

# A survey of phenolic compounds in *Dryopteris* and related fern genera. Part IV. Phloroglucinol derivatives and morphology in the section *Marginatae* (Pteridophyta, Dryopteridaceae)

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The phloroglucinol composition of 29 species of *Dryopteris* Adanson belonging to subgenus *Dryopteris* section *Marginatae* were investigated on a world-wide basis, and the taxonomy is discussed based on both morphology and chemistry. The ferns of this section show relatively variable phloroglucinol patterns in line with their morphological variability. In good agreement with the other sections of subgenus *Dryopteris*, the majority of ferns of sect. *Marginatae* contain considerable amounts of phloroglucinols (crude filicin) and oleo-resin (ether extract) in their rhizomes and stipe-bases. However, *D. porosa* from China and the Hawai'ian species *D. mauianensis* were lacking in these phenolics. The African species, *D. pentheri*, *D. lewalleana* and *D. manniana*, are subdivided here into two separate chemical races, however, this does not affect their taxonomic identity, except in the case of *D. manniana*. *Dryopteris wideniana* Fraser-Jenk. is described as a new species in the *D. manniana* aggregate from S and E Africa.

## Introduction

Most species of *Dryopteris*, and some from several related genera of the Dryopteridaceae contain in their rhizomes and petiolar bases typical phloroglucinol derivatives or acylphloroglucinols (see Widén *et al.* 1976, 1991, 1993, 1996, 1997, 1999, 2001, 2006, Fraser-Jenkins & Widén 1993, and Gibby *et al.* 1992 and refs. therein). *Dryopteris* is divided into three subgenera and

these in turn into several sections (Fraser-Jenkins 1986, Widén *et al.* 1999). In Widén *et al.* (1996, 1999) the phloroglucinols of some of the sections of subgenus *Dryopteris* were discussed, whereas Widén *et al.* (2001) dealt with the sections of subgenera *Erythrovaria* and *Nephrocystis*. In the present and last paper of the series, we report our chemical and botanical investigations on the ferns of the subgenus *Dryopteris*, sect. *Marginatae* (see also previous reports by Puri &

Widén 1978, von Euw *et al.* 1980, Widén *et al.* 1973, 1975, 1978, 1991, 1997, 1998, and Gibby *et al.* 1992\*).

The major part of the material investigated here was collected by C.R. Fraser-Jenkins from different parts of the world, but various herbarium specimens from different collectors were also investigated, particularly from Africa. Most of the present work and many of the taxonomic conclusions were completed some 20 years ago, but not published earlier due to other priorities. Fortunately, this delay enabled us to revise the chemistry of African species while working together with the late Dr. J.P. “Koos” Roux, whose recent death in a road accident has deprived African and world pteridology of one of its most remarkable and energetic workers. His last monograph on sub-Saharan *Dryopteris* appeared in 2012 (Roux 2012).

### Synopsis of *Dryopteris* subgenus *Dryopteris* section *Marginatae*

This section contains mainly large species with tripinnatifid to tripinnate or more fronds with wide lamina-bases and long basal basiscopic pinnules. Within it, there are a number of subgroups of related species that appear to have evolved in different regions, though the area with the greatest morphological diversity is in SW China, as part of the Sino-Himalayan flora. However the section is also the predominant one in Africa, with many critical and often confused species present there, several of which have only recently been described, though in the absence of cytological or phytochemical information. Fraser-Jenkins (1986) recognised 26 species in the section, but since then there have been major changes. *Dryopteris mauritensis*, which had previ-

ously been overlooked was placed in the section *Marginatae* by Fraser-Jenkins (1994). *Dryopteris pteridiiformis*, whose type turned out to be a sterile hybrid, was replaced by *D. camusiae* (Fraser-Jenkins 1997). Roux (2012) treated *D. esterhuyseniae*, formerly misplaced by Fraser-Jenkins (1986) in the section *Cinnamomeae*, as a taxonomic synonym of *D. dracomontana*.

In the present paper we reduce *D. mangindranensis* to a synonym of the formerly unplaced *D. subcrenulata*, here placed in section *Marginatae*. We transfer *D. athamantica* from the section *Cinnamomeae* to *Marginatae*, its sloping, asymmetrical pinnules merely being a parallel development to the species of the section *Cinnamomeae*. Also *D. comorensis* and *D. macrolepidota* are added to the section *Marginatae*, both previously overlooked by Fraser-Jenkins (1986). *Dryopteris bernieri* is separated again from *D. bojeri*, where Fraser-Jenkins (1986) placed it in error. The S and E African “*D. manniana*” *auct.* is here described as a new species, *D. wideniana*.

