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A survey of phenolic compounds in *Dryopteris* and related fern genera. Part III

Phloroglucinol derivatives in subgenera *Erythrovaria* and *Nephrocystis* and related genera (Pteridophyta, Dryopteridaceae)

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The phloroglucinol derivatives of 26 species of *Dryopteris* belonging to the subgenera *Erythrovaria* and *Nephrocystis* are listed and the taxonomy is discussed based on both chemistry and morphology. The ferns of section *Erythrovariae* in general contain aspidin (*6*) in their rhizomes and petiolar bases, whereas those of section *Variae* have margaspidin (*13*) (subgenus *Erythrovaria*). The ferns of sections *Purpurascentes* and *Diclisodon* usually contain only minute amounts of phloroglucinols or are totally lacking these phenolics. Consequently no characteristic compounds appear to occur in subgenus *Nephrocystis*. In addition, 102 species (including varieties) belonging to various genera of the Dryopteridaceae, including subfamilies Dryopteridoideae, Polystichoideae, Peranematoideae and Tectarioideae as well as to the families Davalliaceae and Oleandraceae have been investigated for the occurrence of phloroglucinols and glands. *Dryopsis apiciflora*, *D. clarkei* and *D. nidus* differed from all other taxa in containing great percentages of ether extract (oleo-resin) and phloroglucinols (crude filicin) as well as internal secreting glands in their rhizomes and stipe bases (subfamily Dryopteridoideae). Of the other genera, *Peranema*, *Diacalpe*, *Rumohra*, *Stigmatopteris*, *Arachnioides* and *Polybotrya* usually contained small but clearly detectable amounts of phloroglucinols, whereas in *Nothoperanema* only traces or total lack of these com-

pounds were recorded. The species investigated of *Polystichum* proved to be totally devoid of phloroglucinols with the exception of *P. tsus-simense* and *P. rigens* (subfamilies Dryopteridoideae, Peranematoideae and Polystichoideae). Of the genera *Ctenitis* and *Lastreopsis* (subfamily Tectaroideae), only few species contained trace amounts of phloroglucinols, the great majority were totally lacking these compounds. Also in *Pleiocnemia* some unknown phenolics were observed. In the other tectaroid genera no clear indications of phloroglucinols were found. The same was true of the genus *Davallia* (Davalliaceae) and the genus *Arthropteris* (Oleandraceae). All phloroglucinol containing species contained secretory structures in parenchyma of their rhizomes and stipes or on the epidermis of these organs.

Key words: *Dryopteris*, phloroglucinols, subg. *Erythrovaria*, *Nephrocystis*, Pteridophyta, taxonomy

Introduction

The species of *Dryopteris* and several related genera of the Dryopteridaceae contain in their rhizomes and petiolar bases phloroglucinol derivatives or acylphloroglucinols (cf. Widén *et al*. 1991, 1996, 1997, 1999 and refs. therein). These are located in typical internal secreting glands in the parenchyma and/or in external glands on the epidermis (cf. Widén *et al*. 1976, 1978, 1981, 1983, Gibby *et al*. 1992).

According to Fraser-Jenkins (1986) and Widén *et al*. (1999) the genus *Dryopteris* is divided into three subgenera: *Dryopteris*, *Erythrovaria* (H. Itô) Fraser-Jenk., and *Nephrocystis* (H. Itô) Fras.-Jenk. each of which is subdivided into several sections. In Widén *et al*. 1996 and 1999, the phloroglucinol patterns of subgenus *Dryopteris* except for section *Marginatae* Fras.-Jenk. have been reported. The phenolics of several taxa of subgenus *Erythrovaria* (H. Itô) Fras.-Jenk. and *Nephrocystis* (H. Itô) Fras.-Jenk. were also preliminarily investigated by Hisada (1961, 1966), Hisada and Noro (1961), Hisada *et al*. (1971, 1974), and Widén *et al*. (1973, 1975, 1993) but no comprehensive survey has yet been published.

Phloroglucinol derivatives have been recorded also in several taxa of genera outside *Dryopteris*, which are related to subgenus *Erythrovaria* and especially to subgenus *Nephrocystis*. These consist of 24 species and 19 hybrids of *Arachniodes*, two species of *Polystichum*, four species of *Ctenitis*, *Acrophorus nodosus* C. Presl, *Pleocnemia conjugata* (Blume) C. Presl, *P. irregularis* (C. Presl) Holttum and *Polybotria caudata* Kunze (Widén *et al.* 1976, 1978, 1981, 1983 and refs. therein). These investigations led us to study additional material/species of *Arachniodes*, *Polystichum*, *Ctenitis* and *Acrophorus* and several species of the other more or less related genera. The main part of the material investigated is collected by Christopher R. Fraser-Jenkins from different parts of the world, but herbarium vouchers were also studied.

Synopsis

Dryopteris subgenus *Erythrovaria* (H. Itô) Fras.-Jenk.

Dryopteris subgenus *Erythrovaria* consists of ca. 36 species mainly distributed in E Asia, the main centre of distribution being in Japan and E China including Taiwan, extending to W China, Korea, SE Asia and NE India. Most of the species are apomictic (Hirabayashi 1974, Fraser-Jenkins 1986).

The fronds are similar to those of the ferns of subgenus *Dryopteris* in being once to nearly four times pinnate. However, the petiolar-bases usually bear a tuft of stiff narrow scales and the rest of the petiole is nearly devoid of scales. Subgenus *Erythrovaria* is distinct from subgenus *Dryopteris* in that almost all of its species have small bullate or bullate based scales on the underside of the pinnae or on the upper rachis.

Subgenus *Erythrovaria* shows many mor-

phological similarities with the other subgenera of *Dryopteris*, and also, though less obviuosly to *Nothoperanema*, *Ctenitis* and *Arachniodes*. It may be the most primitive subgenus in *Dryopteris* (Fraser-Jenkins 1986), though it happens to have undergone a recent bust of speciation.

Fraser-Jenkins (1986) has divided subgenus *Erythrovaria* into three sections: *Erythrovariae*, *Politae* and *Variae*.

Section *Erythrovariae*

Fronds with herbaceous or coriaceous lamina. Pinnules without caudate apices and lobes normally rounded (not pointed). Petiolar scales wide or narrow; costae and costules with bullate scales below. Contains ca. 25 species (Fraser-Jenkins 1986) of which those investigated for their phenolics are listed in Table 1.

Section *Politae* Fras.-Jenk.

This section contains a single, diploid sexual species, *Dryopteris polita* Rosenstock (Hirabayashi 1974) of rather uncertain affinity within the genus. It is distributed in S Japan, Indo-China, Thailand, Malay Peninsula, Sumatra, Borneo, Mindanao and Papua New Guinea (Kuo 1985). Section *Politae* differs from section *Erythrovariae* in being completely glabrous and lacking scales, except for a tuft of narrow ones at the very base of the petiole. According to Hisada and Noro (1961) and Hisada (1966) *D. polita* completely lacks phloroglucinols. This section is morphologically intermediate between subgenera *Erythrovaria* and *Nephrocystis*, but apart from the scales its morphology is closer to *Erythrovaria* than to *Nephrocystis* (*see* Fraser-Jenkins 1986).

Section *Variae* Fras.-Jenk.

The species of section *Variae* differ from those of section *Erythrovariae* in having a stiffly coriaceous lamina and the pinnules with caudate apices and pointed lobes. Stipe scales narrow and the costae and costulae with slightly bullate-based scales in contrast to the more bullate scaled species of section *Erythrovariae*. This section contains ca. 10 species of which those investigated for their phloroglucinols are listed in Table 2.

Table 1. Cytology and distribution of the investigated species of *Dryopteris* section *Erythrovariae*.

Species	Cytology[1)]	Distribution	Reference
D. decipiens (Hook.) O. Kuntze	3x, a	S Japan, China	Hirabayashi (1974)
D. fuscipes C. Chr.	3x, a	S Japan, Taiwan, China	Hirabayashi (1974)
D. championii (Benth.) C. Chr.	3x, a 2x, a	S Japan, S Korea, China SW China	Hirabayashi (1974), Gibby (1985)
D. kinkiensis Koidz. ex Tagawa	4x, s	S Japan, S Korea, Cheju-Po	Hirabayashi (1974)
D. erythrosora (D. C. Eaton) O. Kuntze	3x, a	S Japan	Hirabayashi (1974)
D. hondoensis Koidz.	3x, a	Central and S Japan	Hirabayashi (1974)
D. cystolepidota (Miq.) Mak. (= *D. nipponensis* Koidz.)	3x, a	Central and S Japan	Hirabayashi (1974)
D. tenuicula C. G. Matthew & Christ (= *D. indusiata* Mak. & Yamam)	3x, a	S Japan	Hirabayashi (1974)
D. subtriangularis (C. Hope) C. Chr.	3x, a	India, Burma = Mayanmar, China, Taiwan, Thailand, N Vietnam, Philippines	Gibby (1985), Fraser-Jenkins (1989)
D. gymnosora (Makino) C. Chr.	3x	S Japan, S China	Hirabayashi (1974), Gibby (1985)
"*D. truncatulata* Ching ined" (= *D. subtriangularis* or near ?)	?	China	New data

[1)] 2x = diploid, 3x = triploid, 4x = tetraploid, a = apogamous, s = sexual.

Dryopteris subgenus *Nephrocystis* Fras.-Jenk.

The fronds are twice to four times pinnate and similar to those of subgenus *Dryopteris*, all are more or less wide at the base. The petioles are long and smooth and bears only a few scales, which are narrow to ovate and partly decidous unlike those in subgenus *Dryopteris*. The upper rachis and costae are glabrous or bear only a few small and narrow scales unlike the bullate scales in subgenus *Erythrovaria*. The pinnules at the base of the lamina are either catadromous as in subgenus *Dryopteris* or anadromous as in *Arachniodes*. The pinnules are always asymmetrical and sloping. The lamina is usually markedly smoother and more glabrous than in subgenus *Dryopteris*.

Several of the ferns of this subgenus have been considerably confused in their generic placement because the arrangements of the segments can be either anadromous or catadromous. Several species of obvious *Dryopteris* were mistakenly included in *Arachniodes* solely because of their anadromic pinnation, *see* Sledge (1973), Iwatsuki in Widén *et al*. (1976) and Fraser-Jenkins (1986). Subgenus *Nephrocystis* occurs in Africa, Asia, Australasia and Oceania apart from one species in Central America. Most of the species occur in SE Asia and Sri Lanka (Ceylon) (Fraser-Jenkins 1986). According to Fraser-Jenkins (1986) subgenus *Nephrocystis* is divided into two sections: *Purpurascentes* Fraser-Jenkins and *Diclisodon* (T. Moore) C. Chr. (= section *Nephrocystis* (H. Itô) Fras.-Jenk.)

Section *Purpurascentes* Fras.-Jenk.

Similar to section *Diclisodon* except that the fronds are very large, finely dissect, three or four times pinnate, and with small more or less remote ultimate segments. These are usually more or less pointed at their apices and auriculate at their acroscopic bases. The rhizome is often creeping as in many *Arachniodes* species or ascendent as in section *Diclisodon*. In contrast to section *Diclisodon* the petioles bear very narrow scales in a tuft near the base, and the frond usually bears very narrow scales in tufts underneath the junctions of the rachis, costae and costules.

Section *Purpurascentes* contains ca. 13 species, mainly occurring in SE Asia and the Australiasian and Pacific islands extending to Africa and tropical America (Fraser-Jenkins 1986). However *Dryopteris futura* A. Reid Smith has later been transferred to section *Aemulae* (Widén *et al*. 1999).

Only two species have been investigated for their phloroglucinols; the African diploid species *D. kilemensis* (Kuhn) O. Kuntze; and *D. pulvinulifera* (Bedd.) O. Kuntze, a diploid sexual fern

Table 2. Cytology and distribution of the investigated species of *Dryopteris* section *Variae*.

Species	Cytology[1)]	Distribution	Reference
D. saxifraga H. Itô	2x, s	Japan, Korea, N China	Hirabayashi (1974)
D. bissetiana (Baker) C. Chr.	3x, a	Japan, Korea, China..	Hirabayashi (1974)
D. varia (L.) O. Kuntze	2x, 3a	Japan, Korea, Ryukyus, S China, N and E India, Philippines	Hirabayashi (1974) Gibby (1985), Kuo (1985)
D. hikonensis (H. Itô) Nakaike (= *D. pacifica* (Nakai) Tagawa)[2)]	3x, a	Japan, Cheju-Po, Korea, China	Hirabayashi (1974)
D. sacrosancta Koidz.	3x, a	Japan, Cheju Po, Korea, China	Hirabayashi (1974)
D. sordidipes Tagawa	2x, s	S Japan, Ryukyus, Taiwan	Kuo (1985), Hirabayashi (1974)
D. formosana C. Chr.	3x, a	Japan, Taiwan, Philippines	Kuo (1985), Hirabayashi (1974)

[1)] 2x = diploid, 3x = triploid, a = apogamous, s = sexual.

growing in India, E Nepal, Sri Lanka, Bhutan?, and China (Yunnan) (Fraser-Jenkins 1989).

Section *Diclisodon* (T. Moore) C. Chr.

Fraser-Jenkins has recently found that the name section *Nephrocystis* is predated by section *Diclisodon*, *see* Christensen (1905). Rhizomes ascendent, petioles long with ovate-lanceolate scales, rachis and costae more or less glabrous. Fronds normally twice to rarely four times pinnate with small remote segments or large ones; segments normally rounded, asymmetrical.

This section contains a few catadromous species a majority matching subgenus *Erythrovaria* and to some extent coming close to section *Purpurascentes*. It also contains a majority of dissected anadromous species previously placed in the genus *Acrorumohra*. It is noteworthy that *Dryopteris undulata* (Bedd.) O. Kuntze has both kind of fronds. According to Fraser-Jenkins (1986, and present paper) section *Diclisodon* contains ca. 13 species confined to Asia and the Australasian and Pacific islands and Australia. Most species occur in SE Asia and Sri Lanka. The species studied for their phenolics are listed in Table 3.

In addition *Arachniodes maximowicsii* (Baker) Ohwi was placed by Serizawa (1974) in *Dryopteris* as also suggested by Widén *et al*. (1976) on chemical and morphological grounds. However, this was not followed by Fraser-Jenkins (1986) and in the present work it is excluded and is placed within *Arachniodes* on the basis of its segment shape.

In the following the genera related to *Dryopteris* are briefly discussed. According to Crabbe *et al*. (1975), based on Holttum (1947), they belong in two subfamilies: Dryopteridoideae Holttum and Tectarioideae Nayar. However Fraser-Jenkins (1997: 297) has separated two more subfamilies: Peranematoideae Fras.-Jenk. and Polystichoideae Fras.-Jenk.

Subfamily Dryopteridoideae Holttum

Midrib of ultimate leaflets grooved, the groove of the rachis bearing the leaflets being open to admit the leaflet-groove, the margin of the leaflet being decurrent (but not prominent) down

Table 3. Cytology and distribution of the investigated species of *Dryopteris* section *Diclisodon*.

Species	Cytology[1)]	Distribution	Reference
D. hasseltii (Blume) C. Chr.	?	S Japan, Ruykyus, S China (Hainan), Vietnam, N and E Himalaya, Malesia, Philippines, Sumatra, Java, New Guinea etc.	Fraser-Jenkins (1989), Kuo (1985)
D. sparsa (Buch.-Ham ex D. Don) Kuntze ("*D. sparsa* aggregate")	2x, s; 4x, s 3x, a	Tropical Asia, north to S China and S Japan	Kuo (1985), Fraser-Jenkins (1989) and present work, Hirabayashi (1974)
D. subexaltata (Christ) C. Chr. (= *D. hayatae* Tag.)	2x, s	S Japan, Taiwan, Ryukyus	Hirabayashi (1974), Kuo (1985)
D. sabae (Franch. & Savat.) C. Chr.	2x, s	Japan	Hirabayashi (1974)
D. macrochlamys (Fée) Fras.-Jenk. (= *D. obtusissima* (Mett. ex Kuhn.) Christ	2x, s	Sri Lanka	Fraser-Jenkins (1989)
D. undulata (Bedd.) O. Kuntze (= *D. sri-lankensis* Fras.-Jenk.)	?	Sri Lanka	Present work
D. diffracta (Baker) C. Chr.	4x	NE India, Mayanmar, SE Tibet, China, Taiwan, N Vietnam	Fraser-Jenkins (1989)

[1)] 2x = diploid, 3x = triploid, 4x = tetraploid, a = apogamous, s = sexual.

the side of the rachis; ctenitoid hairs lacking (Holttum 1986). The base chromosome number is 41 in all the studied species. Investigated genera are described below (*see* pp. 100–103 for *Dryopteris*).

Nothoperanema (Tagawa) Ching

This genus of ca. 5 species was first published by Tagawa (1938) as a subgenus of *Dryopteris* and later raised up to generic rank by Ching (1966) followed by Price (1977) and Fraser-Jenkins (1989, sub "excluded species"). *Nothoperanema* is closely related to *Dryopteris*. The species that we investigated are listed in Table 4.

Dryopsis Holttum & P. J. Edwards

This genus of 25 species was earlier included in *Ctenitis* of the Tectarioideae, but was described as a new genus by Holttum and Edwards (1986). According to these authors *Dryopsis* is more allied to *Nothoperanema*, *Stenolepia* and *Dryopteris* (subfamily Dryopteridoideae) than to *Ctenitis* (subfamily Tectarioideae). In *Dryopsis* the costae are shallowly grooved and the groove is closed at the base of a costa. In *Dryopteris* the upper surface of costae is hairless and deeply grooved, and at the base of a leaflet the groove of the major axis to which it is attached is open to receive the costal groove. Thus *Dryopsis* differs from *Dryopteris* in the form of the groove, the presence of peculiar hairs and "hair-scales" on its margin and the closure of the groove at the base of a leaflet. Both *Dryopteris* and *Dryopsis* differs from *Ctenitis* in their sulcate costae and in the absence of so-called ctenitoid hairs (Holttum & Edwards 1986). However, hair-scales like those in *Dryopsis* also occur in the margins of the upper surface of *Nothoperanema*, *Stenolepia* and *Peranema*. Thus *Dryopsis* has characters in common with *Nothoperanema* but differs in the closed bases of its costal grooves (Holttum & Edwards 1986). The basic chromosome numbers is 41 (Mehra & Mittal 1961).

