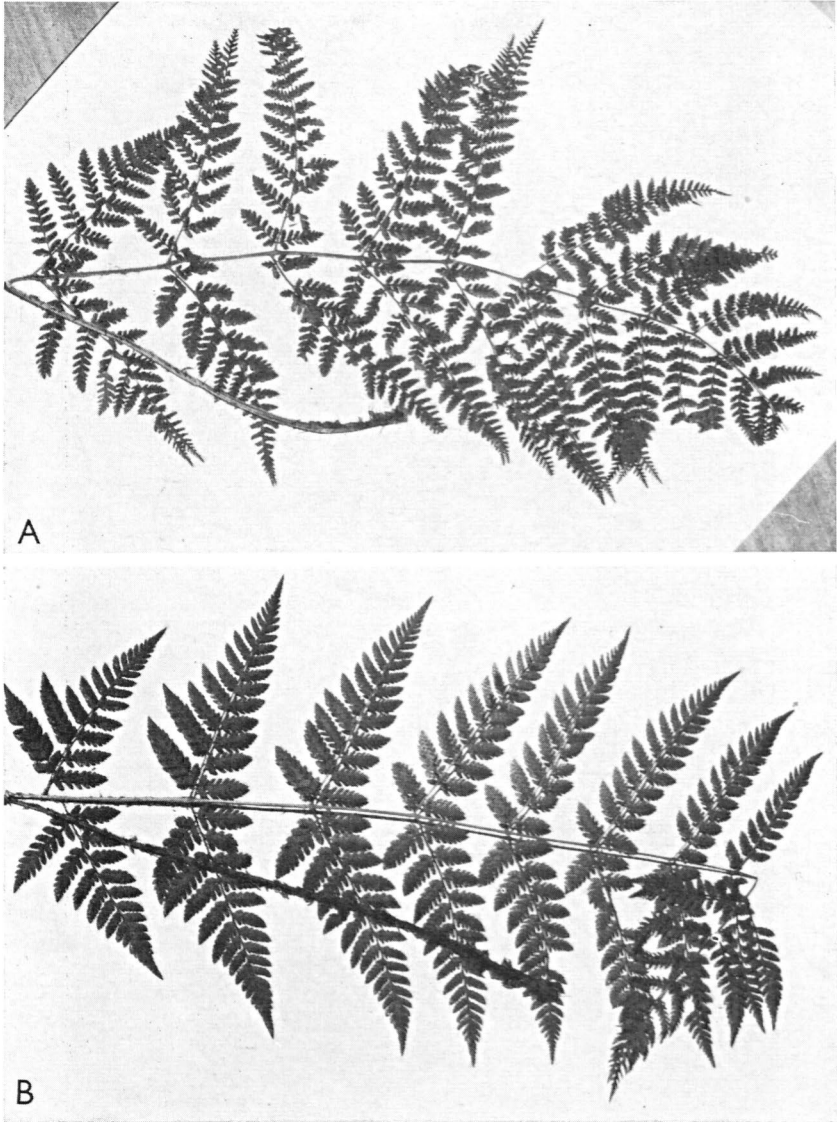


A. *Dryopteris assimilis* ('var. *pseudospinulosa*'), Enontekiö, Malla, 7.VIII.1966, K.-G. Widén (H).
B. *Dryopteris spinulosa*, Pernå, Kabböle, 15.VIII.1965, C.-J. Widén (H).
 $\frac{1}{4}$ of natural size (photo V. Sorsa).