Recently, Roux (2012) described no less than 11 new species in this section from Africa and the Cape Verde Islands, based largely on detailed study of glands, hairs, stomata and spore ornamentation and size, which at least partly correspond with some of the different chemotypes and unpublished new species proposed some ten to twenty years previously by our colleagues, the late Mr. J. Sarvela and Prof. T. Reichstein. They did not publish these at the time pending further study into these difficult entities, which has now been completed in large part. But it is likely that further revision of some of these African species will be necessary, and further cytological investigation, in particular, should be carried out. Some of the species included in the section have their fronds a little more simply dissected than in most of the large species, but they are not close to the adjacent section *Pallidae* and on becoming properly familiar with them it is clear that they are related to and belong in the section *Marginatae*. Thus *D. cochleata*, *D. camusiae*, *D. subcrenulata* and *D. manniana* are placed in this section despite being only bipinnate.

We now recognise 42 species in the section *Marginatae*, of which 15 are Asian (including the Hawai’ian Islands) and 27 are African

\* Correction of Gibby *et al.* 1992. In table 2 on p. 236 the phloroglucinol compositions of *Arachniodes foliosa* and *A. webbiana* are given. However, *A. foliosa* is completely devoid of phenolics as could be confirmed by investigating two herbarium vouchers (H) of *A. foliosa* collected by R. Lampinen from the Meru Mountain in Tanzania. They were lacking in phloroglucinols. On the other hand, the chromatographic results for *A. webbiana* were quite correct. We consider that the above correction hardly alters our taxonomic conclusions on these two taxa.

(including Madagascar, the Mascarenes, Canary and Cape Verde Islands).

### Asian and Hawai'ian species

*Dryopteris cochleata* (D. Don) C. Chr. This is a diploid, sexually reproducing species common at lowish altitudes throughout India and extending W to Pakistan, and east through most of SE Asia (see Fraser-Jenkins 1989). It has large bipinnate fronds showing sterile–fertile dimorphism, the sterile fronds being much laxer and with wide, pointed pinnules; but the more erect fertile fronds have a reduced laminar surface, obtuse pinnule-apices and remarkably thick, tall, button-like, inflected indusia, close-packed on the surface. It appears to be distantly related to *D. marginata*, but the pinnules are mostly unlobed or the lower ones rather shallowly so. Interestingly some uncommon populations in far NE India (Meghalaya, Manipur, Mizoram, etc.) and SW China do not or only partially develop the frond dimorphism and have smaller, lower, spaced out sori with thinner indusia, while their rather smaller fronds have wide fertile pinnules similar to those of sterile fronds. They remain fairly constant in cultivation, but are nevertheless obviously part of the range of variation of *D. cochleata* and not a distinct species, though perhaps a distinct subspecies.

*Dryopteris camusiae* Fraser-Jenk. (1997: 131–132). This was a new species described because the type of the species long called *D. pteridiiformis* Christ is a sterile hybrid with abortive spores. The species was therefore without a name until described as *D. camusiae*. It is a sexually reproducing, tetraploid species, presumably of mixed allopolyploid origin, which was suggested by Fraser-Jenkins (1989) as possibly involving *D. angustifrons*, *D. cochleata*, *D. subimpressa*, or now added, *D. carolihopei* or *D. marginata*. Its fronds are rather narrow and the pinnules are mostly rather shallowly lobed, with small acute teeth. It is a very restricted SW Chinese species (Yunnan), otherwise known only from Nagaland and Mizoram in NE India.

*Dryopteris angustifrons* (T. Moore ex Hook.) Kuntze. This is a very rare and little known species, said to have come from Nepal, though never

since refound there. Its cytotype is unknown but the spores are small. It is close to *D. carolihopei*, which also has a creeping rhizome, but the rhizome of *D. angustifrons* is longer and thinner, with the fronds arising a bit apart. Its erect fronds are narrower and the pinnae shorter and more sloping, while the ultimate segments are smaller and more rectangular. Until our chemical results confirmed a clear qualitative difference from *D. carolihopei*, it was difficult to be confident that it was not just an abnormal form of that species and several records of it were in error for *D. carolihopei* (see Fraser-Jenkins 1989: 413–425). However another collection turned up from Yunnan, which shows its distinctive features and confirmed its separateness, though the illustration by Wu (2000) is not of this species, but probably *D. camusiae*. The question arises as to whether Wallich's original specimen really came from Nepal and it appears possible that it may well not have done. After all the intervening years of collection and study of Nepalese ferns on Wallich's routes and around the Kathmandu Valley it is surprising that no further trace of it has been found, though if really from Nepal it is more likely to have been on the way down to Hetauda at lower altitude. But several of Wallich's specimens, particularly those not included in his *Enumerated List*, which this was not, though assumed by recipients to have been from Nepal [either from the Hon. E. Gardner's 1817–1819 collections or from Wallich's own 1820–1821 collections, see Fraser-Jenkins (2006)], may not have been from there. Fraser-Jenkins (1989) assumed the type collection was likely to have been from 1821, and the other cited collection at Kew was so localised and dated, but it remains possible that it may really have come from Wallich's 1826–1827 Myanmar (Burmese) collections, perhaps up the Chappedong river, S of Kyaikami (Amherst) and Mawlamyaing (Moulmein) in Mon State, SE Myanmar, where he collected many ferns, or from some other area. It is the only one of Wallich's apparently Nepalese ferns that has not been refound in Nepal in modern times, though it is also present in far NE India (Fraser-Jenkins 2008).