The main distribution of the species of *Dryopsis* is from mountains of NE India to N China (Yunnan, Guizhou and Sichuan) with a few species in S China, Taiwan and S Japan. Three species occur in S India and Sri Lanka. Two species are endemic to Malesia. The sole Philippine species, *D. manipurensis* (Bedd.) Holttum & Edwards also occurs in E Nepal to NE India (Holttum & Edwards 1986). This has newly been collected by Fraser-Jenkins in Meghalaya, N of Mairang. The species that we investigated are listed in Table 5.

Subfamily Peranematoideae Fras.-Jenk.

Peranema D. Don and *Diacalpe* Blume

Peranema with two species and *Diacalpe* with one species, both with overlapping areas in

Table 4. Cytology and distribution of the investigated species of *Nothoperanema*.

Species	Cytology[1)]	Distribution	Reference
N. rubiginosa (Brack) A. Reid Smith & D. R. Palmer	?	Endemic in Hawai´i	
N. squamiseta (Hook.) Ching	?	Africa, including Madagascar and the Reunion Island C and E Himalaya	Kuo (1985)
N. hendersonii (Bedd.) Ching	2x, s	S Japan (Isl. Yakushima), Nepal, Taiwan, S China, Thailand, N Philippines (Luzon), Java	Hirabayashi (1974), Kuo (1985)
N. shikokiana (Mak.) Ching	2x, s	S Japan, China	Hirabayashi (1974)

[1)]2x = diploid, s = sexual.

tropical Asia, are two genera which have been described in 1825 and in 1828, respectively. *Peranema* is remarkable because of its sori being elevated on vascularized stalks or pedicels on the veins. *Diacalpe* differs in having sessile, globose sori with a basally attached indusium which entirely covers the sporangia as does the indusium in *Peranema*. In other respects they are closely alike (Sledge 1973). The frond morphology and habit, anatomy, spore characters and gametophyte generation have been taken by some authors to indicate that *Diacalpe* and *Peranema* belong to the same genus, *Peranema*. If so, the traditional distinction based on the sessile and stalked sori should be regarded as a specific and not a generic character (Nayar & Kaur 1963, cf. also Sledge 1973, Kuo 1985). In the present work, however, we have retained the two genera.

Peranema cyatheoides D. Don is distributed in the Himalaya, SW China and Burma = Mayanmar. Its cytology is unknown. *Diacalpe aspidioides* Bl. has a broad distribution in tropical Asia: Sri Lanka, Nepal, Bhutan, NE India, Burma = Mayanmar, N Thailand, Vietnam, S China, Sumatra, Java, Borneo, New Guinea and the Philippines (Kuo 1985). Its cytology is unknown, but another species, *D. christensenii* Ching from Yunnan is diploid (2n = 82; Gibby 1985). These ferns have not previously been investigated for their phloroglucinols. We investigated *P. cyatheoides* and *D. aspidioides* Blume from Nepal.

Acrophorus C. Presl

There are two different opinions about the two closely related species of *Acrophorus*. According to Kramer & Green (1990) there are two species occurring in moist forest from NE India and S Japan: *A. nodosus* C. Presl and *A. blumei* Ching ex C. Chr. However, Picci Sermolli (1977) described a new species, *A. paleolatus* Pic.Ser.

Table 5. Cytology and distribution of the investigated species of *Dryopsis*.

Species	Cytology[1)]	Distribution	Reference
D. apiciflora (Wall. ex Mett.) Holttum & P. J. Edwards (Fig. 1)	2x, s	Kumaon (Uttar Pradesh), Nepal, Sikkim, Bhutan, Arunchal Pradesh, Manipur (NE India), N Burma = Mayanmar, Yunnan, Taiwan	Mehra & Mittal (1961), Holttum & Edwards (1986)
D. clarkei (Bak.) Holttum & J. Edwards (Fig. 2)	?	E Nepal, Sikkim, N Burma = Mayanmar, China (Sichuan, Yunnan, Gyangxi)	Holttum & Edwards (1986)
D. nidus (Bak.) Holttum & J. Edwards (Fig. 3) (*Ctenitis maximovicziana*)	2x, s	C and E Nepal, Darjeeling, Sikkim, Yunnan	Mehra & Mittal (1961), Widén & Puri (1979), Holttum & Edwards (1986)
D. maximovicziana (Miq.)[2)] Holttum & P. J. Edwards (*Ctenitis maximovicziana* (Miq.) Ching)	?	China (Hunan, Guizhow, Taiwan), Japan (Honshu, Kyushu)	Holttum & Edwards (1986)
D. ferruginea (Bak.) Holtt. var. *obtusiloba* Holttum & P. J. Edwards (*Ctenitis ferruginea* (Bak.) Ching var. *obtusiloba* Sledge)[3)]	?	Endemic to Sri Lanka	

[1)] 2x = diploid, s = sexual.
[2)] It has proved to be devoid of phloroglucinols and glands. (Harada 1951–1952, Inagaki *et al.* 1961, Widén *et al.* 1976.)
[3)] It has not previously been tested for phloroglucinols.

Fig. 1. A frond of *Dryopsis apiciflora* (*CRFJ 8514*, H).

Fig. 2. A frond of *Dryopsis clarkei* (*CRFJ 8473*, H).

(= *A. stipellatus auct. non* T. Moore). Another species is *Acrophorus nodosus* C. Presl, which is not the synonym of *A. stipellatus* T. Moore. Moreover, Picci Sermolli (1977a) stated that *A. blumei* must be named *Acrophorus nodosus* C. Presl. In this work, we follow the nomenclature of Picci Sermolli. According to Kuo (1985) *A. paleolatus* is distributed in S Japan, SW China, Indo-China and Himalaya. The cytology is unknown. We investigated material from S Japan of *A. nodosus* and from Taiwan of *A. paleolatus*.

Subfamily Polystichoideae Fras.-Jenk.

Rumohra Raddi

According to Kramer (1990) seven species are retained in the genus, and the remainder are placed in *Arachniodes*. The type specimen, *Rumohra adiantiformis* (Forst.f.) Ching has a circumaustral distribution: S America, Tristan da Cunha and Gough Island, S Africa, Madagascar, Mascarenes, Seychelles, New Guinea, SE Australia, Tasmania and New Zealand. One species is endemic to Juan Fernández, the others occur in Madagascar and tropical America. The base chromosome number is 41. Fraser-Jenkins (1986 and 1997: 38–39) is as convinced, from its sori, that *Rumohra* is in the Dryopteridaceae and closely allied to, if not congeneric with, *Arachniodes*, as Holttum (1947) was that it is in the Davalliaceae, but on its laminar morphology.

Stigmatopteris C. Chr.

This neotropical genus consists of 24 species all of which occur in Central and South America (Moran 1991). For our investigations only one

single herbarium voucher of *Stigmatopteris longicaudata* (Liebm.) C. Chr. from Costa Rica was available. This genus has not previously been investigated for its phenolics.

Polybotrya Humb. & Bonpl.

This genus of ca. 40 species occurring in tropical America (Mexico, Central America), is closely related to *Stigmatopteris* and *Cyclodium* (Moran 1991). The latter has not been studied for phenolics and glands. The sole species investigated is *Polybotrya caudata* Kunze from Guyana.

Arachniodes Blume

This genus comprises ca. 50 species of which the main part is from SE Asia with single species in Australia, Africa, S America and Hawai´i (cf. Widén *et al*. 1976, 1978, 1981, Kuo 1985, Gibby *et al*. 1991, Wagner 1993). The salient features of *Arachniodes* are broad and decompound, normally coriaceous fronds with an anadromic pattern of pinnation and single pointed apices to the segments and to their basal acroscopic auricles; either thick or erect or in most cases thin and long creeping rhizomes with exclusively external glands and orbicular reniform, almost peltate indusia (cf. Sledge 1973, Widén *et al*. 1976). *Arachniodes* is intermediate between *Dryopteris* and *Polystichum* in its morphology in that most species have an indusium similar to *Dryopteris*, but in the rest of its morphology it is much closer to *Polystichum*. We investigated 27 species and 19 hybrids of *Arachniodes* from different sources. However in the present work, we discuss only those species for which we obtained additional material (Table 6).

Polystichum Roth

This widely distributed genus of ca. 160 species occurs in most of the world and all continents; both in temperate regions of the N and S hemispheres and in mountain regions of the tropics.

Fig. 3. A frond of *Dryopsis nidus* (*CRFJ 8464*, H).

There are 27 species in Taiwan and 55 in tropical America (Tryon & Tryon 1982, Kuo 1985) and 45 species in the Indian subcontinent (Fraser-Jenkins 1991, 1997b). The base chromosome number is 41 (Mehra & Mittal 1961, Gibby 1985).

In *Dryopteris* the fronds are broad bipinnate or more finely divided and of herbaceous structure and the indusia are reniform. *Polystichum* clearly differs from *Dryopteris* having 1–2 pinnate fronds of more coriaceous texture and peltate indusia. Furthermore, in *Polystichum* the arrangement of the pinnules is anadromic and in *Dryopteris* it is usually catadromic. The salient features of *Polystichum* is its single-pointed, hair-toothed pinnule apices and a similar single pointed acroscopic basal auricle to the pinnules. The veins are free, whereas in the related genus *Cyrtomium*, which has wider single pinnae, they are anastomosing. The species from Taiwan and Mexico that we investigated are listed in Table 7.

Cyrtomium C. Presl

This genus comprises ca. 16 species with 15 in S and SE Asia and in the Indian subcontinent and one in S Africa. *Cyrtomium* is closely related to *Polystichum* and included in that genus by Kramer & Green (1990). The main centres of distribution are SW China and Japan with the species range extremely west to S Africa and east to Hawai´i. Only one species, the widespread *C. falcatum* C. Presl, was investigated by us from Malaysia and it was completely lacking phloroglucinols and glands (Widén *et al*. 1983). *Cyrtomium falcatum* is distributed in Japan, Ruykyus, S Korea, E and SE China and Indo-China.

Subfamily Tectarioideae Nayar

Midribs of ultimate leaflets more or less prominent (in *Tectaria* sometimes slightly grooved) and often bearing ctenitoid hairs (Holttum 1986). Holttum (1986) divided the ferns into three groups as follows: *Tectaria* and closely allied genera with 40 chromosomes and lacking cylindrical glands; genera having unicellular cylindrical glands and 41 chromosomes; and genera lacking glands and also having 41 chromosomes.

Tectaria Cav. and closely allied genera

Tectaria is a large genus, consisting of about 210 species of which 40 are neotropic. It is divided into two sections (not considered here) (Holttum 1986). Only three species were investigated: *T. bamleriana* (Rosenst.) C. Chr. from Papua New Guinea, *T. gemmifera* (Fée) Alston from Malawi, W Africa and *T. ceylanica* (Houtt.) Copel. from Sri Lanka (Widén *et al*. 1983 and present paper). Of the related genera, *Stenosemia aurita* (Sw.) C. Presl from the Philippines,

Table 6. Cytology and distribution of the investigated species of *Arachniodes*.

Species	Cytology	Distribution	Reference
A. rhomboidea (Wall. ex Mett.) Ching	?	Japan, S China, India, Nepal, Burma = Mayanmar	Kuo (1985)
A. aristata (G. Forst.) Tindale (*A. exilis* (Hance) Ching)	?	Tropics and subtropics of Asia and Australia, north to S China, Korea, Japan	Kuo (1985)
A. miqueliana (Fr. & Savat) Ohwi	?	Taiwan	
A. maximovicsii (Baker) Ohwi	?	Japan	
A. assamica (Kuhn) Ohwi	?	SE Asia and China, W to NE India	
A. superba Fras.-Jenk. (*Lithostegia foeniculacea* (Hook.) Ching) *See* Fraser-Jenkins 1997a: 39–40	?	China	

Table 7. Cytology and distribution of the investigated species of *Polystichum*.

Species	Cytology	Distribution	Reference
P. hancockii (Hance) Diels	?	S China (Fukien, Kwangtung, Kwangsi), Japan, Ryukyus	Kuo (1985)
P. parvipinnulum Tagawa	?	Taiwan (endemic)	Kuo (1985)
P. prionolepis Hayata	?	Taiwan (endemic)	Kuo (1985)
P. deltodon (Baker) Diels	?	Japan, China (Yunnan, Sichuan, Kweichow, Hupeh, Anhwei, Kwangtung), Indo-China	Kuo (1985)
P. speciosissimus (Kunze) F. Moore	?	Mexico	

Fadyenia prolifera Hook. (of unknown origin) and *Heterogonium sagenoides* (Mett.) Holttum from Borneo have been investigated (Widén *et al*. 1981, 1983). All these ferns proved to lack both phloroglucinols and glands on their rhizomes and petiolar bases.

Genera having unicellular cylindrical glands

The following three genera have unicellular cylindrical hairs on the stalks of sporangia, many of the species also on the margins of indusia and on the rhizomes and petiolar bases (Widén *et al*. 1976, 1978, 1981, Holttum 1986).

Ctenitis C. Chr.

According to Holttum (1986) the genus comprises about 100 species and is considerably diversified in both the Old World and the New World. *Ctenitis* differs from *Tectaria* in its glands, its fragile-fringed indusia, in having abundant scales which are at least in part clathrate on all the smaller axis of the frond, also in having fronds which in almost all species are more finely divided, the ultimate leaflets almost always deeply lobed and always with free veins. *Ctenitis* is distributed worldwide in the tropics and the subtropics, and have been subdivided into three groups (not considered here) (Tryon & Tryon 1982, Holttum 1985, 1986, Stoltze 1990). Six species of *Ctenitis* were studied for phloroglucinols and glands. Of these *C. setosa* (C. Presl) Holttum, *C. subglandulosa* (Hance) Ching and *C. mannii* (C. Hope) Ching proved to contain trace amounts of phloroglucinols and glands. However, Harada (1951, 1952) reports an absence of phenolic compounds in *C. subglandulosa* but employed less sensitive methods (cf. discussions in Widén *et al*. 1976). The three other investigated species *C. maximowicziana*, *C. ferruginea* var. *obtusiloba* and *C. protensa* (Afzel. ex Sw.) Ching have since then been transferred to other genera; i.e *Dryopsis* (*see* p. 104) and *Triplophyllum* (*see* p. 110). They proved to lack both glands and phenolics. The following species were studied in the present work: *C. crinita* (Poir.) Ching ("*C. crinita* aggregate") (Tardieu-Blot 1955a) from the Comoro Islands, *C. crinita* var. *crinita* from Mauritius, *C. crinita* var. *hispida* (Kühn) Tardieu-Blot from Madagascar, *C. borbonica* (Bak.) Tardieu-Blot and *C. pseudoperrieriana* (C. Chr.) Tardieu-Blot from Madagascar, *C. honoluluensis* (Hook.) Copel. from Hawai´i, *C. hemslayana* (Baker) Copel. from Mexico and *C. sloanei* (Spreng.) C. Morton from Jamaica.

Lastreopsis Ching, emend. Tindale

This genus consisting of ca. 35 species is closely related to *Ctenitis*, but differs in scales (more like those of *Tectaria*) and in the thickened decurrent basiscopic margins of leaflets which form wings on the axes to which the are attached. The hairs are variable; ctenitoid hairs occur in most species. *Lastreopsis* is pantropical in distribution (Tindale 1965, Holttum 1986) and has not previously been studied for phloroglucinols. Species studied in the present paper: *L. boivinii* (Baker) Tardieu-Blot from Madagascar, *L. effusa* (Sw.) Tindale var. *effusa* from Jamaica, *L. exculta* (Mett.) Tindale from Mexico and *L. decomposita* (R.Br.) Tindale, *L. marginans* (F. Muell.) D. A. Sm. & Tindale, *L. microsora* (Endl.) Tindale, *L. munita* (Mett.) Tindale, *L. silvestris* D. A. Sm. ex Tindale, *L. smithiana* Tindale, *L. wurunuran* (Domin) Tindale, all from Australia.

Pleocnemia C. Presl

This genus comprises 19 species, mainly Malaysian. The most distinctive characters are the presence of teeth in the sinuses between pinnule-lobes and of cylindrical glands which are usually yellow or orange in contrast to the usually pallid glands of most species of *Ctenitis* (Holttum 1986, Widén *et al*. 1981). Species investigated: *P. conjugata* (Bl.) C. Presl and *P. irregularis* (C. Presl) Holttum both from Borneo (Kalimantan).

Genera lacking glands

These ferns like the gland bearing ones, in having 41 chromosomes, but in other ways they are not closely related.

Triplophyllum Holttum

There are twenty species with a centre of distribution in Africa, five species in tropical America and two in Madagascar. Most species have previously been placed by recent authors in *Ctenitis* and two in *Tectaria*. Most scales are *Tectaria*-like, also their spores. Investigated species: *T. heudeloti* Pic.Serm. (= *Ctenitis protensa* (Afzel.) Copel.); *T. securidiforme* (Hook.) Holttum (*Ctenitis securidiformis* (C. Chr.) Copel.) and *T. vogelii* (Hook.) Holttum, all from W Africa, Cameroon.

Megalastrum Holttum

There are thirty neotropical species and five more in Africa including Madagascar and the Mascarene Islands. The African species lack the dentate scales which are characteristic of most of the neotropical ones. Investigated species: *M. magnum* (Baker) Holttum (= *Ctenitis magna* (Baker) Tardieu-Blot from Madagascar and *M. subinsicum* (Willd.) A. Reid Smith & R. C. Moran from Mexico.

Pseudotectaria Tardieu-Blot

This genus shows some morphological resemblance to *Heterogonium* and *Tectaria* section *Sagenia* (Tardieu-Blot 1955b, Holttum 1986). Two species have been investigated: *P. biformis* (Mett.) Holttum (*Ctenitis biformis* (C. Chr.) Tardieu-Blot) from the Mayotte Island and *P. decaryana* (C. Chr.) Tardieu-Blot from Madagascar. The chromosome number of *P. decaryana* was found to be 2n = 82 (Holttum & Lin 1990).

Trichoneuron Ching

Pichi Sermolli (1977b) following Ching (1964) considered this genus to belong to the Athyriaceae, but Crabbe *et al*. (1975) listed it in the Tectaroidaceae. Fraser-Jenkins does not except it as in the Athyriaceae, but it is not clear to what it belongs. We have investigated *T. microlepioides* Ching from China (Yunnan).