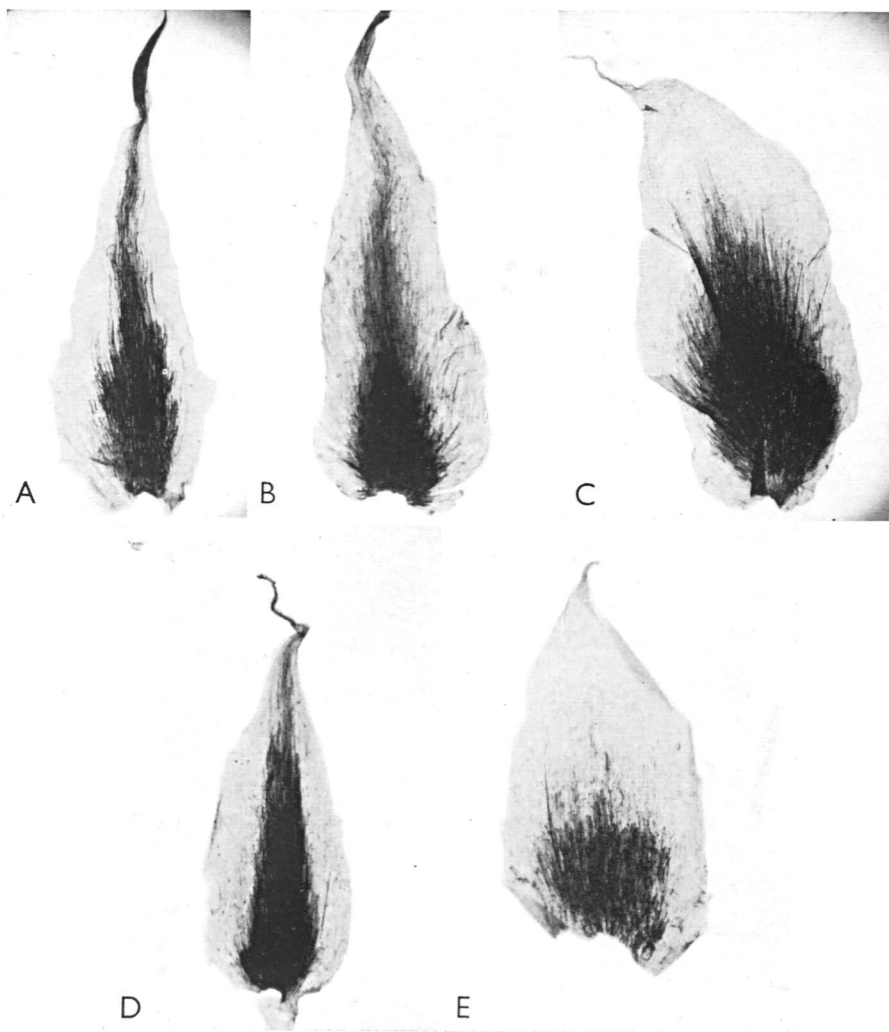


A. *Dryopteris dilatata*, Ekenäs parish, Gullö, 15.VII.1966, C.-J. Widén & V. Sorsa (H).
B. *Dryopteris assimilis* × *dilatata*, as above.
 $\frac{1}{5}$ of natural size (photo V. Sorsa).

PLATE 4



- A. *Dryopteris dilatata* × *spinulosa*, Ekenäs parish, Gullö, 15.VII.1966, C.-J. Widén & V. Sorsa (H).
B. *Dryopteris assimilis* × *spinulosa*, Espoo, Luukki, 10.IX.1966, J. Sarvela no. 19 (H).
 $\frac{1}{3}$ of natural size (photo V. Sorsa).



Basal scales on petioles of *Dryopteris*.

A. *D. dilatata*, Ekenäs parish, Gullö, 15.VII.1966, C.-J. Widén & V. Sorsa (3.7 x).

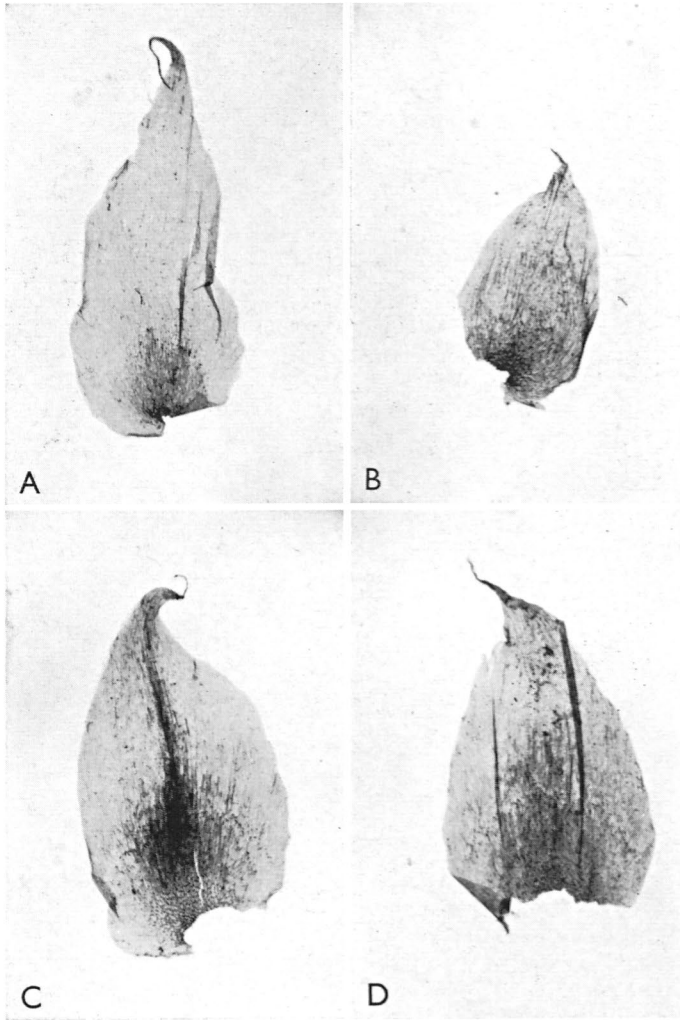
B. As above (4.6 x).

C. *D. assimilis* × *dilatata*, as above (4.0 x).

D. *D. assimilis*, Borgå parish, Hasselö, 5.IX.1965, C.-J. Widén (5.0 x).

E. As above.

PLATE 6



Basal scales on petioles of *Dryopteris*.

A. *D. assimilis*, Parikkala, Surumäki, 9.IX.1966, C.-J. Widén, (5.2 x).

B. *D. spinulosa*, Pernä, Kabböle, 15. VIII. 1965, C.-J. Widén (4.7 x).

C. *D. assimilis* × *spinulosa*, Espoo, Luukki, 10.IX.1966, J. Sarvela (5.0 x).

D. As above (4.8 x).

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