*Dryopteris subimpressa* Loyal. This is a diploid, sexually reproducing species (Gibby 1985) with a robust, scaly stipe and rachis and tripin-

nate fronds, though it can also become precociously fertile when small and only bipinnate. It has large, tall sori with thick indusia and is in general similar to *D. carolihopei* and *D. marginata*, but differs from either by its more erect, narrower fronds, less deeply dissect segments and obviously larger, thicker and taller indusia. It was almost certainly described from near Lachen, N Sikkim, though the locality was erroneously said to be at the eastern edge of Darjeeling town due to a confusion (see Fraser-Jenkins 1989). It occurs scattered through the W Himalaya from Himachal Pradesh eastwards, in Nepal, Sikkim, Bhutan, Arunachal Pradesh and in SW China.

*Dryopteris approximata* Sledge. This species is cytologically unknown, though it has small spores. It is somewhat intermediate between *D. carolihopei* and *D. ramosa*, with large, wide, rather delicate, tripinnate fronds and small, narrowish acute segments; the pinnules are markedly closely sessile so that the lowest opposite-pair of pinnulets overlaps the pinna-costa. The indusia are small and turned down at the edges, becoming pale brown. It is endemic to S India and Sri Lanka.

*Dryopteris goeringiana* (Kunze) Koidz. This is a diploid, sexually reproducing species (from Japan, under the synonym, *D. laeta* (Kom.) C. Chr.). It has large, thin, tripinnate fronds, with the lowest pinna often a bit shorter than the next, the pinnae usually somewhat narrowed to their bases, and the pinnulets sloping. The indusia are thin and flat. It occurs in N China, eastern Siberia, N Korea and N Japan. The epithet *goeringiana* has sometimes been misapplied to *Athyrium niponicum* in the past.

*Dryopteris ramosa* (C. Hope) C. Chr. This is a diploid, sexually reproducing species with thick, horizontal rhizomes, brown stipe-scales and large, finely dissect, tripinnate fronds, the lowest pinnae having very long lower basiscopic pinnules and small, acute well toothed segments. It belongs to an interesting category of W Himalayan endemics, being found at higher altitude only from NE Afghanistan east to the westernmost part of Nepal (where it is rare). Its nearest relatives are *D. goeringiana* and the Japanese endemic, *D. shiroumensis*, the latter being very close to it in morphology and probably a vicariant form of it.

*Dryopteris shiroumensis* Sa. Kurata & T. Nakam. (mistakenly put as "Nakaike" by Fraser-Jenkins 1986, 1989). This is a very rare Japanese endemic species, but is very similar indeed to *D. ramosa*, differing only in being slightly less toothed. It is quite likely that it may represent the same species, as a minor geographical race of it, though it might then be expected to occur somewhere in China in an intervening area. Unfortunately we were not been able to examine material of *D. shiroumensis* chemically to compare with *D. ramosa*, as if it were basically similar with relatively few differences it could provide grounds to unite them or separate them only as subspecies.

*Dryopteris carolihopei* Fraser-Jenk. (Fig. 1). This is a diploid, sexually reproducing species, with long, thickish, horizontal underground rhizomes, lacerate, scurf-like stipe-scales and a large, wide, tripinnate frond bearing small sori with thin indusia. The frond texture is matt and bears many fine striations from the slightly impressed veinlets, while the rounded-pointed segments are markedly toothed with small, acute teeth that often stick up slightly out of the surface. This rather lower altitude species replaces the more easterly *D. marginata* in the W and C Himalaya, but also extends eastwards through Nepal, Sikkim, Bhutan, Arunachal Pradesh, Manipur, Meghalaya, Mizoram, N Burma, Tibet and SW China. Although previously widely misidentified as being *D. marginata* and superficially similar it is quite distinct from it.

*Dryopteris marginata* (Wall. ex C.B. Clarke) Christ. (Fig. 2). Clarke's main concept and type (lectotype, here designated, "Aspidium Napa-lia 1821 [Wallich] 391," second sheet, the first sheet, as pointed out by Clarke (1880: 521) in the protologue, being different and actually belonging to *Diplazium spectabile*, were of the present species, while he separated *D. carolihopei* as another, more serrate, but unnamed plant from Khasia. The origin of Wallich's specimen must be somewhat doubtful as the only species present in C Nepal, where he or his collectors visited, is *D. carolihopei*, while *D. marginata* begins to occur much further east in the Arun Valley. It is likely that some confusion may have occurred and it may have come from Darjeeling or further east, which might also explain the sur-



**Fig. 1.** A frond of *Dryopteris caroli-hopei* (C.R. Fraser-Jenkins 8199, H).

prising mixture under Wallich's *Numerical List* number 391. *Dryopteris marginata* is a diploid, sexually reproducing species. It has a short, erect rhizome, glossy, pale stipe-scales and a very large, tripinnate frond with a smooth lamina and rectangular, often rather less toothed, or only tooth-lobed ultimate segments. It has thin, flat indusia. It occurs from E Nepal eastwards but is seldom very common; E Nepal, Darjeeling,

Sikkim, Bhutan, Arunachal Pradesh, Manipur, Meghalaya, SW and across S China, Taiwan, Thailand and N Vietnam.