Family Davalliaceae Mett. ex A. B. Frank

Davallia J. Sm.

In a broad sence, this genus consists of ca. 90 species occurring in tropical and oceanic-temperate areas of Asia, from the Himalaya and N Japan to Australia and Tahiti; only two species in Africa and Madagascar; one in NW Africa, Macaronesia, and SW Europe. We have investigated *Davallia canariensis* (L.) J. Sm. from Madeira, *D. solida* (G. Forst.) Sw. of unknown origin, and *D. sessifolia* (Blume) Mett. from India. The latter species previously belonged to an own genus *Humata*, which was sunk into *Davallia* by Fraser-Jenkins (1997a: 100) following Kato (1985). They all proved to lack both glands and phloroglucinols. (Widén *et al*. 1983 and present work).

Family Oleandraceae Ching ex Pic. Ser.

Arthropteris beckleri (Hook.) Mett. and *A. tenella* (Forst. f.) J. Sm. from Australia were investigated. No phloroglucinols were detected in *Arthropteris*. In addition *Nephrolepis exaltata* (L.) Schott of unknown origin was studied by Widén *et al*. (1981); no phenolics or glands were observed.

Material

The collection data of the material not previously investigated are presented below. Voucher specimens are deposited in H if not indicated otherwise.

Phloroglucinol positive taxa
(included in Tables 8–13)

Dryopteris subtriangularis: *CRFJ field no. 529* and *530* with Rajkumar Khatri Chhetri and Sunil Gotami & P.D.

Gurung, and *CRFJ field no. 528* ditto, 6.II.1993, NE India, Meghalaya, forest beside and on E side of road, ca. 3 km S of Sohrarim, 42 km S of Shillong (Cherrapunjee). *Pei-Hsi Yuan 1750*, 8.VIII.1958, China, Fujian, Siung Mu Hsien, Can Crang, She Li Toi (village) (PE).

"*Dryopteris truncatulata* Ching ined.": *Collector no.6158*, China, Sichuan (PE).

Dryopteris sparsa: *CRFJ 8627–34*, *8636–37*, *8639–40*, *8642–43*, *8647–50*, *8652–60*, *8662*, 19.XI.1978, N India, W Bengal, 1550 m, below *Cryptomeria*, Lebong Forest, N of and below Lebong, N of Darjeeling, 29 rhizomes = 180 g. *CRFJ 8698–99*, 20. XI. 1978, N India, W Bengal, ca. 1250 m, stream gully, 0.5 km above Sidrapong power house, W of and below Darjeeling, 2 rhizomes. *CRFJ 9091*, *9093–96*, 15.XII.1978, S India, Tamil Nadu, 1600 m, woods by stream below Shevaroy Temple, S of Bauxite mine and Kakasholai stream, N of Yercaud, Shevaroy hills, Salem, 5 rhizomes. *CRFJ 9110*, *9112–9119*, 15.XII.1978, S India, Tamil Nadu, ca. 1650 m, dense woods beside Kakasholai stream, near Bauxite mine, NW of Yercaud, NE of Salem, Shevaroy hills, 9 rhizomes. The ploidy level is not counted in the above collections. *Dryopteris sparsa* hybrids: CRFJ 8625, 8635, 8641, same place and date, 3 rhizomes.

Dryopteris undulata: *CRFJ field no. 95*, 4.IX.1993, Sri Lanka, ca. 1300 m SE of Gombanya mountain, above Hilloomally, Kallebokka, NE of Knuckles Range, Kandy, 4 rhizomes.

Dryopteris macrochlamys: *CRFJ field no. 381–382*, IX.1993, Sri Lanka, upper part of S side of Mt. Pedrotalagalla, Nuwara Eliya, 2 rhizomes.

Dryopteris diffracta: *Collector no. 430*, 1.XI.1954, China, Hainan (PE).

Nothoperanema rubiginosa: *CRFJ 14877–78*, with R. Hobdy, 28.II.1988, Hawai´i, West Maui, 4000 feet, forest on shoulder of Hana´aula mountain, W of Waikapu.

Nothoperanema squamiseta: *CRFJ 12295–96*, 25.VII.1986, Réunion Island, ca. 1950 m, Path to Fonds de la Riv. d´Est, La Fournaise. *CRFJ field no. 391*, with A. C. Jermy & Rajkumar Khatri Chhetri, 16.I.1993, Nepal, Kathmandu Valley, NE side of Sheopuri Mt., ca. 7500 feet.

Nothoperanema hendersonii: *CRFJ field no. 528*, with Rajkumar Khatri Chhetri and Sunil Gotami, 6.II.1993, NE India, Meghalaya, forest beside and on E side of road, ca. 3 km S of Sohrarim, 42 km S of Shillong, on road to Sohra (Cherrapunjee), 3 rhizomes.

Dryopsis apiciflora: *CRFJ 8515–21*, 16.XI.1978, N India, W Bengal, 2700 m, *Rhododendron* forest by stream, Gairibas to Tonglo, W of Darjeeling, 7 rhizomes = 1640 g.

Dryopsis clarkei: *CRFJ 8470–76*, *8482*, same place and date as *D. nidus* (*CRFJ 8458–60* etc.).

Dryopsis nidus: *CRFJ 8458–60*, *8462–67*, 15.XI.1978, N India, W Bengal, *Rhododendron* forest 3000 m, Kalapokhri to Sandakphoo, N of Tonglo, W of Darjeeling, 9 rhizomes = 500 g. *CRFJ 15709*, *15744–52*, 10.XI.1989, C Nepal, ca. 13 000 feet, on E side of and below Khurpudanda ridge, above Army headquarters, E of Somdang, W of Langtang, above Syabrubensi and Gatlang, Rasuwa District, Bagmati Zone. 10 rhizomes.

Peranema cyatheoides: *CRFJ 15639*, 9. XI. 1989, Nepal, forest above and half way from Ramche to Dhunche, N of Trisuli Bazaar on road to Rasuwa District, 2 rhizomes.

Diacalpe aspidioides: *CRFJ 15823–33*, 17.XI.1981, C Nepal, ca. 1650 m, SE side of Jamachok Mt., W of Balaju, NW of Kathmandu, 12 rhizomes.

Acrophorus paleolatus: *J. Hyvönen 4194*, 1.XII.1987, Taiwan, Taichung Co, piece of rhizome from herbarium specimen, not weighed.

Rumohra adiantiformis: *R. Coveny 9485*, 12.VI.1977, Australia, Minnamurra Falls, 7 km WNW of Jamberoo. *J. Zizich & H. Roivainen 2139*, 30.I.1970, Argentina, Puerto Descado, Canadon Aquada Barril, fisura grande de roca volcania, bastante escasamente. *A. Kalela 656*, 6.XI.1977, Argentina, Correntoso, steep slope. *A. Burkhart 27433*, 23.I.1969, Chile, Bio-Bio, Lago Laja, Salto de Trubunleo. Rhizome pieces of herbarium material investigated of all the above numbers.

Stigmatopteris longicaudata: *R. C. & C. K. R. Moran 5872*, 19. V. 1992, Costa Rica, Puntarenos, Santa Elena Rainforest, 6 km N of Santa Elena, cloud forest, 10°21´ N, 84°07´ W, piece of rhizome from herbarium specimen.

Ctenitis crinita var. *hispida*: *CRFJ 12011–12*, 19.VI.1986, Madagascar, ca. 975 m, Lac Vert, SW of Anamalazaotra, Andasibe. *CRFJ 12034*, 21.VI.1986, same place as above.

Lastreopsis marginans: *R. Coveny 9402*, 4.V.1977, Australia, New South Wales, Brunswick Heads. *R. Coveny 9413*, 5.V.1977, New South Wales, Mt. Tomewin. *R. Coveny 9942 & Haegi*, 5.XII.1977, New South Wales, Tyalgum Ridge.

Lastreopsis decomposita: *R. Coveny 9243*, 10.IV.1977, Australia, New South Wales, Culoul Range. *R. Coveny 9414*, 5.V.1977, New South Wales, Mt. Tomewin. *R. Coveny 9945 & Haegi*, 5.XII.1977, New South Wales, Tyalgym Ridge.

Arachniodes rhomboidea: *M. J. Lai 13162–67*, 2.V.1982, Taiwan, Taipei co, Sanchih. Piece of rhizome from herbarium specimen.

Arachniodes aristata: *R. Coveny 8473*, 4.X.1976, Australia, New South Wales, O'Sullivan's Gap. *R. Coveny 9668. R. Coveny 9868 & Haegi*, 28.XI.1977, O'Sullivan's gap, Bangalow creek.

A. miqueliana: *T. Seki, M. Higuchi & S. Piippo 5954*, 31.V. 1986, Japan, Honshu, Hiroshima Pref., Nebudani Valley, ca. 300 m, Piece of rhizome from herbarium specimen.

A. maximoviczii: *S. Mitsuta s.n.*, 13.VIII.1975, Japan, Iochigi Pref., Mt Koshin, ca. 1500 m. Piece of rhizome from herbarium specimen.

Arachniodes assamica: *S. Piippo 5949* with S. Hattori and M. Mizutani, 7.V.1986 Japan, Kuyshu, Mizazaki-Ken, Nichinan-Shi, Inotani Valley, mixed forest. Piece of rhizome from herbarium specimen.

Phloroglucinol negative taxa
(not included in Tables 8–13)

Arthropteris beckleri: *R. Coveny 9418*, 5.V.1977, Australia, New South Wales, Bilambil Creek, SW of Bilambil.

Arthropteris tenella: *R. Coveny 8456*, 2.X.1976, Australia, New South Wales, Craven Plateau.

Ctenitis borbonica: *CRFJ 12263*, 25.VII.1986, Réunion Island, ca. 1500 m, Pass above Plaine des Palmistes.

Ctenitis crinita "aggregate": *CRFJ 12228–29*, 18.VII.1986, Comoro Islands, NW Mayotte, forest around Majimbini, W of Mamoutsou, below Mt. M'Sapore, ca. 620 m.

Ctenitis crinita var. *crinita*: *CRFJ 12116–17*, *12123*, *12130*, 9.VII.1986, Mauritius, SE of Port Louis, S side of La Pouce mountain, scrub forest below cliff, ca. 600 m.

Ctenitis hemsleyana: *CRFJ & A. Monef Ali, field no. 38*, *39*, 23.X.1992, Mexico, Vera Cruz State, ca. 5–7 km N of Paz de Enriques, ca. 20 km S of Misantla on road to Jalapa, Forest.

Ctenitis honoluluensis: *CRFJ 14879–80* with R. W. Hobdy, 28.II.1988, Hawai´i, W Maui, W of Waikapu, forest on S shoulder of Hana´aula mountain, W of Waikapu, 4000 feet.

Ctenitis pseudoperrieriana: *CRFJ 11996*, *12005–08*, 19.VI.1986, Madagascar, ca. 975 m, Lac Vert, SW of Anamalazaotra, Andasibe.

Ctenitis sloanei: *CRFJ 14696–97*, 11.II.1988, Jamaica, Surrey, S Portland, John Crow Mountains, W of Eccleston, NW of Manchioneal.

Davallia solida: Cambridge, Botanical Gardens of unknown origin.

Dryopsis ferruginea var. *obtusiloba*: *CRFJ field no. 360*, *362*, 25.X.1993, with Brahakmanagiri Abeysiri, 1700–1800 m, on S side of ridge, ca. 1–2 km along track from ca. 1 km below top of Top Pass (Ramboda Pass) on W side, heading towards NW and Maturata, W of Nuwara Eliya.

Lastreopsis boivinii: *CRFJ 11985–86*, 18.VI.1986, Madagascar, ca. 975 m, Lac Vert, SW of Anamalazaotra, Andasibe.

Lastreopsis exculta: *CRFJ field no. 102*, *104*, with A. Monef Ali, 23.X.1992, Mexico, Vera Cruz, forest on W side of road from Misantla to Yecuatla, ca. 1 km N of Plan de Almensa, S of Misantla, N of Jalapa.

Lastreopsis effusa: *CRFJ field no. 101*, Mexico, Vera Cruz, 2 rhizomes, same place and date as *L. exculta*.

L. effusa var. *effusa*: *CRFJ 14647*, 6.II.1988, Jamaica, Surrey, S Portland, NE side of Uncommon Hill, ca. 450 m.

Lastreopsis microsora: *R. Coveny 9409*, 5.V.1977, Australia, New South Wales, Mt. Tomewin.

Lastreopsis munita: *R. Coveny 9410*, 5. V. 1977, Australia, New South Wales, Mt. Tomewin.

Lastreopsis silvestris: *R. Coveny 9943 & Haegi*, 5.II.1977, Australia, New South Wales, Tyalgum Ridge.

Lastreopsis smithiana: *R. Coveny 9951 & Haegi*, 4.II.1977, Australia, Brindle Creek, Wiangaree State Forest.

Lastreopsis wurunuran: *I. Kukkonen 11002*, 13.IX.1981, Australia, Queensland, Atherton Tableland Lamin's Hill, E of Malanda, Rain forest patch.

Arachniodes superba: *C.W. Wang* in 1935–1936, China, Yunnan (PE). *C. W. Wang 72074*, II.1936, China, Yunnan, Shan-Ning, Hsien, 3200 m (PE).

Megalastrum magnum: *CRFJ 12040*, 21.VI.1986, Madagascar, ca. 975 m, Lac Vert, SW of Anamalazaotra, Andasibe.

Megalastrum subincisum: *CRFJ field no. 41* with A. Monef Ali, 23.X.1992, Mexico, Vera Cruz, ca. 5–7 km N of Paz de Enriques, ca. 20 km S of Misantla on road to Jalapa, Forest. *CRFJ field no. 103* with A. Monef Ali, same place and date as *L. exculta*.

Polystichum speciosissimum: *CRFJ 13313*, 5.V.1987, Mexico, Oaxaca, Ixlán de Juarez, on road to Valle Nacional and Tuxtepec, ca. 2500 m.

Polystichum hancockii: *J. Hyvönen 4191*, 1. XII. 1987, Taiwan, Taichung Co. Piece of rhizome from herbarium specimen.

Polystichum parvipinnulum: *J. Hyvönen 4214*, 1.XII.1987, Taiwan, Taichung Co. Piece of rhizome from herbarium specimen.

Polystichum prionolepis: *J. Hyvönen 4197*, 1.XII.1987, Taiwan, Taichung Co. Piece of rhizome from herbarium specimen.

Polystichum deltodon: *S. Stenroos 3109*, 17.XI.1987, Taiwan, Nantou Co. Piece of rhizome from herbarium specimen.

Pseudotectaria biformis: *CRFJ 12222–23*, 18.VII.1986, Comoro Islands, NW Mayotte Island, forest around Majimbini, W of Mamoutsou, below Mt. M'Sapore, ca. 620 m.

Pseudotectaria decaryana: *CRFJ 11997*, 12047, 19–21.VII.1986, Madagascar, ca. 975 m, Lac Vert, SW of Anamalazaotra, Andasibe.

Tectaria gemmifera: *L. Junikka 1378*, 8.IV.1989, W Africa, Malawi, S Reg., Mulanje D., Mt Mulanje Ruo Gorge. Moist evergreen forest, Lat. 15°56´58´´ S, Long. 35°38–39´´ E, Alt. 1050 m.

Trichoneuron microlepioides: *PE 3432a*, China, Yunnan, Xizangpanna area, Isotype!, collector no. 578. Piece of rhizome from herbarium sheet (PE).

Triphophyllum heudelotii: *CRFJ 14416*, 5.VI.1985 with C. D. Fraser Jenkins, Cameroon, SW Province, ca. 200 m, forest a few km W of Bokwa, on main road E of Mamfé.

Triplophyllum securidiforme: *CRFJ 11428–29*, 5.VI.1985, Cameroon, NW province, ca. 750 m., above Bokwa, SW of Bamenda.

Triplophyllum vogelii: *CRFJ 11423–24*, 5.VI.1985, Cameroon, NW Province, above Bokwa, ca. 450 m, between Bokwa and Batibo, E of Mamfé.

Results

The fern genera investigated can be divided into two main groupings based on occurrence of phloroglucinols and secreting glands (or other secretory structures), though these were not considered here to be taxonomic groupings.

Phloroglucinol negative genera or groups

The following genera were totally lacking phloroglucinols and glands: *Cyrtomium* (subfamily Polystichoideae); *Tectaria*, *Stenosemia*, *Heterogonium*, *Fadyenia*, *Trichoneuron*, *Triplophyllum*, *Megalastrum*, *Pseudotectaria* (subfamily Tectarioideae); *Davallia* (family Davalliaceae); *Arthropteris*, *Nephrolepis* (family Oleandriaceae).

Phloroglucinol positive genera

Dryopteris (main part), (*Nothoperanema*), *Dryopsis* (main part), *Peranema*, *Diacalpe*, (*Acrophorus*), (*Polystichum*), *Arachniodes* (main part), *Stigmatopteris*, *Polybotria*, *Rumohra* (*see* text). In the genera within parentheses, only few species contain phloroglucinols and glands, others are totally lacking these phenolics and secreting organs.

Previous and new analytical results from the taxa studied are summarized in Tables 8–12. Compounds not present in the appropriate sections are omitted from the Tables. Amounts of crude extractive products and secretory structures are given in Table 13. Tables 14 and 15 list the approximative total amount of side chain homologues after reductive alkaline cleavage of the crude filicins and study of the acylfilicinic acids (*36*) or aspidinols (*2*) formed. In the following the compounds isolated from *Dryopsis apiciflora*, *D. clarkei* and *D. nidus* are described (Fig. 4), for details *see* Experimental procedures.

Dryopsis apiciflora: Trispara-aspidin as a mixture of the homologues VBB/BBV (*20*-VBB/BBV), *BBB* (*20*-BBB) and PBB/BBP (*20*-PBB/BBP) containing minute amounts of higher and lower homologues; margaspidin consisting of the homologues VB/BV (*13*-VB, BV), BB (*13*-BB), PB/BP (*13*-PB / BP) also containing small amounts of higher and lower homologues; phloraspin as a mixture of homologues VB/BV (*11*-VB, BV) and BB (*11*-BB) with traces of lower homologues.

Dryopsis clarkei: Phloraspidinol as a mixture of homologues VB/BV (*13*-VB, BV) and BB (*13*-BB); margaspidin -BB (*13*-BB), -PB/BP (*13*-PB/BP) and -PP (*13*-PP).