*Dryopteris porosa* Ching. This is diploid, sexually reproducing species (Gibby 1985) confined to SW China. It is very close to *D. marginata*, but has a thicker frond, with almost untoothed margins which usually have a rather obvious cartilaginous edge. The sori are tall and



**Fig. 2.** A frond of *Dryopteris marginata* (C.R. Fraser-Jenkins 8422, H).

the indusia thick. It is inexplicable as to why we were unable to detect phloroglucinols in the material investigated as it is obviously a very typical member of this section and related to *D. marginata*. It would be desirable to investigate it again from sufficient fresh material.

*Dryopteris mauiensis* C. Chr. This endemic Hawaiian species, of unknown cytotype (but with small spores) was often confused and placed

under the name *D. sandwicensis* (Hook. & Arn.) C. Chr. (see Fraser-Jenkins 1994) in error. *Dryopteris mauiensis* was unfortunately omitted by Fraser-Jenkins (1986). It is a very large species with tall, wide, tripinnate fronds and the sori are exindusiate. It is probably related to *D. chaerophyllifolia*, *D. subarborea* and *D. macrolepidota* and thus in turn related more distantly to *D. marginata*. Some of the African species may also be

more related to *D. marginata* and such species as *D. mauiensis* than to most others in the section. The presence or absence of an indusium is a somewhat secondary specific characteristic in the section, rather than a basic feature indicating species groups. Our material did not contain any phloroglucinols which is also the case with some other large species that probably belong to the section *Aemulae* from Hawai'i.

*Dryopteris subarborea* Baker. This is a cytologically unknown species generally similar to a very large *D. marginata*, but is larger, with a massive rhizome and stipe and wide, tripinnate frond. It occurs in tropical rainforests in the Malaysian and Indonesian Islands, the Philippines and New Guinea and is sometimes mistaken for *D. arborescens* (Baker) Kuntze from Oceania, which latter is easily separable by its asymmetrical, sloping pinnules and belongs to the subgenus *Nephrocystis*, sect. *Purpurascentes*.

*Dryopteris chaerophyllifolia* (Zipp.) C. Chr. This cytologically unknown species is generally similar to *D. subarborea* and thus more distantly to *D. marginata* and is a similarly large species, but has more-or-less numerous stiff, narrow exserted scales on the stipe, rachis and costae. The ultimate segments are rectangular but often obviously shallowly lobed at the edges and the sori are exindusiate. It occurs in Sumatra, Java, Sulawesi and N Borneo.

*Dryopteris macrolepidota* Copel. This cytologically unknown species is obviously very closely related to *D. chaerophyllifolia* and is similar in its segments and scales, but is indusiate. It occurs in Oceania (Tahiti and the New Hebrides) and may turn out merely be a vicariant of *D. chaerophyllifolia* showing some slight geographical variation.

### African and Macaronesian species

*Dryopteris subcrenulata* (Baker) C. Chr. (syn. *D. mangindranensis* Tardieu). This species is cytologically unknown, though it has small spores. It is a less developed member of the section *Marginatae*, with fronds only bipinnatifid to bipinnate below due to its smaller size, though larger plants become somewhat tripinnatifid below and correspond with the type of *D. mangindranen-*

*sis*. But in other ways it is similar to the general morphology of members of this section and shows its allegiance here. It is a Madagascarian endemic, perhaps very distantly connected to *D. cochleata* from Asia.

*Dryopteris dracomontana* Schelpe & N.C. Anthony (syn. *D. esterhuyseniae* Schelpe & N.C. Anthony). This species is cytologically unknown, but it has stomata (40–)52(–66)  $\mu\text{m}$ , and spores (38–)43(–48)  $\times$  (26–)31(–36)  $\mu\text{m}$ , that fall within the size range of tetraploid taxa. It is the only species in Africa and the Malagassy region that has truly dimorphic sterile and fertile fronds that are bipinnate–pinnatifid. *Dryopteris dracomontana* is restricted to the Drakensberg Mountain range of South Africa and Lesotho where it occurs at elevations ranging from 1850 to 3050 m a.s.l., an altitudinal range which is only occasionally shared by *D. pentheri*, and then only at lower levels. It shows no clear affinity to any other taxon within the region, but its overall morphology supports its inclusion in the section *Marginatae*. *Dryopteris esterhuyseniae* is merely a large, shade-growing form of *D. dracomontana*.