Dryopsis nidus: Methylene-bis-aspidinol containing the homologues BV (*18*-BV) and BB (*18*-BB); albaspidin mainly consisting of the homologues *10*-VB, *10*-BB and *10*-PB; margaspidin -BV/VB (*13*-BV, VB) and -BB (*13*-BB) with traces of higher and lower homologues. In addition phloropyrone mainly consisting of the homologues -BB (*15*-BB) and PB/BP (*15*-PB, BP) but also containing minute amounts of homologues VB/BV (*15*-VB, BV) and PP (*15*-PP). This is the first time that a variation of the length of the side-chain of the pyrone ring (ring B) has been observed.

Secretory structures

Dryopteris taxa

The morphology and occurrence of secreting glands and other secretory structures of the taxa investigated are given in Table 13. In general, the species of *Dryopteris* contain typical internal secreting glands in the parenchyma of the rhizomes and stipe bases (cf. Mehra & Mittal 1961, Widén *et al*. 1983 and literature therein). Of the *Dryopteris* taxa discussed in the present paper internal glands were studied only in *D. pulvinulifera* and *D. hasseltii* (Mehra & Mittal 1961, Widén *et al*. 1978). The rest of the species investigated (*D. sparsa*, *D. subexaltata* and *D. diffracta*) contained only external glands rather sparsely on the epidermis of the stipe bases and rhizomes (Widén *et al*. 1976). Exclusively external glands also occur in *D. fragrans* (L.) Schott, *D. aemula* (Ait.) O. Kuntze and *D. hayatae* (Widén *et al*. 1970, 1971, 1976).

Table 8. Semiquantitative results showing the phloroglucinol composition in different taxa of *Dryopteris* subgenus *Erythrovaria* section *Erythrovariae*. Estimated from intensity of spots in TLC and yield in preparative column chromatography. +++ = 20% or more of the crude filicin mixture; ++ = 10%–20%; + = 5%–10%; (+) = 1%–5%; – = < 1%; His. = Hisada.

Taxon and ploidy, reproduction[1]	Collection number or lit. ref.[2]	Origin	Aspidinol-B (*2*-B)[3]	Subtriangularin-iB (*34*-iB)	Flavaspidic acid-BB (*5*-BB)[4]	Flavaspidic acid-AB (*5*-AB)	Aspidin-BB (*6*-BB)[4]	Aspidin-iBiB (*6*-iBiB)	Aspidin-AB (*6*-AB)	Aspidin-AA (*6*-AA)	Para-aspidin-BB (*7*-BB)[4]	Para-aspidin-AB (*7*-AB)	Albaspidin-BB (*10*-BB)[5]	Albaspidin-iBiB (*10*iBiB)	Albaspidin-AB (*10*-AB)[6]	Desaspidin-BB (*8*-BB)[5]	Trisdesaspidin-BBB (*21*-BBB)[7]	Trisflavaspidic acid-BBB (*23*-BBB)[7]
D. decipiens	His. & Noro 1961,																	
3x, a	His. 1961, 1966	Japan	–	–	?	–	++	–	–	–	–	–	+	–	–	–	–	–
D. fuscipes	His. & Noro 1961,	Japan	?/–	–	?	–	++/+	–	–	–	–	–	+/–	–	–	–	–	–
3x, a	His. 1961, 1966																	
D. championi	Widen *et al.* 1975	Japan	–	–	(+)	–	+++	–	+	–	–	–	(+)	–	(+)	++	+++	(+)
3x, a																		
2x, a	His. & Noro 1961,																	
	His. 1961	Japan	–	–	+/–	–	+	–	–	–	–	–	+	–	–	++	–	–
D. kinkiensis	His. & Noro 1961,	Japan	?	–	+/–	–	+	–	–	–	–	–	+	–	–	++	–	–
4x, s	His. 1961, 1966																	
D. hondoensis	His. & Noro 1961,	Japan	?/–	–	?	–	++	–	–	–	–	–	+	–	–	–	–	–
3x, a	His. 1961, 1966																	
D. erythrosora	His. & Noro 1961,	Japan	–	–	–	–	++	–	–	–	–	–	+	–	–	–	–	–
3x, a	His. 1961,1966																	
	Widén *et al.* 1975	Japan	–	–	(+)	–	+++	++	++	–	–	–	++	+	+	–	–	–
D. cystolepidota	His. & Noro 1961	Japan	–	–	–	–	++	–	–	–	–	–	+	–	–	–	–	–
(=*D. nipponensis*)	His. 1961, 1966																	
3x, a																		
D. subtriangularis	Widén *et al.* 1993	N India	–	+++	–	–	–	–	–	–	–	–	++	+++	+	–	–	–
3x, a																		
	P.H. Yan 1750	China	–	++	–	–	–	–	–	–	–	–	++	++	+	–	–	–
	CRFJ field nr. 530	N India	–	–	–	–	–	–	–	–	–	–	++	++	+	–	–	–
"*D. truncatulata*" [8]	PE collector 6158	China	–	–	–	–	++	–	–	–	–	–	–	++	–	–	–	–
D. tenuicula	His. & Noro 1961,	Japan	–	–	–	–	+	–	–	–	–	–	+	–	–	–	–	–
(=*D. indusiata*)	His. 1966																	
3x, a																		
D. gymnosora	His. & Noro 1961,	Japan	–	–	–	–	+	–	–	+	–	–	+	–	–	–	–	–
3x, a	His. *et al.* 1974																	

[1] 2x = diploid, 3x = triploid, 4x = tetraploid, a = apomictic, s = sexual.
[2] CRFJ = C.R. Fraser-Jenkins, PE = refers to unidentified collectors in PE (Beijing) herbarium.
[3] Aspidinol (*2*) is mostly an artefact (cf. Widén *et al.* 1996, 1997).
[4] This spot is often a mixture of BB, BP/PB homologues which do not separate in TLC. In some cases V homologues may be present too.
[5] This spot, which was formerly often designated as "albaspidin 1", may be provoked by a mixture of the homologues *10*-BB, PB and PP.
[6] This spot is often designated as "albaspidin 2" and may be formed by a mixture of homologues *10*-BA, -PA.
[7] This spot may be a mixture of homologues BBB, PBB and PBP. In some also cases V homologues may be present.
[8] This is only a provisional name (Ching ined.), given by Ching in PE herbarium.

Non *Dryopteris* taxa

Of the ferns not belonging to *Dryopteris* internal glands in the rhizomes have so far been observed only in *Dryopsis apiciflora* and *D. nidus* (Mehra & Mittal 1961). In Fig. 5, we present a transverse section of *D. nidus* showing three amphicribral vascular bundles and many sclerenchymatic cell bundles. Noteworthy also are large, schizogenously developed intercellular

Table 9. Semiquantitative results showing the phloroglucinol composition in the investigated taxa of *Dryopteris* subgenus *Erythrovaria,* sections *Politae* and *Variae.* Estimated from intensity of spots in TLC and yield in preparative column chromatography. +++ = 20% or more of the crude filicin mixture; ++ = 10%–20% ;+ = 5%–10% ; (+) = 1%–5%; – = < 1%; His. = Hisada.

Taxon and ploidy, reproduction[1)]	Ref.	Origin	Aspidinol-B (*3*-B)	Flavaspidic acid-BB (*5*-BB)	Aspidin-BB (*6*-BB)	Albaspidin-BB (*10*-BB)	Albaspidin-BA (10-BA)	Phloraspidinol-BB (*12*-BB)[3)]	Margaspidin-BB (*13*-BB)[3)]	Methylene-bis-aspidinol-BB (*18*-BB)[3)]	Filixic acid-BBB (*19*-BBB)[4)]	Trispara-aspidin-BBB (*20*-BBB)[4)]
Section *Politae*												
D. polita	His. & Noro 1961	Japan	–	–	–	–	–	–	–	–	–	–
2x, s	His. 1966											
Section *Variae*												
D. saxifraga	His. & Noro 1961,											
2x, s	His. 1966,	Japan	++[2)]	–	–	–	–	–	++	–	–	–
	His. *et al.* 1971											
D. bissetiana	His. & Noro 1961,											
3x, a	His. 1966,	Japan	++[2)]	–	–	–	–	–	++	–	–	–
	His. *et al* 1971											
	Widén *et al.* 1975	Japan	–	++	–	+	?	–	+++	(+)	+	(+)
D. varia	His. & Noro 1961,											
2x, 3x, a	His. 1966	Japan	?	++	–	+	–	–	–	–	–	–
D. hikonensis	His. & Noro 1961,											
(= *D. pacifica*)	His. 1966,	Japan	++[2)]	?	–	–	–	–	++	–	–	–
3x, a	His. *et al.* 1971											
D. sacrosancta	His. & Noro 1961,											
3x, a	His. 1966,	Japan	++[2)]	–/++	–	–	–	–	++	–	–	–
	His. *et al.* 1971											
	Widén *et al.* 1975	Japan	–	++	–	(+)	?	–	+++	(+)	+	(+)
D. sordidipes	His. & Noro 1961,											
2x, s	His. 1966	Japan	?	?	–	++	–	–	–	–	–	–
D. formosana	His. & Noro 1961,	Japan	–	?	+	–	–	–	–	–	–	–
3x, a	His. 1966											

[1)] 2x = diploid, 3x = triploid, 4x = tetraploid, a = apomictic, s = sexual.

[2)] Presumably an artefact formed from margaspidin (*13*) in the isolation procedure, *see* Widén *et al.* 1999 (Part II).

[3)] These compounds may include the homologues PB and BP as well.

[4)] These substances may also include the homologues PBB and PBP.

Table 10. Semiquantitative results showing the phloroglucinol composition in different taxa of *Dryopteris* subgenus *Nephrocystis* section *Purpurascentes* and section *Nephrocystis* and genus *Nothoperanema*. Estimated from intensity of spots in TLC and yield in preparative column chromatography. +++ = 20% or more of the crude filicin mixture; ++ = 10%–20%; + = 5%–10%; (+) = 1%–5%; – = < 1%; His. = Hisada.

Taxon and ploidy, reproduction[1)]	Collection number or lit. ref.[2)]	Origin	Aspidinol-B (*2*-B)	Para-aspidin-BB (*7*-BB)	Flavaspidic acid-BB (*5*-BB)	Flavaspidic acid-AB (*5*-AB)	Aspidin-BB (*6*-BB)	Aspidin-AB (*6*-AB)	Albaspidin-BB (*10*-BB)	Albaspidin-AB (*10*-AB)	Albaspidin-AA (*10*-AA)	Phloraspidinol-BB (*12*-BB)	Pulvinuliferin-VV (*33*-VV)	Filixic acid-BBB (*19*-BBB)	Filixic acid-ABB (*19*-ABB)[3)]	Trisflavaspidic acid-BBB (*23*-BBB)[4)]	Pu-1[5)]
Section *Purpurascentes*																	
D. kilemensis 2x, s	Widén *et al.* 1973	Kenya	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
D. pulvinulifera	Widén *et al.* 1993	N India	–	–	–	–	–	–	–	–	–	–	+++	–	–	–	+
2x, s	Widén *et al.* 1978	Phil	–	–	(+)	–	++	+	+	–	–	–	–	–	–	–	–
Section *Diclisodon*																	
D. hasseltii	Widén *et al.* 1976	Japan	–	–	+	+	–	–	++	++	++	–	–	–	–	–	–
D. sparsa aggregate	Widén *et al.* 1978	Japan	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
(2x, 4x, s or 3x, a)	His. & Noro 1961	Japan	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Widén *et al.* 1976[7)]	Japan	–	–	–	–	–	–	+	+	+	–	–	(+)	(+)	–	–
"2x"	CRFJ 8625,8627–34[6)]	N India	(+)	(+)	–	–	–	–	(+)	(+)	(+)	(+)	–	(+)	(+)	–	–
hybrid	CRFJ 8635–41	N India	–	(+)	–	–	–	–	(+)	(+)	(+)	(+)	–	(+)	(+)	–	–
"2x"	CRFJ 8998–99	N India	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	CRFJ 9091,9093–96	S India	(+)	(+)	–	–	–	–	(+)	(+)	(+)	(+)	–	+	(+)	–	–
	CRFJ 9110,9112–19	S India	(+)	(+)	–	–	–	–	(+)	(+)	(+)	(+)	–	+	(+)	–	–
D. subexaltata	His. & Noro 1961	Japan	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
(= *D. hayatae*)	Widén *et al.* 1976	Japan	–	–	(+)	–	–	–	+	++	+	–	–	–	–	–	–
2x, s																	
D. sabae	His. & Noro 1961,	Japan	–	–	?	–	?	–	–	–	–	–	–	–	–	–	–
2x, s	His. 1966																
	Widén *et al.* 1975	Japan	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
D. undulata	CRFJ field no. 95,	Sri La	–	–	–	–	–	–	++	(+)	–	–	–	–	–	–	–
D. macrochlamys	CRFJ field no.	Sri La	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2x, s	381–382																
D. diffracta	PE collector 430	China	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4x																	
Nothoperanema																	
N. rubiginosa	CRFJ 14877–78	Hawai´i	–	–	–	–	–	–	(+)	(+)	–	–	–	–	–	–	–
N. squamiseta	CRFJ 12295–96	Réunion	–	–	–	–	–	–	–	(+)	–	–	–	–	–	–	–
	CRFJ 16.I.1993	Nepal	–	–	+	–	–	–	+	+	+	–	–	++	+	–	–
	Widen *et al.* 1973	Kenya	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
N. hendersonii	Widén *et al.* 1978	Japan	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2x, s		India	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
N. shikokiana	Widén *et al.* 1978	Japan	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2x, s																	

[1)] 2x = diploid, 3x = triploid, 4x = tetraploid, a = apomictic, s = sexual.
[2)] CRFJ = C. R. Fraser-Jenkins, PE = refers to unidentified collectors in PE (Beijing) herbarium.
[3)] Filixic acid-ABB (*19*-ABB) may include the homologue ABP (*19*-ABP) as well.
[4)] Trisflavaspidic acid-BBB (*23*-BBB) may also contain homologues PBB (*23*-PBB) and ABP (*23*-ABP).
[5)] This is a non phloroglucinolic compound of unknown structure (von Euw *et al.* 1985, Widén *et al.* 1993).
[6)] CRFJ 8625, 8635 and 8641 are hybrids. The ploidy level is not counted.
[7)] Widén *et al.* (1976) report aspidin-BB (*6*-BB), which proved to be wrong. It should be filixic acid (*19*), which is now corrected in the table.

Table 11. Semiquantitative results showing the phloroglucinol composition in different taxa of *Dryopsis, Peranema, Diacalpe* and related genera. Estimated from intensity of spots in TLC and yield in preparative column chromatography. +++ = 20% or more of the crude filicin mixture; ++ = 10%–20% ;+ = 5%–10% ; (+) = 1%–5% ; – = < 1%

Taxon and ploidy, reproduction[1]	Collection number or lit. ref.[2]	Origin[3]	Aspidinol-B (*2*-B)	Norflavaspidic acid-BB (*4*-BB)	Flavaspidic acid-BB (*5*-BB)	Flavaspidic acid-AB (*5*-AB)	Para-aspidin-BB (*7*-BB)	Desapidin-BB (*8*-BB)	Albaspidin-BB (*10*-BB)	Albaspidin-AB (*10*-AB)	Albaspidin-AA (*10*-AA)	Phloraspin-BB (*11*-B)	Phloraspidinol-BB (*12*-BB)	Margaspidin-BB (*13*-BB)	Methylene-bis-aspidinol-BB (*18*-BB)	Phloropyrone-BB (*15*-BB)	Phloraspyrone-BB (16-BB)	Filixic acid-BBB (*19*-BBB)	Filixic-acid-ABB (*19*-ABB)	Filixic acid-ABA (*19*-ABA)
Dryopsis																				
D. apiciflora[4]	CRFJ 8115–21	N India	+	–	–	–	(+)	–	–	–	–	+++	(+)	+++	(+)	–	–	–	–	–
	Widén & Puri 1979[5]	N India	+	–	(+)	–	+	–	+	–	–	++	–	++	(+)	+++	–	–	–	–
D. clarkei	CRFJ 8470–76	N India	+	–	–	–	(+)	(+)	(+)	–	–	+++	+	+++	(+)	(+)	+	–	–	–
	CRFJ 8482	N India	+	–	–	–	(+)	(+)	(+)	–	–	+++	+	+++	(+)	(+)	+	–	–	–
	Widén & Puri 1979	N India	+	–	(+)	–	(+)	(+)	–	–	–	+++	+	++	+	–	–	–	–	–
D. nidus	CRFJ 8458–60	N India	+	–	–	–	+	–	(+)	–	–	–	(+)	+++	+	++	+	–	–	–
2x, s	CRFJ 8462–67	N India	+	–	–	–	+	–	(+)	–	–	–	(+)	+++	+	++	+	–	–	–
	CRFJ 15709, 15744–52	Nepal	+	–	+	–	++	–	(+)	–	–	–	–	+++	+	+	–	–	–	–
Peranema																				
cyatheoides	CRFJ 15639	Nepal	–	–	++	+	–	–	–	–	–	–	–	–	–	–	–	+	++	+
Diacalpe																				
aspidioides	CRFJ 15823–15833	Nepal	–	–	+	–	–	–	+	–	–	–	–	–	–	+++	–	–	–	–
Rumohra																				
adiantiformis	RC 9485	Aust	–	–	–	–	–	–	–	–	–	–	–	–	–	++	–	–	–	–
	IZ 2139, AK 656	Arg	–	–	–	–	–	–	–	–	–	–	–	–	–	++	–	–	–	–
	AB 27433	Chile	–	–	–	–	–	–	–	–	–	–	–	–	–	++	–	–	–	–
Stigmatopteris																				
longicaudata	RC & CKM	Co Ric	–	+++	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ctenitis																				
C. crinita	CRFJ 12011	Madg	–	–	–	–	–	–	–	–	–	–	(+)	–	–	–	–	–	–	–
var. *hispida*	CRFJ 12034	Madg	–	–	–	–	–	–	–	–	–	(+)	(+)	(+)	–	–	–	–	–	–
	CRFJ 12012	Madg	–	–	–	–	–	–	–	–	–	(+)	(+)	(+)	–	–	–	–	–	–
C. setosa	Widén & Puri 1979	Japan	–	–	(+)	–	–	–	–	–	–	(+)	–	–	(+)	(+)	–	–	–	–
C. subglandulosa	—"—	Japan	–	–	–	–	–	–	–	–	–	(+)	–	–	(+)	(+)	–	–	–	–
C. mannii	Widén *et al.* 1981	Borneo	–	–	(+)	(+)	–	–	+	++	++	–	–	–	–	–	–	–	–	–
Lastreopsis																				
L. marginans[6]	RC 9402, 9413, 9942	NSW	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
L. decomposita[7]	RC 9243–9414, 9945	NSW	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

[1] 2x = diploid, 3x = triploid, 4x = tetraploid, a = apomictic, s = sexual.
[2] CRFJ = C. R. Fraser-Jenkins, RC = R. Coveny, IZ = I. Zizich, AK = A. Kalela, AB = A. Burkhart, RC & CKM = R. C. & C. K. Moran.
[3] Aust = Australia, Arg = Argentina, Co Ric = Costa Rica, Madg = Madagascar, May = Mayotte Island, NSW = New South Wales.
[4] In *D. apiciflora* trace amounts of trispara-aspidin (*20*-BBB) were also found.
[5] In this sample traces of trisflavaspidic acid (*23*-BBB) was detected.
[6] In TLC two unknown compounds, R_f 0.40 and 0.37, were detected in solvent system hexane–chloroform 50:50. The colorations with fast blue salt B were orange and red respectively.
[7] In TLC (same system as above) two unknown compounds, R_f 0.50 and 0.07, were detected. The coloration with fast blue salt B was violet in both cases.

cavities. Cross sections of *D. apiciflora* and *D. clarkei* are similar to those of *D. nidus*, but sclerenchymatic bundles were lacking in *D.clarkei* and the intercellular cavities are of minor size in *D. apiciflora* as compared with the two other species. In addition resinous cells were present in *D. apiciflora* and *D. clarkei*.