*Dryopteris schimperiana* (Hochst. ex A. Braun) C. Chr. This variable species with tripinnate fronds is widespread in East and tropical Central Africa at elevations ranging between 1400 and 2600 m a.s.l. (in Ethiopia). It is diploid and sexually reproducing (see below under Material; however the diploid “*D. schimperiana*”, RBF-71/468, of Widén *et al.* (1973), which was later corrected to “*D. sp. not identified*” (Widén *et al.* 1991: 87, table 2), has now been reidentified as *D. tricellularis*) and can be confused with *D. pentheri*, but differs from it in the sessile or short-stalked scales, the rigid isocytic hairs occurring along the frond axes and abaxially along the veins, and the large indusium with strongly involute margins. The occurrence of 2- and 3-celled hairs along the lamina axes and veins suggest that it may be related to the exindusiate *D. tricellularis*.

*Dryopteris ruwenzoriensis* C. Chr. (Fraser-Jenkins 1986). This little known but distinctive species with fronds that can be up to 1.35 m long and become tripinnate, is restricted to the Ruwenzori Mountains of the Democratic Republic of Congo, Rwanda, and Uganda at an elevation ranging between 1350 and 3500 m a.s.l.

It is cytologically unknown, but Roux (2004d) postulated from its morphology that it could be tetraploid species related to, or derived from *D. fadenii* and *D. rodolfii*. It reproduces sexually with 64 spores per sporangium, and the almost unique tuberculate perispore sculpture suggests an affinity with *D. rodolfii*. It is normally exindusiate, but Christensen suggested it possible that fugaceous indusia might be found in young sori, though he did not find them.

*Dryopteris pentheri* (Krasser) C. Chr. This is perhaps the most widely distributed species in Africa with a distribution that extends to Madagascar. In the past this sexually reproducing, tetraploid species (Widén et al. 1991, sub "*D. inaequalis*"), with fronds that can be up to 1.9 m long, and a lamina that can be up to tripinnate, was generally included within *D. inaequalis*, but was clearly separated and lectotypified by Pichi Sermolli (1985). *Dryopteris pentheri* is characterised by unicellular oblong hairs, (60–)137.02(–260)  $\mu\text{m}$  long, and 2-cellular hairs occurring abaxially along the axes and veins, which suggest it may be related to *D. tricellularis*. Although the species occurs in evergreen forests it also occupies more exposed habitats at elevations ranging from near sea-level to 2425 m a.s.l. in Lesotho.

*Dryopteris filipaleata* J.P. Roux. Roux (2004b) found that this sexually reproducing species has stomata (40–)50(62)  $\mu\text{m}$ , and spores (32–)41(–54)  $\times$  (18–)26(–34)  $\mu\text{m}$ , that fall within the size range of a tetraploid cytotype. In agreement with this, the tetraploid specimen RBF-71/885 (= TR-3305), originally listed by Widén et al. (1973, 1991) as "*D. sp. not identified*" has now been reidentified by Roux as *D. filipaleata*. The fronds are up to 1.2 m long and the lamina becomes tripinnate. It is clearly closely related to *D. pentheri*, but differs from it in the exindusiate sori, the absence of unicellular oblong hairs and 2-celled hairs, and the narrow lamina scales. The species appear to be restricted to moist evergreen forests in Kenya and Tanzania at elevations ranging between 1350 and 2000 m a.s.l. *Dryopteris filipaleata* forms part of a small group of exindusiate species which appear not to be related to each other.

*Dryopteris tricellularis* J.P. Roux. The cytotype of this species is unknown, but its stomatal

size (32–)47.53(–64)  $\mu\text{m}$ , is within the size range of tetraploids. On the other hand, the specimens here identified as *D. tricellularis* viz. RBF 71/468 (= TR-3248 and R. Bonnefille A/212) are both diploid. The former specimen is also listed by Roux (2012). The plant has fronds up to 1.1 m long and the lamina can become tripinnate. The most diagnostic features of the species is the occurrence of predominantly 3-celled hairs along the lamina axes and veins, the oblong glands along the scale margins, the exindusiate or indusiate sori, and the granulate perispore. The species is known from 2075 to 3600 m a.s.l. in Kenya, Uganda and Ethiopia. Roux (2002, 2012) tentatively suggested that it might be related to *D. fadenii*.

*Dryopteris amblyodonta* J.P. Roux. This is a poorly known species, which appears to be endemic to the Loma and Tingi Mountains in Sierra Leone and forms part of a group of species clearly related to *D. pentheri*. Its chromosome number is unknown, but it is sexually reproducing with 64 spores per sporangium, spores that are (34–)38(–46)  $\times$  (24–)28(–34)  $\mu\text{m}$  long and stomata that are (42–)53(–66)  $\mu\text{m}$  long. It differs from other species in the region by the long stipe relative to lamina length, the occasional occurrence of glands and pluricellular hairs along the indusium margin and surface, and the sporangium stalk with large capitate glands and pluricellular hairs. The clavate glands (60–)88(–130)  $\mu\text{m}$  long, the absence of 2-celled hairs, and smaller spores separate it from *D. pentheri*.

*Dryopteris glandulosopaleata* J.P. Roux. This sexually reproducing species has an obvious affinity with *D. pentheri*, but differs from it in the scales regularly set with glands along the margin and faces, the absence of 2-celled hairs from the lamina axes and veins, and in the lamina closely set abaxially with clavate glands (62.0–)111.01(–146.0)  $\mu\text{m}$  long, along and between the veins. The spore and stomatal sizes [(48.0–)55.59 (–68.0)  $\times$  (34.0–)37.08(–48.0)  $\mu\text{m}$  and (44.0–)53.96(–70.0)  $\mu\text{m}$ , respectively] compare well to those of *D. pentheri* and are within the range of tetraploid species. It is only known from the mountainous regions of Cameroon and adjacent Nigeria.

*Dryopteris occidentalis* J.P. Roux. This is a sexually reproducing species with 64 spores



per sporangium and has an obvious affinity with *D. pentheri* and *D. glandulosopaleata*. The fronds are up to 0.95 m long and the lamina becomes bipinnate-pinnatifid. As in *D. glandulosopaleata*, this species also lacks the 2-celled hairs diagnostic of *D. pentheri*, and the unicellular glands are clavate and shorter, (56.0–)76.78(–92.0)  $\mu\text{m}$ , than in both those species. The stomata [(48.0–)55.31(–64.0)  $\mu\text{m}$ ] are slightly larger than in *D. pentheri*, but the spores [(38.0–)39.95(–46.0)  $\times$  (24.0–)26.81(–30.0)  $\mu\text{m}$ ] are smaller. It differs from *D. glandulosopaleata* in its scales not bearing glandular cells on their face. It appears to be restricted to forests in Côte d'Ivoire, Guinea and Nigeria.

*Dryopteris cicatricata* J.P. Roux. This is a sexually reproducing species with 64 spores per sporangium. The small stomatal and spore sizes [(40–)46(–52)  $\mu\text{m}$  and (36–)38(–40)  $\times$  (24–)27(–30)  $\mu\text{m}$ , respectively] are within the range of diploid taxa. *Dryopteris cicatricata* is known only from São Tomé and differs from *D. pentheri* in the absence of oblong hairs and 2-celled hairs, the echinulate spores, and the muriccate-cicatricate stipe and rachis. The echinulate spores and exindusiate sori may suggest some affinity with *D. ruwenzoriensis* C. Chr., but it differs from that species in its smaller stomata and spores.

*Dryopteris caperata* J.P. Roux. This is a sexually reproducing species with 64 spores per sporangium. The stomatal and spore sizes, [(32–)42(–52)  $\mu\text{m}$  and (28–)34(–38)  $\times$  (22–)22(–24)  $\mu\text{m}$ , respectively] are within the range of diploid species in the section. This and the absence of laminar glands separates it from *D. pentheri*. This species also appears to be endemic to São Tomé, but it differs from *D. cicatricata* in the stipe and rachis scales being lacerate and irregularly set with numerous long and twisted pluricellular outgrowths, and in the perispore which has short reticulate ridges.

*Dryopteris aurantiaca* J.P. Roux. This sexually reproducing species with 64 spores per sporangium is endemic to tiny Annobon Island, Equatorial Guinea. It can be readily separated from other species in the region by the large, deep orange to ferruginous rhizome scales with few marginal outgrowths, the margins and faces variously set with small clavate glands. Another

diagnostic feature of the species is the indusium which bears large pyriform glands and pluricellular hairs. Glands [(50–)56(–64)  $\mu\text{m}$ ] occurring on the lamina are clavate and half as long as those in *D. pentheri*.

*Dryopteris katangaensis* J.P. Roux. This species appears to be endemic to the copper belt in the Mwinilunga District of the Northwestern Province of Zambia and adjacent higher lying areas of the Upper Katanga Province of the Democratic Republic of Congo. Most African *Dryopteris* species in the section *Marginatae* tend to have short to long decumbent, branched rhizomes, but in *D. katangaensis* the rhizome is short, simple and erect. The fronds are up to 0.95 m long and the lamina becomes tripinnate. Roux (2003) suggested it may be related to *D. schimperiana* and listed the features of difference from that species. The stomatal and spore sizes [(30.0–)39.25(–48.0)  $\mu\text{m}$  and (38.0–)43.0(–52.0)  $\times$  (26.0–)30.72(–38.0)  $\mu\text{m}$ , respectively] are within the range of diploid species in the section.