The internal glands of the above species cannot be studied from cross sections as they are transversely cut. Also in longitudinal sections of the rhizome or petiolar bases they are difficult to observe. However, in KOH macerates the form

Table 12. Semiquantitative results showing the phloroglucinol composition in the investigated taxa of *Arachniodes* and related genera. Estimated from intensity of spots in TLC and yield in preparative column chromatography. +++ = 20% or more of the crude filicin mixture; ++ = 10%–20%; + = 5%–10%; (+) = 1%–5%; – = < 1%

Taxon and ploidy, reproduction[1)]	Collection number or lit. ref.[2)]	Origin[3)]	Aspidinol-B (*2*-B)	Flavaspidic acid-BB (*5*-BB)	Flavaspidic acid-AB (*5*-AB)	Aspidin-BB (*6*-BB)	Aspidin-AB (*6*-AB)	Para-aspidin-BB (*7*-BB)	Para-aspidin-AB (*7*-AB)	Desaspidin-BB (*8*-BB)	Desaspidin-AB (*8*-AB)	Albaspidin-BB (*10*-BB)	Albaspidin-AB (*10*-AB)	Albaspidin-AA (*10*-AA)	Abbreviatin-BB (*30*-BB)	Trisdesaspidin-BBB (*21*-BBB)	Trisflavaspidic acid-BBB (*23*-BBB)	Trisflavaspidic acid-ABB (*23*-ABB)
Arachniodes																		
A. rhomboidea	MJL 13162–67	Taiwan	–	(+)	(+)	++	++	–	–	+	–	–	–	–	–	–	+	+
(= *A. amabilis*)	Widén *et al.* 1976	Japan	–	(+)	–	–	(+)	–	–	++	–	–/(+)	–	–	–	+	–	–
	Widén *et al.* 1978	Phil	–	(+)	–	–/+	–	–/++	–	++	–	–	–	–	–	–	–	–
A. aristata	RC 8473	NSW	–	+	–	++	++	–	–	–	–	–	–	–	–	–	–	–
(= *A. exilis*)	RC 9668	NSW	–	+	–	++	++	–	–	–	–	–	–	–	–	–	–	–
	Widen *et al.* 1976, 1981	Japan	–	+	–	++	++	–	–	–	–	–	–	–	–	–		–
	Widén *et al.* 1978, 1981	Phil	–	+	–	+	(+)	–	–	++	++	(+)	(+)	–	–	–	–	–
A. miqueliana	SP 5954	Japan	–	(+)	–	–	–	–	–	++	–	–	–	–	–	(+)	–	–
	Widén *et al.* 1976	Japan	–	++	–	(+)	–	–	–	+	(+)	–	–	–	–	–	–	–
A. maximowiczii	SM *s.n.*	Japan	–	(+)		–	–	++	–	–	–	–	–	–	–	–	–	–
	Widén *et al.* 1976	Japan	–	+		–	–	++	(+)	–	–	(+)	(+)	–	–	–	–	–
A. assamica	SP 5949	Japan	–	(+)		–	–	–	–	++	–	–	–	–	–	+	–	–
	Widen *et al.* 1978	Japan	–	(+)		–	–	–	–	++	–	–	–	–	–	–	–	–
Polystichum																		
P. tsus-simense	Widén *et al.* 1976,	Japan	–	++	–	++	(+)	–	–	++	–	–	–	–	–	–	–	–
3x, a	1978	Japan	–	++	–	–	–	–	–	++	–	(+)	(+)	–	–	–	+	–
P. rigens[4)]	Widén *et al.* 1978	Japan	–	(+)	–	–	–	++	–	–	–	(+)	–	–	–	–	–	–
Acrophorus																		
A. nodosus	Widén *et al.* 1978	Japan	–	–	–	++	–	–	–	–	–	–	–	–	–	–	–	–
A. paleolatus	JH 4194	Taiwan	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pleocnemia																		
P. conjugata	Widén *et al.* 1981	Borneo	–	–	+	–	–	–	–	–	–	–	–	–	+	–	–	+
P. irregularis	Widén *et al.* 1981	Borneo	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Polybotrya																		
P. caudata	Widén *et al.* 1983	Guyana	–	+	–	++	–	–	–	+	–	+	–	–	–	–	–	–

[1)] 2x = diploid, 3x = triploid, 4x = tetraploid, a = apomictic, s = sexual.
[2)] MJL = M. J. Lai, RC = R. Coveny, SP = S. Piippo, SM = S. Mitsuta, JH = J. Hyvönen.
[3)] Phil = Philippines, NSW = New South Wales.
[4)] In addition to the compounds listed in the table phloropyrone (*15*) was detected.

Table 13. Crude extractives and secretory structures in the phloroglucinol positive fern material investigated. Ex = external glands, Int = internal glands, n.s. = not studied.

Taxon	Collection number or lit. ref.	Origin	Dry rhizome in g	Ether extract in g (in %)		Crude filicin in g (in %)				Secretory structures
						MgO		$Ba(OH)_2$		
Dryopteris										
Subgenus *Erythrovaria*										
Section *Erythrovariae*										
D. championii	Widén *et al.* 1975	Japan	97	4.7	(4.9)	0.961	(1.0)	2.096	(2.2)	n.s.
D. erythrosora	—"—	Japan	51.5	2.3	(4.5)	0.750	(1.5)	1.332	(2.6)	n.s.
D. subtriangularis	Widén *et al.* 1993	N India	97	2.62	(2.66)	0.71	(0.72)	0.27	(0.28)	n.s.
	PHY 1750	China	2.8	0.08	(2.95)	n.s.		n.s.		n.s.
	CRFJ field no. 130	N India	90	3.5	(3.87)	n.s.		n.s.		n.s.
"*D. truncatulata*"	PE 6158	China	7.8	0.08	(1.0)	n.s.		n.s.		n.s.
Section *Variae*										
D. bissetiana	Widén *et al.* 1975	Japan	3.7	0.55	(14.9)	0.145	(3.9)	0.118	(3.2)	n.s.
D. sacrosancta	—"—	Japan	28	3.9	(3.99)	0.758	(2.7)	0.783	(2.8)	n.s.
Subgenus *Nephrocystis*										
Section *Purpurascentes*										
D. kilemensis	Widén *et al.* 1973	Kenya	182	0.49	(0.26)	–			–	n.s.
D. pulvinulifera	Widén *et al.* 1993	N India	23.9	1.55	(6.50)	0.17	(0.77)	0.34	(1.53)	n.s.
	Widén *et al.* 1978	Phil.	18.0	1.07	(5.97)	0.313	(1.74)	n.s.		Ex abundant, long stalked, 38–53 μm; Int: abundant, clavate, 85–105 μm
Section *Diclisodon*										
D. hasseltii	Widén *et al.* 1976	Japan	26	0.55	(2.1)	0.328	(1.25)	n.s.		Int: abundant, 48–77 μm (also Ex present)
D. sparsa	Widén *et al.* 1976	Japan	2	0.015	(0.75)	n.s.		n.s.		Ex few, short stalked.
	—"—	Japan	15	0.140	(0.93)	0.017	(0.11)	n.s.		
	CRFJ 8625, 8627–34	N India	10.5	0.105	(1.0)	n.s.		n.s.		
	CRFJ 8635–41	N India	5.0	0.053	(1.06)	n.s.		n.s.		
	CRFJ 8698–99	N India	12.8	0.134	(1.05)	0.031	(0.05)	0.99	(0.17)	
	CRFJ 9091, 9093–96	S India	21.0	0.093	(0.44)	n.s.		n.s.		n.s.
	CRFJ 9110, 9112–19	S India	10.7	0.087	(0.82)	n.s.		n.s.		n.s.
D. hayatae	Widén *et al.* 1976	Japan	2	0.022	(1.10)	n.s.		n.s.		Ex few in herbarium specimens
D. sabae	Widén *et al.* 1975	Japan	30.7	0.80	(2.6)	–		–		n.s.
D. undulata	CRFJ field no. 95	Sri La	12.1	0.073	(0.60)	n.s.		n.s.		n.s.
D. macrochlamys	CRFJ field no. 381–82	Sri La	3.2	0.023	(0.73)	–		–		n.s.

continued

Table 13. Continued.

Taxon	Collection number or lit. ref.	Origin	Dry rhizome in g	Ether extract in g (in %)	Crude filicin in g (in %)		Secretory structures
Dryopteris					MgO	$Ba(OH)_2$	
D. diffracta	PE 4080	China	2.6	0.007 (0.27)	–	–	Ex few in herbarium specimens (Widén *et al.* 1978)
Nothoperanema							
N. rubiginosa	CRFJ 14877–78	Hawai´i	3.3	0.012 (0.36)	n.s.	n.s.	Ex few
N. squamiseta	CRFJ 12295–96	Réunion	21.9	0.078 (0.36)	n.s.	n.s.	n.s.
	CRFJ 16.1.1993	Nepal	1.55	0.005 (0.32)	n.s.	n.s.	n.s.
	Widén *et al.* 1973	Kenya	150	0.58 (0.38)	–	–	–
N. hendersonii	Widén *et al.* 1978	Japan	9.49	0.036 (0.38)	–	–	–
		N India	1.79	0.003 (0.17)	–	–	–
N. shikokiana	Widén *et al.* 1978	Japan	0.16	0.005 (0.31)	–	–	–
Dryopsis							
D. apiciflora	CRFJ 8115–21	N India	44.3	1.290 (2.91)	0.110 (0.27)	0.562 (1.39)	Int: abundant long cylindrical, 150–210 μm; also resinous cells present
	Widén & Puri 1979	N India	135.0	7.3 (5.4)	0.697 (0.51)	0.878 (0.65)	n.s.
D. nidus	CRFJ 5758–60 8462–67	N India	24.7	1.076 (4.36)	0.041 (0.16)	0.098 (0.40)	n.s.
	CRFJ 15709, 15744–52	Nepal	7.6	0.295 (3.90)	n.s.	n.s.	Int: abundant, very long, cylindrical, 150–280 μm; no resinous cells present
D. clarkei	CRFJ 8770–76, 8482	N India	27.0	1.368 (5.07)	0.118 (0.47)	0.449 (1.80)	Int: abundant, very long, cylindrical, 150–280 μm; also resinous cells present
	Widén *et al.* 1979	N India	85.0	6.00 (7.1)	0.446 (0.52)	2.678 (3.15)	n.s.
	Widén *et al.* 1979	N India	135.0	9.35 (6.9)	1.125 (0.83)	3.138 (2.32)	n.s.
Peranema							
P. cyatheoides	CRFJ 15639	Nepal	2.7	0.008 (0.30)	n.s.	n.s.	Resinous cells, light brown, containing resinous bodies; no glands
Diacalpe							
D. aspidioides	CRFJ 15823–33	Nepal	24.2	0.374 (1.55)	n.s.	n.s.	Ex rather frequent, 60–80 μm
Rumohra							
R. adiantiformis	RC 9485	Aust	0.79	0.022 (2.77)	n.s.	n.s.	Resinous, hair-like cells in parenchyma, 50–60 μm; Ex few, ca. 100 μm
	IZ 2139	Arg	0.93	0.018 (1.95)	n.s.	n.s.	n.s.
	AK 656	Arg	1.01	0.027 (2.68)	n.s.	n.s.	n.s.
	AB 27433	Chile	1.75	0.041 (2.31)	n.s.	n.s.	n.s.

Stigmatopteris									
S. longicaudata	RC & CKM	Co Ric	0.95	0.046	(4.84)	n.s.		n.s.	n.s.
Ctenitis									
C. crinita									
var. *hispida*	CRFJ 12011	Madg	10.6	0.030	(0.30)	n.s.		n.s.	n.s.
	CRFJ 12034	Madg	5.7	0.020	(0.30)	n.s.		n.s.	n.s.
	CRFJ 12012	Madg	8.6	0.057	(0.66)	n.s.		n.s.	n.s.
C. crinita agg.	CRFJ 12228	May	21.4	0.092	(0.40)	n.s.		n.s.	n.s.
C. crinita agg.	CRFJ 12229	May	5.9	0.030	(0.50)	n.s.		n.s.	n.s.
C. setosa	Widén *et al.* 1978	Japan	13.0	0.080	(0.61)	0.013	(0.10)	n.s.	Ex very abundant, clavate, 110–154 μm.
C. subglandulosa	—"—	Japan	31.0	0.211	(0.68)	0.019	(0.06)	n.s.	Ex abundant clavate, short stalked, 86–120 μm; abundant stalked with round heads, 38–40 μm.
	—"—	Japan	105.0	0.417	(0.40)	0.129	(0.129	n.s.	As in the former
C. mannii	Widén *et al.* 1981	Borneo	84.1	0.330	(0.39)	n.s.		n.s.	Ex abundant, some stalked, with round to orbicular heads, transparent to yellowish, 42–63 μm.
Lastreopsis									
L. marginans (D)	RC 9413	NSW	37.9	0.269	(0.71)	0.063	(0.59)	n.s.	Ex abundant, clavate, and bent 60–70 μm
(E)	RC 9402	NSW	24.3	0.340	(1.40)				
	RC 9942	NSW	14.6	0.192	(1.32)	0.046	(0.32)	n.s.	n.s.
L. decomposita (A)	RC 9243	NSW	10.1	0.081	(0.80)	–		n.s.	Ex very few, clavate, 47–62 μm
(G)	RC 9414	NSW	182.5	0.587	(0.44)	0.009	(0.01)	n.s.	Ex abundant, clavate, 52–85 μm
	RC 9945	NSW	14.5	0.076	(0.52)	0.026	(0.19)	n.s.	n.s.
Arachniodes									
A. rhomboidea									
(*A. amabilis*)	MJL 13162–67	Taiwan	5.0	0.028	(0.57)	n.s.		n.s.	n.s.
	Widén *et al.* 1976	Japan	26.0	0.061	(0.23)	0.030	(0.11)	n.s.	Ex rather abundant, stalked, 48–67 μm
	—"—	Japan	37.0	0.287	(0.78)	0.015	(0.04)	n.s.	n.s.
	Widén *et al.* 1978	Phil	2.0	0.012	80.60)	n.s.		n.s.	Ex abundant, stalked, 48–68 μm
	—"—	Japan	10.1	0.056	(0.55)	0.007	(0.07)	n.s.	Ex few, stalked, 38–56 μm
A. aristata	RC 8473	NSW	11.5	0.140	(1.21)	n.s.		n.s.	Ex abundant, long stalked 60–90 μm
(= *A. exilis*)									
	RC 9668	NSW	50.8	0.168	(0.33)	0.069	(0.14)	n.s.	n.s.
	Widén *et al.* 1976	Japan	27.0	0.196	(0.72)	0.032	(0.12)	n.s.	Ex rather abundant, stalked, 38–53 μm.
	Widén *et al.* 1976	Japan	21.5	0.139	(0.65)	n.s.		n.s.	n.s.
	Widén *et al.* 1978	Phil	8.0	0.036	(0.45)	n.s.		n.s.	Ex few stalked, 48–68 μm.
	—"—	Japan	15.0	0.086	(0.57)	0.013	(0.09)	n.s.	Ex abundant, stalked 38–56 μm.

continued

Table 13. Continued.

Taxon	Collection number or lit. ref.	Origin	Dry rhizome in g	Ether extract in g (in %)	Crude filicin in g (in %)		Secretory structures
					MgO	$Ba(OH)_2$	
Dryopteris							
A. miqueliana	SP 5954	Japan	8.7	0.070 (0.81)	n.s	n.s.	n.s.
	Widén *et al.* 1976	Japan	29.0	0.110 (0.38)	–	–	–
	—"—	Japan	24.0	0.178 (0.759	0.017 (0.07)	n.s.	Ex rather abundant, stalked, 40–60 μm.
A. maximovicsii	SM *s.n.*	Taiwan	5.4	0.070 (1.30)	n.s.	n.s.	n.s.
	Widén *et al.* 1978	Japan	8.0	0.198 (2.48)	0.090 (1.13)	n.s.	Ex abundant, short stalked, 43–58 μm.
A. assamica	SP 5949	Taiwan	6.4	0.050 (0.78)	n.s.	n.s.	n.s.
	Widén *et al.* 1978	Japan	3.4	0.041 (1.22)	+	n.s.	n.s.
Acrophorous							
A. nodosus	Widén *et al.* 1978	Japan	20.8	0.116 (0.55)	0.008 (0.04)	n.s.	Ex locally abundant, short stalked, 24–42 μm
A. paleolatus	JH 4194	Taiwan	4.3	0.011 (0.26)	n.s.	n.s.	n.s.
Pleocnemia							
P. conjugata	Widén *et al.* 1981	Borneo	15.3	0.110 (.73)	n.s.	n.s.	Ex two kinds, one clavate, abundant, 42–57 μm, another hairly transparent with round heads, 67–118 μm
P. irregularis	Widén *et al.* 1981	Borneo	84.1	0.330 (0.39)	n.s.	n.s.	Extwo kinds, one clavate abundant, 65–70 μm, another hairly, few with round heads, transparent, 68–154 μm
Polybotrya *P. caudata*	Widén *et al. 1983*	Guyana	16.2	0.085 (052)	n.s.	n.s.	Ex few short stalked with large rounded heads, 54–56 μm

[1] PHY = Pei-His Yan, CRFJ = Christopher Fraser-Jenkins, Pe = unidentified collectors in PE (Beijing) herbarium, RC = R. Coveny, IZ = I. Zizich, AK = A. Kalela, AB = A. Burkhart, RC & CKM = R. C. & C. K. Moran, MJL = M. J. Lai, SP = S. Piippo, JH = J. Hyvönen, SM = S. Mitsuta.