*Dryopteris rodolfi* J.P. Roux. This species is unknown cytologically. Roux (2004d) suggested it may be related to *D. fadeonii* and *D. ruwenzoriensis*. It has larger stomata, (44.0–)59.48(–80.0)  $\mu\text{m}$ , and spores, (42.0–)48.43(–56.0)  $\times$  (24.0–)31.82(–38.0)  $\mu\text{m}$ , than either of those species. The tuberculate spores suggest an affinity with *D. ruwenzoriensis*. At present *D. rodolfi* is only known from the Bale mountains in Ethiopia and from Mt. Kenya where it occurs at elevations ranging between 3250 m and 3500 m a.s.l.

*Dryopteris gorgonea* J.P. Roux. The cytology of this species is unknown. Until recently it was confused with *D. pentheri* (Fraser-Jenkins 1982, who first recognised the species on the Cape Verdes as morphologically distinct from *D. oligodonta*), but Roux (2004c) treated it as representing a distinct species perhaps partly related to *D. oligodonta* and confined to the Cape Verde Islands. It differs from *D. pentheri* in the occurrence of capitate glands on the scale faces and frond axes, and from *D. oligodonta* in its segment shape, longer clavate glands, (50–)68.48(–98)  $\mu\text{m}$ , and larger stomata, (42–)53.31(–64)  $\mu\text{m}$  vs. (30–)37.54(–48)  $\mu\text{m}$ , which are within the range of tetraploid species,

rather than diploids like *D. oligodonta*. It may possibly have been derived partly from *D. oligodonta*. *Dryopteris gorgonea* is known only from old material from the Cape Verde island of São Nicolau, and may now be extinct.

*Dryopteris fadenii* Pic. Serm. This species is diploid and sexually reproducing (Widén et al. 1973, sub "*D. pentheri*"; see Widén et al. 1991: 82, table 2, where its identity and cytotype were corrected by J. Sarvela, T. Reichstein with CRFJ, and R.E.G. Pichi Sermolli 1984) and occurs in Burundi, Ethiopia, Kenya and Tanzania at from 1700 to 3250 m a.s.l. Its small bullate scales, occurring abaxially along the lamina axes, and its small, erose indusium are diagnostic. The lamina is eglandular. Roux (2004a) considered this species, *D. ruwenzoriensis*, and *D. rodolfi* as cryptic, related taxa, though the two latter are immediately distinguishable by their tuberculate spores. But due to Widén et al. (1973) having initially reported it as tetraploid, it is possible that Roux may also have referred some different species to this name.

*Dryopteris lewalleana* Pic. Serm. This species is a large member of the group related to *D. pentheri*, described and only known from Burundi, by Pichi Sermolli (1985). It differs from it in the entire or fimbriate scales mainly being confined to the stipe base and terminating in a long hair, the lamina thinner, pinna-costae more winged and the pinnules usually opposite; the pinnules are almost glabrous but bear occasional hair-like fibrils. The sori are small and bear small, denticulate indusia that do not cover the whole sorus. The spores are small, suggesting that it is within the range of diploid species in the section,  $36\text{--}44 \times 24\text{--}30 \mu\text{m}$ .

*Dryopteris athamantica* (Kunze) Kuntze. This diploid, sexually reproducing species (Widén et al. 1973) is widespread in Africa, but in spite of this it appears to be relatively uniform in overall morphology throughout its wide distribution. It is more or less restricted to open habitats, chiefly occurring in small sinkholes along drainage lines, at cliff bases, and at the foot of boulders in grasslands, but rarely also in forest margins where it forms small clonal stands and its fronds may become laxer in the shade. The relatively thick decumbent rhizome, erect fronds, angled pinna orientation resulting in a

3-dimensional lamina, somewhat asymmetrical and usually sloping pinnules and the closely spaced veins can be used to separate it readily from other *Dryopteris* species in the region.

*Dryopteris inaequalis* (Schltdl.) Kuntze. This name has been widely and incorrectly applied to several *Dryopteris* species throughout much of Africa, including especially *D. pentheri* and its relatives, with a wide lamina-base. But *s. stricto* it was confined by Fraser-Jenkins (1982 and *ined.*) and Pichi Sermolli (1985) to the smallish South African species with a rather narrower lamina-base and prominent teeth. Detailed study by Roux (2012) confirms that *D. inaequalis* is confined to South Africa, occurring from Table Mountain on the Cape Peninsula, where the type was collected, along the eastern mountainous regions to the Waterberg in the Limpopo province. Its cytology is unknown, but its stomatal size,  $(30\text{--})42.24\text{--}(58) \mu\text{m}$ , is within the range of diploid species in the section. Characteristic of the species is the relatively thin, shortly creeping rhizome, the basal pinna pair usually being slightly reduced, and the indusium generally bearing glands along the margin and on the surface.