[2] Phil = Philippines, Sri La = Sri Lanka, Austr = Australia, Arg = Argentina, Co Ric = Costa Rica, Madg = Madagascar, May = Mayotte Island, NSW = New South Wales.

and shape of the glands without secretion can be readily observed (Fig. 6). In all three species long-stalked, cylindrical glands with elongated heads occur (cf. also Mehra & Mittal 1961). They differ in morphology from those in most *Dryopteris* species but are relatively similar to the long-stalked, club-shaped glands of *D. pulvinulifera* and *D. wallichiana* (Spreng.) Hyl. (Mehra & Mittal 1961, Widén *et al*. 1978). Large internal glands of unknown morphology are reported to occur also in the leaf parenchyma of *Stigmatopteris* (Moran 1991). However, in the sole available leaf of *S. longicaudata* no glands were observed by us.

Interestingly, apart from in *Dryopsis apiciflora* and *D. clarkei*, resinous cells occur also in parenchyma of *Rumohra adiantiformis* (brown, gland-like cells) and *Peranema cyatheoides* (light brown cells containing resin bodies) (Fig. 6). In the latter sclerenchymatic cells were frequent, but no external/internal glands were observed. Both *P. cyatheoides* and *Diacalpe aspidioides* contained only small internal cavities. It seems likely that the phloroglucinols are stored also in the resinous cells in *P. cyathoides* discussed above, as no glands could be observed (cf. also discussions by Mehra & Mittal 1961). In the taxa of all other genera except *Dryopteris* only external glands occur (Table 6). In Figs. 7–9, we present the glands of *Rumohra adiantiformis* with secretion, and *Lastreopsis marginata* and *L. decomposita* without secretion. The glands of *Lastreopsis* are often bent as observed in *L. marginans*.

Of the four species of *Nothoperanema* investigated for occurrence of phloroglucinols *N. rubiginosa* contained small locally frequent glands on the epidermis of the stipe bases. Some resin-

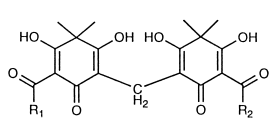
Table 14. The semiquantitative composition of the acylfilicinic acids (36) and homologues, *see* Widén *et al*. 1991) after reductive cleavage of the crude filicins. V = valeryl, iB = *iso*butyryl, B = butyryl, P = propionyl, A = acetyl. For abbreviations and further data *see* Table 1.

Taxon	Collection no. or lit. ref.	Origin	Acylfilicinic acids (36) in % of or total amount				
			V	iB	B	P	A
Subgenus *Erythrovaria*							
Section *Erythrovariae*							
D. championii	Widén *et al*. 1975	Japan	–	–	90	6	4
D. erythrosora	Widén *et al*. 1975	Japan	8	18	60	2	12
D. subtriangularis	Widén *et al*. 1993	N India	–	60	30	–	10
Section *Variae*							
D. sacrosancta	Widén *et al*. 1975	Japan	–	–	40	40	20

Table 15. The semiquantitative composition of the aspidinols (*2*) obtained after reductive cleavage of the crude filicins of the different taxa of *Dryopsis*[1)].

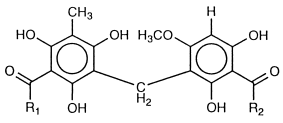
Taxon	Collection no.	Origin	Aspidinol V(*2*-V)	Aspidinol B(*2*-B)	Aspidinol P(*2*-P)	Aspidinol A(*2*-A)
D. apiciflora	CRFJ 8515–21	N India	45	45	10	–
D. clarkei	CRFJ 8470–76 CRFJ 8482	N India	10	85	5	–
D. nidus	CRFJ 8458–60 CRFJ 8462–67	N India	20	40	40	–

[1)] Due to the very small amounts of compounds containing acylfilicinic acids (*36*) in their molecules, no spots of these acids were found in the present material.



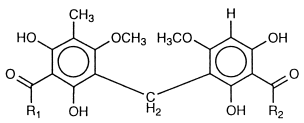
10

$R_1 = R_2 = C_3H_7$ Albaspidin-BB (***10***-BB)
$R_1=C_2H_5$; $R_2=C_4H_9$ Albaspidin-PV (***10***-PV)
$R_1=C_2H_5$; $R_2=C_3H_7$ Albaspidin-PB (***10***-PB)



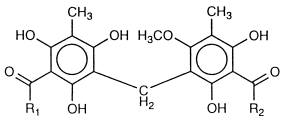
11

$R_1=C_4H_9$; $R_2=C_3H_7$ Phloraspin-VB (***11***-VB)
$R_1=C_3H_7$; $R_2=C_4H_9$ Phloraspin-BV (***11***-BV)
$R_1 = R_2 = C_3H_7$ Phloraspin -BB (***11***-BB)



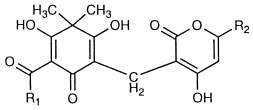
12

$R_1=C_4H_9$; $R_2=C_3H_7$ Phloraspidinol-VB (***12***-VB)
$R_1=C_3H_7$; $R_2=C_4H_9$ Phloraspidinol-BV (***12***-BV)
$R_1 = R_2 = C_3H_7$ Phloraspidinol-BB (***12***-BB)



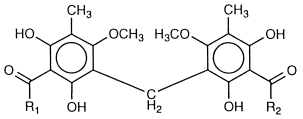
13

$R_1=C_4H_9$; $R_2=C_3H_7$ Margaspidin-VB (***13***-VB)
$R_1=C_3H_7$; $R_2=C_4H_9$ Margaspidin-BV (***13***-BV)
$R_1 = R_2 = C_3H_7$ Margaspidin-BB (***13***-BB)
$R_1=C_2H_5$; $R_2=C_3H_7$ Margaspidin-PB (***13***-PB)
$R_1=C_3H_7$; $R_2=C_2H_5$ Margaspidin-BP (***13***-BP)
$R_1 = R_2 = C_2H_5$ Margaspidin-PP (***13***-PP)



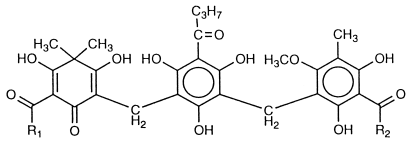
15

$R_1 = R_2 = C_3H_7$ Phloropyrone-BB (***15***-BB)
$R_1=C_2H_5$; $R_2=C_3H_7$ Phloropyrone-PB (***15***-PB)
$R_1=C_3H_7$; $R_2=C_2H_5$ Phloropyrone BP (***15***-BP)



18

$R_1=C_4H_9$; $R_2=CH_3$ Methylene-bis-aspidinol-VB (***18***-VB)
$R_1 = R_2 = C_3H_7$ Methylene-bis-aspidinol-BB (***18***-BB)



20

$R_1=C_4H_9$; $R_2=C_3H_7$ Trispara-aspidin-VBB (***20***-VBB)
$R_1=C_3H_7$; $R_2=C_4H_9$ Trispara-aspidin-BBV (***20***-BBV)
$R_1 = R_2 = C_3H_7$ Trispara-aspidin-BBB (***20***-BBB)
$R_1=C_2H_5$; $R_2=C_3H_7$ Trispara-aspidin-PBB (***20***-PBB)
$R_1=C_3H_7$; $R_2=C_2H_5$ Trispara-aspidin-BBP (***20***-BBP)

Fig. 4. Chemical structures of the compound isolated from the three Himalayan *Dryopsis* species.

ous cells in the parenchyma of the rhizome were detected. In *N. hendersonii* both glands and phloroglucinols were lacking.

The glands of *Arachniodes*, *Polystichum*, *Pleocnemia* and *Polybotria* have been discussed in detail in Widén *et al*. (1976, 1978, 1981, 1983) and Gibby *et al*. (1991), *see also* Table 13.

For comparison we present hairs with glandular tops from *Arthropteris tenella* (Fig. 10). They are multicellular and quite different from those in the other ferns investigated (cf. Sen & Sen 1973). No resinous secretion was present.

Discussion

As in part I and II of the present series (Widén *et al*. 1996, 1999), the main purpose of the present work was to find out how chemical composition reflects taxonomic relationships in the taxa of *Dryopteris* material investigated and those of related genera. It was found that in some sections of subgenus *Dryopteris* the phloroglucinol patterns were relatively constant (e.g. sections *Fibrillosae*, *Hirtipedes*, *Pandae*, *Dryopteris* and *Lophodium*), whereas in others (sections *Splendentes*, *Aemulae* and *Remotae*) a wide variation of

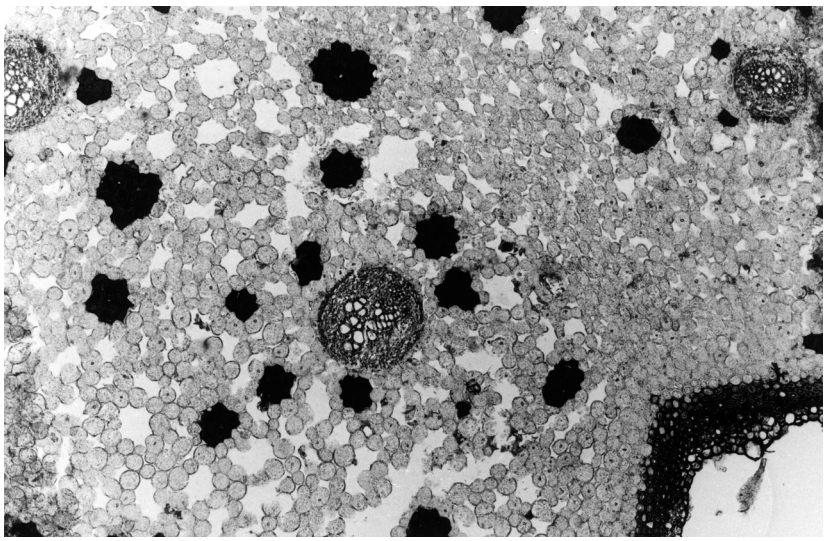


Fig. 5. A cross section of a petiolar base of *Dryopsis nidus* from Nepal showing three amphicribral vascular bundles and numerous sclerenchymatic bundles (black) as well as large intercellular cavities in the ground parenchyma. The long-stalked, cylindrical internal glands are transversely cut and are not visible in the cross sections (or only fragments of these can be seen). Magnification 43×.

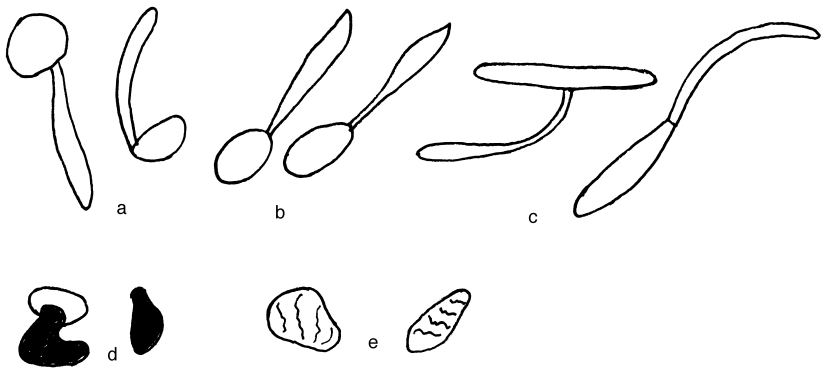


Fig. 6. Macerated gland-bearing cells of: (**a**) *Dryopsis apiciflora*, (**b**) *D. clarkei*, (**c**) *D. nidus*, (**d**) brown resinous gland-like cells from *Rumohra adiantiformis*, and (**e**) light brown resinous cells from *Peranema cyatheoides* with resin bodies. All these are from parenchyma of the rhizomes, 90×.

the phenolics was found. As in Widén *et al*. (1999) the previously investigated species are not usually discussed in detail if no new results are available. Literature references including those of other research groups (Hisada & Noro 1961, Hisada 1961, 1966, Hisada *et al*. 1971, 1972, 1974) are also included in the tables. Concerning the reliability of the older investigations, *see* detailed discussions in Widén *et al*. (1996, 1999).

Dryopteris

Subgenus *Erythrovaria*

Section Erythrovariae (Table 8)

This section contains approximately 25 species (Fraser-Jenkins 1986, subsequently modified) of which 11 were studied by Hisada and Noro (1961), Hisada (1961, 1966) Hisada *et al*. (1974) and Widén *et al*. (1975, 1993 and present paper). Aspidin (*6*) is regularly present in the taxa investigated except for *Dryopteris subtriangularis* in which it is totally absent, though it is a typical member of the section. Also albaspidin (*10*) usually occurs in these ferns.

Dryopteris championii shows a somewhat different phloroglucinol composition from the other taxa in containing desaspidin (*8*) and trisdesaspidin (*21*). Desaspidin (*8*) but no trisdesaspidin (*21*) was reported from *D. kinkiensis* (Hisada & Noro 1961, Hisada 1966), probably due to the fact that the Japanese authors were lacking the latter compound. Therefore we consider that trisdesaspidin (*21*) may occur also in *D. kinkiensis* as *8* and *21* usually occur together (cf. Widén *et al*. 1999). Both species are typical members

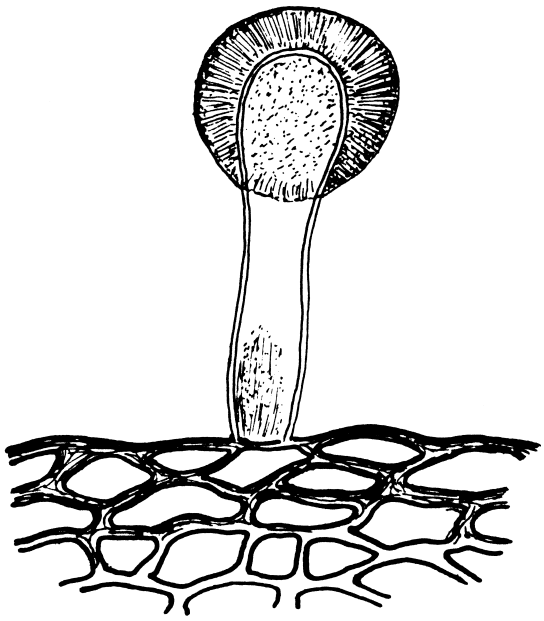


Fig. 7. An external gland of *Rumohra adiantiformis* on the leaf epidermis. Observe lipophilic secretion between the outer cell wall and cuticle (lined area), 450×.

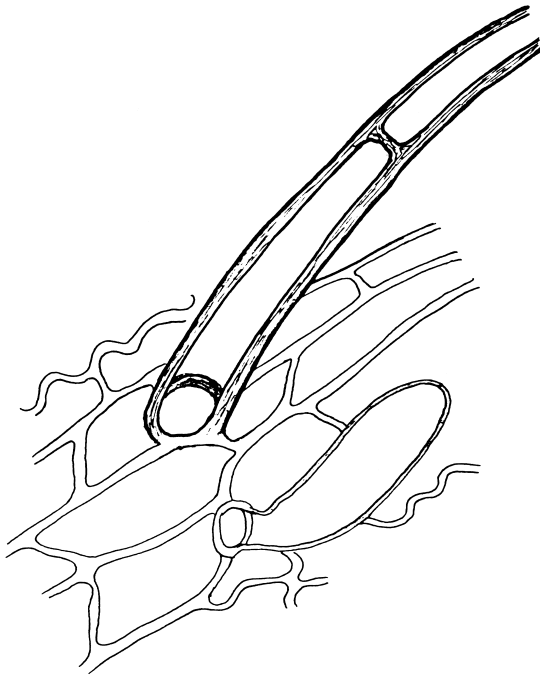


Fig. 9. Longitudinal section of a leaf of *Lastreopsis decomposita* showing a clavate glandular hair and part of a two-cellular hair. Secretion is removed, 400×.

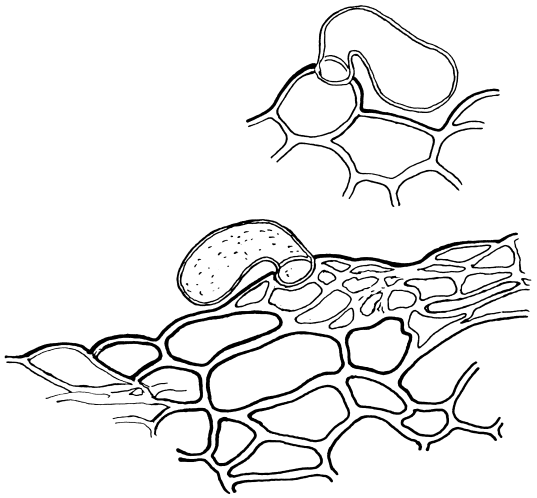


Fig. 8. Cross section of a rhizome (upper part) of *Lastreopsis marginans* and longitudinal section of the same showing typical clavate, bent glands. Secretion is removed by treatment with 5% KOH, 400×.

of the section.

The finding of aspidin -iBiB (*6*-iBiB) and albaspidin -iBiB (*10*-iBiB) in *Dryopteris erythrosora* is most interesting (Widén *et al.* 1975). Later on *10*-iBiB was found also in *D. subtriangularis* (Widén *et al*. 1993 and present work). We were also able to isolate a new compound subtriangularin -iB (*34*-iB), the structure of which could not be evaluated in every single detail (Widén *et al*. 1993). *34*-iB was also present in Chinese material of *D. subtriangularis*. However, our efforts to isolate more subtriangularin -iB (*34*-iB) from additional NE Indian material of that fern (also from Meghalaya, where the previous NE Indian material was from) failed because *34*-iB was totally absent from the new fern material (CRFJ field nos. 528, 530). Consequently subtriangularin (*34*-iB) is not regularly present in *D. subtriangularis*. "*D. truncatulata*" from China, which is most likely closely related to *D. subtriangularis*, was also totally lacking subtriangularin (*34*-iB). However, "*D. truncatulata*" did contain aspidin (*6*).

Phloroglucinols with branched isobutyryl (iB) side chains have never before been reported from *Dryopteris* and are consequently very interesting from a biochemical point of view. However, related phloroglucinols with branched,

mainly *iso*butyryl side chains, occur in kousso flowers, *Hagenia abyssinica* Gmelin (Rosaceae) (Lounasmaa *et al.* 1973a, 1973b).

Interestingly aspidin-AA (*6*-AA) with both side chains consisting of acetyl groups (A) has been reported only from *Dryopteris gymnosora* (Hisada *et al.* 1974). So far this compound has not found in any other *Dryopteris* species, though its existence has been postulated in *Arachniodes mutica* (Fr. & Sav.) Ohwi; *see* Widén *et al.* (1976: table 2, footnote 3).

With the exception of *Dryopteris subtriangularis* the phloroglucinol composition of section *Erythrovariae* is relatively constant.

Section *Politae* (Table 9)

The sole species of this section has been investigated only by Hisada and Noro (1961) and Hisada (1966), and was found to be totally devoid of phloroglucinols. *Dryopteris polita* is a species of somewhat uncertain relationship, but is perhaps related to section *Erythrovariae*, but is without bullate scales. It also shows some features of subgenus *Nephrocystis* and may be an ancient and primitive species in that subgenus, *see* p. 101.

Section *Variae* (Table 9)

Fraser-Jenkins (1986) listed 10 species of which 7 were investigated by Hisada and Noro (1961), Hisada (1966), Hisada *et al.* (1971), and Widén *et al.* (1975). Margaspidin (*13*) is usually present except in *Dryopteris sordidipes* and *D. formosana*, which lack this compound. It may be observed that the aspidinol (*2*) reported by Hisada and Noro (1961) and Hisada (1966) is not a naturally occuring compound. It is most probably formed by decomposition from margaspidin (*13*) when preparing crude filicins. Para-aspidin (*7*), the other probable source, is lacking in these ferns (Table 2; cf. also discussions in Widén *et al*. 1996 and 1999). It seems likely that a similar block in the biosynthesis of para-aspidin (*7*), from margaspidin (*13*) that was found in *D. marginalis, D. panda* and some other ferns (subgenus *Dryopteris*), may also occur in *D. saxifraga, D. bissetiana, D. hikonensis* and *D. sacrosancta* of section *Variae* (cf. discussion in Widén *et al*. 1999).

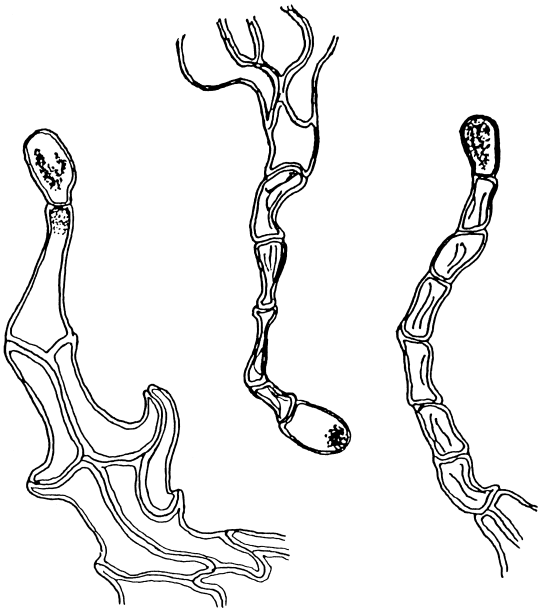


Fig. 10. Multicellular hairs of *Arthropteris tenella* with glandular tips from stipe bases, 160×.

With the exception of *Dryopteris sordidipes* and *D. formosana* section *Variae* is fairly uniform as far as the phenolics here studied are concerned. The latter species is, however, slightly atypical in the section and in its morphology towards section *Erythrovariae*.

When considering the entire subgenus *Erythrovaria* phloroglucinols are regularly present except in *Dryopteris polita* (section *Politae*). Section *Erythrovariae* is characterized by the occurence of aspidin (*6*) whereas section *Variae* usually contains margaspidin (*13*).

Subgenus *Nephrocystis*

Section *Purpurascentes* (Table 10)

Of the 13 species listed by Fraser-Jenkins (1986, subsequently modified, included) only two have been studied by Widén *et al.* (1976, 1978, 1993). One of these, *Dryopteris kilemensis*, proved to lack phloroglucinols totally (Widén *et al.* 1973). The other one, *D. pulvinulifera,* showed a varia-

ble phloroglucinol spectrum in material from different sources. The Philippine material contained aspidin (*6*), whereas that from N India was devoid of *6* and proved to contain a new closely related substance, pulvinuliferin (*33*) (Widén *et al.* 1978, 1993). Apparently two different geographically separated chemical races, a "aspidin-race" and a "pulvinuliferin-race", are present in *D. pulvinulifera*, which demonstrates how sensitive the phloroglucinol chemistry can be.

Because of the limited material investigated no final conclusions can so far be drawn on the phloroglucinol patterns of section *Purpurascentes,* although the two species here investigated proved to vary considerably. The morphology of *Dryopteris pulvinulifera* is not very typical of the section and apart from the narrow stipe-base scales, it may be closer to section *Diclisodon*.

Section *Diclisodon* (Table 10)

Fraser-Jenkins (1986) listed 14 species subsequently modified, (*see* Darnecki *et al*. 1989a, 1989b, 1990) of which seven were investigated by Hisada and Noro (1961), Hisada (1966), and Widén *et al.* (1975, 1976 and present work). Of the species studied *Dryopteris sabae, D. macrochlamys* and *D. diffracta* and *pro parte D. sparsa* were totally devoid of phloroglucinols and *D. sparsa* (major part), *D. subexaltata* and *D. undulata* contained only traces or minute amounts of these compounds. Only *D. hasseltii* proved to contain a somewhat greater percentages of ether extract and crude filicin (Table 13; *see also* Widén *et al.* 1976), though this species is obviously closely related to *D. sparsa*. "*D. sparsa*" consists of quite a large aggregate of closely related species of various different or similar cytotypes. The common taxa in the Himalayan region appears to be the diploid sexual true *D. sparsa*, but a tetraploid sexual taxa considered by Fraser-Jenkins (1989 and present paper) to be *D. viridescens*, occurs sympatrically with it from C Nepal eastwards. Other species in the aggregate occur in Japan and SE Asia, including triploid apomicts. These taxa should be carefully separated when examining new or previous phytochemical reports. *Dryopteris diffracta* may belong here or could belong to a distinct genus, *Acrorumohra*.

Albaspidin (*10*) seems to be the most common phloroglucinol in this section; it occurs in *Dryopteris hasseltii, D. sparsa* (p.p.), *D. subexaltata* and *D. undulata.* In *D. sparsa* trace amounts of para-aspidin (*7*), phloraspidinol (*12*) and filixic acid (*19*) occur as well. However, the aspidin (*6*) reported by Widén et al.(1976) from Japanese *D. sparsa* was erroneous; it should be corrected to filixic acid (19) as was found in connection with the present work. Hisada and Noro (1961) and Hisada (1966) report a total absence of phloroglucinols in Japanese *D. sparsa*. However, at that time they worked with less sensitive paper chromatography. We, therefore, consider that their material of *D. sparsa* may have at least in part contained some phloroglucinols as most of the material studied by us with more sensitive TLC. However, it must be borne in mind that at least some of the Japanese material may have been different from true *D. sparsa*, which is very uncommon there, while *D. viridescens* appears to be the common representative of the group and other taxa are also present in Japan.

As the fairly extensive material of *Dryopteris sparsa* studied so far proved to contain only traces of phenolics or even totally lacks these compounds, no conclusions can be drawn on the taxonomy and cytology of these plants from chemistry. Section *Diclisodon* proved to be very phloroglucinol poor although external glands were found in several species investigated. *Dryopteris hasseltii* is an exception with its internal glands and relative high content of phloroglucinols. This species has several times been included in *Arachniodes*, but in its morphology it is obviously closer to that of section *Diclisodon*. In the entire subgenus *Nephrocystis* phloroglucinols are often lacking or only traces or small amounts of these compounds are present.

Other genera

Dryopsis (Table 11)

Of the 26 species listed by Holttum and Edvards (1986) we have investigated five. Two of these, *Dryopsis maximowicziana* and *D. ferruginea* var. *obtusiloba* proved to be totally devoid of phenolics (Widén *et al*. 1976 and present paper). However, in three of the Himalayan representives of *Dryopsis*, namely *D. apiciflora*, *D. clarkei* and *D. nidus*, considerable amounts of ether extract (oleo-resin) and crude filicin were found (Mehra & Mittal 1961, Widén & Puri 1979, present paper). All these taxa also contained large intercellular cavities and typical long cylindrical internal glands (*see* Fig. 6, p. 125, cf. also Mehra & Mittal 1961). It would be interesting to study other species of *Dryopsis* for occurrence of phloroglucinols and glands. The *D. apiciflora* group, consisting of species with narrow bipinnatified fronds, is somewhat distinct from the rest of the genus.

Dryopsis apiciflora. The main compounds in both samples investigated were phloraspin (*11*) and margaspidin (*13*) accompanied by minute amounts of aspidinol (*2*, artefact), para-aspidin (*7*) and trispara-aspidin (*20*). The major difference between the two collections investigated was the occurrence of much phloropyrone (*15*) in Puri 20.6 whereas those from W Bengal (CRFJ 8115–21) were totally lacking phloropyrone (*15*); i.e two chemotypes are present, one "phloropyrone type" and another "type lacking phloropyrone" (*15*). Trace amounts of albaspidin (*10*), flavaspidic acid (*5*) and trisflavaspidic acid were also detected in Puri 20.6.

Dryopsis clarkei. This species showed a similar phloroglucinol composition to that of *D. apiciflora.* Phloraspin (*11*) and margaspidin (*13*) were the main phloroglucinols accompanied by traces or small amounts of aspidinol (*2*, artefact), flavaspidic acid (*10*) p.p., phloraspidinol (*12*), methylene-bis-aspidinol (*18*), albaspidin (*10*), phloropyrone (*15*) and phloraspyrone (*16*).

Dryopsis nidus. The main compound was margaspidin (*13*) along with huge amounts of phloropyrone (*15*), but phloraspin (*11*) was totally lacking in distinct contrast to the two other species. Minute amounts of aspidinol (*2*, artefact), flavaspidic acid (*5*) p.p., para-aspidin (*7*), methylene-bis-aspidinol (*18*), albaspidin (*10*) and phloraspyrone (*16*) were also present.

The almost exclusive presence of fully aromatic compounds *11, 12, 13* and *18* in the three Himalayan representatives of *Dryopsis* is most interesting. Presumably an even more effective block in the biosynthesis of para-aspidin (*7*) and desaspidin (*8*), than that which has been concluded to exist in *Dryopteris marginalis* L. A. Gray and some other taxa of *Dryopteris* subgenus *Dryopteris* and several taxa of subgenus *Erythrovaria*, (section *Variae*; *see* pp. 100–101), also occurs in *D. apiciflora, D. clarkei* and *D. nidus*.

Peranema cyatheoides (Table 11)

In this species only flavaspidic acids (*5*) and filixic acids (*19*) were found.

Diacalpe aspidioides (Table 11)

The phloroglucinol composition is considerably different from that of *Peranema cyatheoides*; the main compound was phloropyrone (*15*) accompanied by small amounts of flavaspidic acid (*5*) and albaspidin (*10*). The chemical differences between these two species could perhaps be interpreted as a factor strengthening the decision to keep *Peranema* and *Diacalpe* as two different genera. There are also differences in the glandularity of the rhizome and petiolar bases (Table 13).

Rumohra adiantiformis (Table 11)

In this species only phloropyrone (*15*) was detected in material from widely different parts of the world.

Stigmatopteris (Table 11)

For our investigations only a single herbarium voucher of *Stigmatopteris longicaudata* sent by Dr. R. C. Moran was available. In this species only flavaspidic acids (*5*) and norflavaspidic acids (*4*) were observed. The presence of glands (Moran 1991) and phloroglucinol derivatives makes this interesting fern genus worth of further study.

Ctenitis (Table 11)

Ten species were investigated by us of which 6 were totally devoid of phloroglucinols and the rest, four taxa, contained only traces of these compounds (Widén *et al.* 1978, 1983, present work). In this respect, they were different from the three Himalayan representatives of *Dryopsis* which were formerly included in *Ctenitis* (Holttum & Edwards 1985, 1986). However, in *Ctenitis* as well the occurence of the fully aromatic compounds *11, 12, 13, 18* is noteworthy as these are found in trace amounts in *C. setosa*, *C. subglandulosa* and *C. crinita* var. *hispida* pointing to the relationship between these two genera. Furthermore it is interesting to note that *C. mannii* is quite different from the above species in containing flavaspidic acids (*5*) and albaspidins (*10*). Thus *Ctenitis* is still a heterogenous genus from at least a chemical point of view.

Lastreopsis (Table 11)

Of the 10 species investigated only two proved to contain clearly detectable amounts of phenolic compounds of unknown structure (*see* Table 13). These were the Australian species *Lastreopsis marginans* and *L. decomposita*. All the other were devoid of phloroglucinols, though some external glands were observed also in the other species investigated. The difference in chemistry and in the morphology of glands point to the modern separation of *Ctenitis* and *Lastreopsis* as distinct genera.

Arachniodes (Table 12)

We investigated 27 species of which 24 proved to contain minute amounts of phloroglucinols and glands (Widén *et al.* 1976, 1978, 1981, Gibby *et al.* 1991). Only three species, *Arachniodes pseudo-aristata* (Tagawa) Ohwi, *A. standishii* (T. Moore) Ohwi and *A. superba* (*see* Table 6) totally lacked phloroglucinols.

Arachniodes rhomboidea (*A. amabilis*) shows a slightly varying phloroglucinol composition in material from different sources: The Taiwan ferns contain considerable amounts of aspidin-BB (*6*-BB) and -AB (*6*-AB) in contrast to the Japanese and Philippine ferns.

Arachniodes aristata appears to consist of two geographically separated races; an "aspidin race" occurring in Australia and Japan and a "desaspidin race" in the Philippines (cf. also Widén *et al.* 1976, 1981).

Arachniodes miqueliana seems to vary somewhat in its phloroglucinol composition, but is not considered here to consist of any different chemotypes or races; the contents of flavaspidic acid (*5*) and desaspidin (*8*) vary considerably.

Both samples of *Arachniodes maximoviczii* investigated were fairly uniform with para-aspidin (*7*) as the main compound (cf. Widén *et al.* 1976).

Arachniodes assamica also proved to be uniform with considerable percentages of desaspidin (*8*) in its phloroglucinol pattern (cf. Widén *et al.* 1978).

Nothoperanema (Table 10)

In previous investigations *Nothoperanema squamiseta*, *N. shikokiana* and *N. hendersonii* had been found to be totally devoid of phloroglucinols (Hisada & Noro 1961, Widén *et al.* 1973, 1978). In the present work however, trace amounts of albaspidin (*10*) and abbreviatin (*30*) were detected in *N. squamiseta* from the Reunion Island and minute amounts of several phloroglucinols in the material from Nepal. *Nothoperanema rubiginosa*, which was investigated for

the first time in the present work, contained only traces of albaspidin (*10*) (Table 10). Although the genera *Dryopteris* and *Nothoperanema* are undoubtedly closely related the total lack of or occurrence of only minute amounts of phloroglucinols point to the chemical diversity of these two genera. However, subgenus *Nephrocystis* is closely similar in this respect.

Acrophorus (Table 12)

Acrophorus nodosus from S Japan was found to contain aspidin (*6*) and phloroglucinols of unknown structure (Widén *et al*. 1978). However, *A. paleolatus* from Taiwan was totally lacking these compounds. In this respect, *Acrophorus* is much different from the related genera *Peranema* and *Diacalpe*.

Polybotrya (Table 12)

Minute amounts of phloroglucinols were observed in *Polybotrya caudata* (Widén *et al.* 1983). Also in this case the phloroglucinol composition is very different from the related genus *Stigmatopteris*.

Polystichum (Tables 12 and 13)

All five species investigated, *Polystichum speciosissimus*, *P. hancockii*, *P. parvipinnulum*, *P. prionolepis* and *P. deltodon* were totally devoid of phloroglucinols. Of the ca. 22 species investigated on a worldwide basis (Ackermann 1947, Harada 1951, 1952, Inagaki *et al*. 1961, Mehra & Mittal 1961, Puri *et al*. 1976, Widén *et al*. 1976, 1978, 1983) only *P. tsus-simense* (Hook.) J. Sm. and *P. rigens* Tagawa have been found to contain some phenolics.

Conclusions

Although we have not yet published our results on section *Marginatae* of subgenus *Dryopteris* (Widén *et al.* in prep.) we are now able to draw conclusions on the occurrence of phloroglucinols in *Dryopteris* and other related fern genera.

In general, with only few exceptions (*see* Widén *et al*. 1999), the ferns of *Dryopteris* subgenus *Dryopteris* contain considerable amounts of oleo-resin (ether extract) and phloroglucinols (crude filicin) in their rhizomes and stipe bases.

In subgenus *Erythrovaria* huge amounts of phloroglucinols are present, except for section *Politae*, in which the sole taxon present is totally lacking in phloroglucinols. Interestingly compounds with branched isobutyryl (iB) side chains have been found in section *Erythrovariae* (*6*-iBiB, 34-iB) exclusively. Fully aromatic compounds *13* and *18*, that are found in certain taxa of subgenus *Dryopteris*, also occur in subgenus *Erythrovaria* and in the three Himalayan representatives of the genus *Dryopsis*. Phloropyrone (*15*) occurs in several species of section *Lophodium* and some species of sections *Cinnamomae* and *Aemulae* (subgenus *Dryopteris*). It is noteworthy that (*15*) also has been detected in *Dryopsis*, *Rumohra* and *Diacalpe* outside *Dryopteris*.

Considering the absence of phloroglucinols in section *Politae*, this may well reflect the possibility that its sole species, *Dryopteris polita*, is not closely related to the rest of the subgenus *Erythrovaria*. Fraser-Jenkins has long been unsure where this species fits and what its closest relatives are. In the light of the finding that it is without phloroglucinols he now thinks that it might be a member of subgenus *Nephrocystis*, perhaps belonging to section *Diclisodon*, which would also tie in with its lack of bullate scales. We therefore now sink section *Politae* within section *Diclisodon*, which is a further demostration of how phloroglucinol-chemistry can sometimes be utilized taxonomically above the level of species provided it ties in with morphological considerations.

However subgenus *Nephrocystis* differs from the other subgenera of *Dryopteris* in containing only trace amounts of phloroglucinols. Many of its species even totally lack these compounds. In

this respect it resembles *Arachniodes*, perhaps its closest relative outside of *Dryopteris*.

Of the genera outside *Dryopteris*, substantial amounts of phloroglucinols have been observed only in three *Dryopsis* species (*D. apiciflora, D. clarkei, D. nidus*). From a morphological point of view the three Himalayan *Dryopsis* species are similar to the ferns of section *Fibrillosae* within *Dryopteris*, especially *D. wallichiana* (*see* Widén *et al*. 1996). Like section *Fibrillosae* all these ferns contain much phloroglucinols and internal glands, although there are certain differences in the chemical structures of the phloroglucinols and in morphology of the glands (cf. Mehra & Mittal 1961). However it is not possible to decide whether or not this indicates any kind of taxonomic relationship. Small but clearly detected amounts of these compounds also occur in *Peranema cyatheoides* and *Diacalpe aspidioides*, several *Arachniodes* species, *Stigmatopteris longicaudata, Polystichum tsus-simense*, *P. rigens*, *Polybotrya caudata* and *Acrophorus nodosus.* In addition trace amounts of phenolics have also been observed in *Nothoperanema squamiseta* and *N. rubiginosa.* All other genera or species of the dryopteroid ferns investigated proved to be totally devoid of phloroglucinols.

Of the Tectarioideae only a few *Ctenitis* and *Lastreopsis* species as well as *Pleocnemia conjugata* and *P. irregularis* proved to contain any detectable amounts of phloroglucinols. All the remaining species of *Ctenitis* and *Lastreopsis* and other related genera investigated were lacking in these phenolics. These findings agree with the placement of these genera in a different subfamily in contrast to our earlier statement (Widén *et al*. 1983). At that time the profusely phloroglucinol rich Himalayan *Dryopsis* species were included in *Ctenitis* and consequently belonged to the tectarioid ferns.

Rumohra adiantiformis, which has been considered to belong either within Dryopteridaceae or the Davalliaceae by different authors, e.g. Holttum (1947), Crabbe *et al*. (1975) and Pichi Sermolli (1977b), contains phloroglucinols and secretory structures. In this respect, it is closer to the dryopteriod ferns as the davallioid ferns investigated totally lack the phenolics studied. Fraser-Jenkins (1986: 185) and more recently Fraser-Jenkins (1997a: 38–39) backed up Pichi Sermolli (1977b) that *Rumohra adiantiformis* belongs to the Dryopteridaceae. In the latter work (Fraser-Jenkins 1997a), he says that *Rumohra* and *Arachniodes* may be congenic.

The occurence of phloroglucinols is always connected with presence of secretory structures. With only few exceptions (*see* Widén *et al.* 1983) internal secretory glands occur in *Dryopteris*. Such glands are also present in the three *Dryopsis* species listed above. In the other taxa of genera outside *Dryopteris* only external glands occur. Apparently the phloroglucinols can also more rarely be located in resinous cells in the parenchyma of the rhizomes and petiolar bases as found in the present work (cf. Mehra & Mittal 1961).

Experimental procedures

Extraction procedure and analysis of rhizomes

For the preparation of crude extractives and isolation of pure compounds we used both the old standard method and the new improved method (*see* von Euw *et al*. 1980, 1985, Patama & Widén 1991, Widén *et al*. 1996). In the present paper only *Dryopsis apiciflora*, *D. clarkei* and *D. nidus* were preparatively separated, *see* below.

For final identification of individual phloroglucinols we had a complete set of pure reference substances. For structure and numbering *see* Table 4 in Widén *et al*. (1991) and Widén *et al*. (1993, 1996, 1997). Phloraspyrone (*16*) was not available for us during the isolation procedure. Its occurence in *Dryopsis clarkei* and *D. nidus* was later detected in TLC using synthetic *16* as standard (cf. Penttilä & Sundman 1963).

Thin layer (TLC) and paper chromatography (PC)

For details *see* Widen *et al*. (1993, 1996) and references therein.

Investigation of secreting glands (hairs)

The secreting glands were studied from lactic acid preparations and the lipophilic secretions were stained red with Sudan III colouring matter. The morphology of the internal glands was studied from rhizome pieces macerated with 5% KOH (*see* Mehra & Mittal 1961, Widén *et al.* 1976). The glands retain their shape and form perfectly in the macerates.

Treatment of ether extract of *Dryopsis apiciflora*

The crude filicin ether extract of *D. apiciflora* (*CRFJ 8115–21*; 15.54 g) was dissolved in 50 ml ether (Fraction A), whereupon 2.073 g of an insoluble part (Fraction B) remained unsolved.

Fraction A (12.694 g) was shaken with aqueous HCl and H_2O to give 11.351 g cation-free ether extract after removal of the solvent. The cation free ether extract was devided in a methanol fraction (8.303 g) and a hexane fraction (1.732 g).

The methanol fraction was separated by chromatography on silica gel buffered at pH 4.0 (cf. von Euw *et al.* 1980), *see* below next section.

The hexane fraction contained only traces of phloroglucinols (para-aspidin, methylene-bis-aspidinol) and was therefore not further worked up.

Fraction B consisted of phloraspin contaminated by some margaspidin and melted at 172°/185–191 °C. It was not further processed.

Separation of the methanol fraction

Fractions 1–219 were eluted with hexane–chloroform 4:1.

Fractions 54–87 (10 ml each) contained para-aspidin, methylene-bis-aspidinol and trispara-aspidin, no crystals obtained. Fractions 88–99 contained the same compounds as above and phloraspidinol. They gave 1.6 mg trispara-aspidin, m.p. 140–147 °C, after crystallisation from acetone.

Fractions 100–126 contained methylene-bis-aspidinol, trispara-aspidin, phloraspidinol, margaspidin and aspidinol and afforded 1.0 mg trispara-aspidin, m.p. 165–166 °C, when crystallised from acetone.

Fractions 127–162 contained the same phenolics as 100–126 except for phloraspidinol. They gave 20.3 mg margaspidin, m.p. 154–162 °C (acetone), containing traces of aspidinol and 320.5 mg margaspidin, m.p. 159–162 °C, from methanol.

Fractions 163–219 contained margaspidin, aspidinol and phloraspidinol and afforded 603.2 mg margaspidin, m.p. 175–176 °C (acetone).

The last fractions were eluted with hexane–chloroform 1:1 and chloroform.

From fractions 220–249, 5.2 mg margaspidin, m.p. 119–124 °C (methanol) were collected.

Fractions 250–264 contained only margaspidin and phloraspin. They gave the following crystallates: (1) 283.7 mg phloraspin, m.p. 202 °C from acetone; (2) 557 mg margaspidin, 125–135 °C from methanol.

Fractions 265–290 contained the same compounds as fractions 250–264. They afforded 61.4 mg phloraspin, m.p. 170–172 °C from acetone.

The following crystallates were investigated in detail:

— *Trispara-aspidin*, m.p. 165–166 °C. After reductive alkaline cleavage aspidinol V, B and P were detected at pH 8.6 in paper chromatocraphy (PC). In negative fast atom bombardment mass spectrometry (FAB/MS) peaks at m/z (695), 681, 667, 653 and 639 were detected in the molecular region. They correspond to homologues *20*-VVB/BVV, *20*-VBB/BBV, BBB (main homologue), *20*-PBB/BBP and *20*-PPB/BPP.

— *Margaspidin*, m.p. 175–176 °C. After reductive alkaline cleavage aspidinol-V (trace), aspidinol-B, and aspidinol-P were found in PC. In MS peaks at m/z (474), (460), 446, 432, and 418 were detected in the molecular region. They correspond to homologues *18*-VV, *18*-BV/VB, *18*-BB, *18*-PB/BP and *18*-PP.

— *Phloraspin,* m.p. 202 °C. After reductive alkaline cleavage desaspidinol-V (trace), desaspidinol-B, and desaspidinol-P (trace) were

found in PC at pH 8.6. In MS molecular peaks at m/z (446), 432 and (418) were detected. They correspond to *11*-VB/BV, *11*-BB and *11*-PB/BP.

Treatment of ether extract of *Dryopsis clarkei*

The crude ether extract of *D. clarkei* (*CRFJ 8470–76, 8482*; 6.20 g) was dissolved in 50 ml ether (Fraction A), whereupon 1.576 g of an insoluble part (Fraction B) was left.

Fraction A (4.634 g) was shaken with 3 × 10 ml 1N HCl and 3 × 10 ml H_2O to give 3.84 g cation-free ether extract after evaporation *in vacuo*. The latter was divided into a methanol fraction (2.636 g) and a hexane fraction (0.866 g), which were separated by column chromatography on silica gel buffered at pH 4.0 and pH 6.0, respectively.

Fraction B consisted of margaspidin, phloraspin and some phloraspidinol and was treated with benzene. It gave two impure crystallates of phloraspin; 1 527.7 mg (Fraction B_1) and 2 103 mg (Fraction B_2). Both were purified by recrystallisation from acetone–H_2O (8:2). From Fraction B_1, 144.8 mg pure phloraspin, m.p. 185–190 °C, and 56.7 mg of the same substance, m.p. 199–200 °C, were collected. From Fraction B_2, 13.3 mg of pure phloraspin, m.p. 194–196 °C, was obtained.

Separation of the methanol fraction

Fractions 1–165 were eluted with hexane–chloroform 1:1.

Fractions 61–87 contained para-aspidin, methylene-bis-aspidinol and desaspidin, no crystals obtained.

Fractions 88–96 contained desaspidin, as above.

Fractions 97–111 contained desaspidin and phloraspidinol. They gave 41.5 mg phloraspidinol, m.p. 190 °C and a further crystallate, 5.3 mg of m.p. 181–183 °C, of the same substance from acetone.

Fractions 112–120 contained phloraspidinol, margaspidin and some aspidinol. They afforded 31.2 mg phloraspidinol, m.p. 186–187 °C, from acetone.

In fractions 121–135 the same compounds were found as in fractions 112-120. They gave 180.9 mg phloraspidinol, m.p. 187–189 °C (acetone).

Fractions 136–165 contained some phloraspidinol, margaspidin, aspidinol and phloraspin. They afforded 29.4 mg margaspidin, m.p. 175–176 °C (acetone).

Fractions 166–195 were eluted with hexane–chloroform 1: 1 and contained some margaspidin and phloraspin. They gave 16.4 mg phloraspin, m.p. 201–203 °C (ether).

Separation of the hexane fraction

Fractions 1–156 were eluted with hexane–chloroform 4:1 and the fractions 157–173 with hexane–chloroform 1:1. No crystals were obtained.

Fractions 1–108 contained albaspidin and methylene-bis-aspidinol, the fractions 109–144 para-aspidin and aspidinol, the fractions 145–156 para-aspidin, aspidinol, (phloraspidinol) and phloropyrone, the fractions 157–173 phloraspidinol, aspidinol and (para-aspidin).

The following crystallisates were investigated in detail:

— Phloraspidinol, m.p. 190 °C. In MS molecular peaks at m/z 460 and 446 were recorded. They correspond to *12*-VB/ BV and BB (main homologue).
— Margaspidin, m.p. 175–176 °C. After reductive alkaline cleavage aspidinol-V (small spot) aspidinol-B and -P were found in PC at pH 8.6. In MS in the molecular region peeks at m/z 460 (weak), 446 (small), 432 and 418 were detected. They correspond *13*-VB/BV, *13*-BB, *13*-PB/BP and PP.
— Phloraspin, m.p. 199–200 °C (from Fraction B). In MS molecular peaks at m/z 460 (weak), 446, 432 (small), 418 (small) and 404 (weak) in the molecular region. They correspond to *11*-VV, *11*-VB/BV, *11*-BB and *11*-PB/BP and *11*-PP.

Treatment of the ether extract of *Dryopsis nidus*

The ether extract of *D. nidus* (CRFJ 8458–60, 8462–67; 15.01g) was dissolved in 50 ml ether and treated with 3 × 20 ml 1 N HCl to give 13.32 cation-free ether extract. The latter was devided in the usual way in a hexane fraction (7.64 g) and a methanol fraction (3.83 g). The methanol fraction was chromatographed on 96 g SiO_2 buffered at pH 4.0 without further purification, *see* below next section.

The hexane fraction was treated with: (a) 3 × 20 ml saturated $NaHCO_3$-solution (Fraction A), (b) 3 × 20 ml 10% Na_2CO_3 solution (Fraction B), and (c) a carbonate insoluble part was left (Fraction C).

Separation of the methanol fraction

Fractions 1–270 were eluted with hexane–chloroform 4:1.

Fractions 1–120 contained albaspidin, para-aspidin, phloropyrone and aspidinol. They afforded 1 mg albaspidin, m.p. 141–144 °C from acetone.

Fractions 121–189 contained (albaspidin), (para-aspidin), phloropyrone and aspidinol, no crystals obtained.

In fractions 190–204 para-aspidin, phloropyrone and (aspidinol) were found. They gave 11 mg of phloropyrone, m.p. 127–128 °C/136–137 °C, from methanol.

Fractions 205–213 contained para-aspidin, phloropyrone and aspidinol, no crystals obtained.

In fractions 214–246 methylene-bis-aspidinol, para-aspidin, margaspidin and aspidinol were observed, but no crystals obtained.

Fractions 247–270 contained mainly margaspidin of which a crop of 32.7 mg melting at 168–169 °C, was collected.

Fractions 271–300 eluted with hexane–chloroform 1:1 contained a mixture of margaspidin, phloraspidinol and aspidinol, no crystals obtained.

Separation of Fraction A of the hexane phase

443.6 mg of Fraction A was acidified with 10% HCl and taken in ether. After evaporation of the solvent the residue (372.6 mg) was again dissolved in a small portion of ether. Two different crystallates of phloropyrone, 19.5 mg m.p. 132–134 °C, and 20.2 mg, m.p. 124–128 °C were obtained on cooling.

Separation of Fraction B of the hexane phase

376.5 mg of Fraction B was chromatographed on 23 g SiO_2 buffered at pH 6. It gave 3.8 mg albaspidin, m.p. 148–151 °C.

Separation of Fraction C of the hexane phase

8.09 g of Fraction C was chromatographed on 162 g SiO_2 buffered at pH 6. The fractions 211–225 contained para-aspidin and methylene-bis-aspidinol and gave 1.7 mg, m.p. 165–168 °C, of the latter substance from methanol.

Fractions 226–230 para-aspidin and methylene-bis-aspidinol were found, but no crystals obtained.

Fractions 231–252 contained para-aspidin, aspidinol and phloraspidinol, no crystals obtained.

Fractions 253–310 contained virtually only aspidinol, but no crystals were recovered.

The following crystallisates were investigated in detail:

— Margaspidin, m.p. 168–169 °C. In MS molecular peaks at m/z 474 (weak), 460, 446, 432 (small) and 418 (weak) were recorded. They correspond to to *13*-VV, *13*-BV/VB, *13*-BB, *13*-PB/BP and *13*-PP respectively.

— Phloropyrone, m.p. 132–134 °C. It was studied by MS and hydrolytic cleavage in two different conditions. In MS molecular peaks at m/e 404 (trace), 390, 376, and 362 (small),

were observed. These correspond to *15*-VB/BV, *15*-BB, *15*-PB/BP and *15*-PP, respectively. After reductive alkaline cleavage in mild conditions (Widén *et al.* 1970) propionylfilicinic acid (small spot), butyrylfilicinic acid (main spot) and valeryfilicinic acid (small spot) were found in PC at pH 4. To study the pyronone part of the phloropyrone (it is completely destroyed in the former treatment) the molecule was broken up by very gentle treatment with dilute sodium carbonate solution in the following way (Penttilä & Sundman 1963): 5 mg phloropyrone was dissolved in 5 ml 2% $NaCO_3$ solution and boiled for 5 minutes. The cooled solution was acified with 10% HCI and kept at room temperature overnight. The clear liquid was poured off and extracted with 3×20 ml chloroform. The solution was concentrated to a small volume and studied by TLC on SiO_2-G plates buffered at pH 6.0 (hexane–chloroform–ethanol 45:45:10) using synthetic samples of 6-propyl-2,3-dihydropyrane-2,4-dione, m.p. 94–95 °C, 6-ethyl-2,3-dihydropyrane-2,4-dione, m.p. 99–102 °C, and 6-methyl-2,3-dihydropyrane-2,4-dione, m.p. 188–189 °C, as standards. Orange coloured spots of the propyl-derivative (Rf. 0.47) and ethyl-derivative (Rf 0.42) were detected after spraying with fast blue salt B. The methyl-derivative (Rf 0.37) was not observed.

In the light of the above results the sample of phloropyrone (*15*) mainly consisted of the homologues *15*-BB, *15*-BP and *15*-PB containing minute amounts of higher (*15*-VB) and lower (*15*-PP) homologues.

— Albaspidin, m.p. 148–151 °C (artefact). In MS molecular peaks at m/7 460, 446 (small), 432 (weak) and 418 (weak) were observed. They correspond to *10*-BB (main homologues), *10*-PB, (*10*-PP) and (*10*-AP), respectively.
— Methylene-bis-aspidinol, m.p. 165–168 °C. In molecular peaks at m/z 488 (weak), 474 and 460 were detected. They correspond to *18*-VV, *18*-VB and *18*-BB, respectively.

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