*Dryopteris bernieri* Tardieu. The cytology of this Réunionaise (in the Mascarene Islands) endemic is not known. It shows no obvious affinity to any of the other species in Africa and the Malagassy region, but the occurrence and distribution of laminar glands perhaps suggests an affinity with *D. oligodonta*. It is a rather small to medium sized species and its prominent capitate glandular cells occurring on the lamina, scales, and indusium are diagnostic. The scale morphology might suggest a relationship to *D. aquilinoidea*, but their overall frond-morphology and chemistry are markedly different.

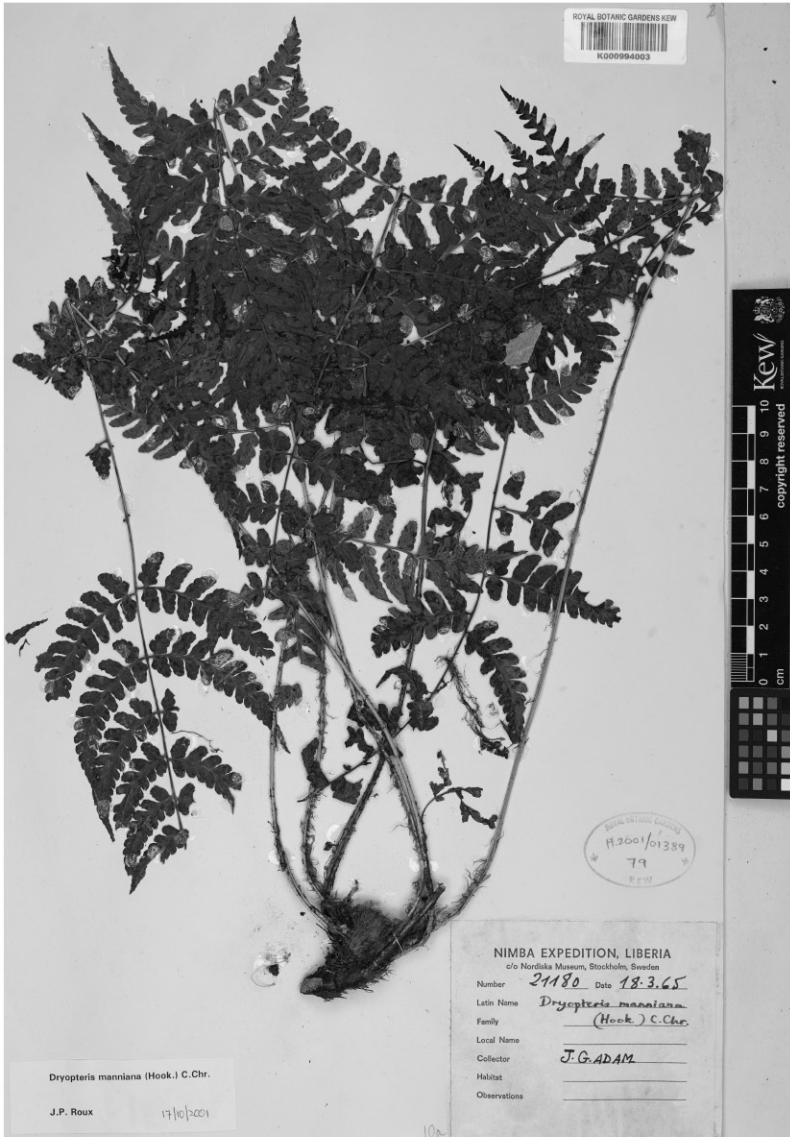
*Dryopteris manniana* (Hook.) C. Chr. (Figs. 3 and 4). This tetraploid species was described from Bioko (Fernando Po), Equatorial Guinea, and as construed here is confined to W Africa, being well known from Sierra Leone, Liberia, Guinea, Nigeria, Côte d'Ivoire and Cameroon. It is always a small species, often only 10 cm tall, becoming fertile at an early stage, and has a delicate, narrowly triangular, bipinnate frond, bearing a subapical bud, and has exindusiate sori. Although the next species has long been



**Fig. 3.** Two fronds of *Dryopteris manniana* (C.R. Fraser-Jenkins 11355, H).

identified as *D. manniana*, the two are separated here. In some respects this and *D. wideniana* are reminiscent of the species of the Asian *D. sparsa* (D. Don) Kuntze group in the subgenus *Nephrocystis*, sect. *Diclisodon* (T. Moore) C. Chr. (syn. section *Nephrocystis* (H. Itô) Fraser-Jenk.), with their smooth lamina and scattered, glossy stipe-scales, but their overall frond-morphology is more like the section *Marginatae*.

*Dryopteris wideniana* Fraser-Jenk., *sp. nova* (Fig. 5). *Species insignis a turma D. manniana; frons multo maiora, tripinnatifidis, lobis ultimis rectangularis, gemma subapiculata instructis.* — Holotype: E Africa, Rhodesia N.C. Chase 5705, 5 Aug. 1955 Zimbabwe, Umtali District, Vumba Mts., 1590 m. (K). — This South and East African "*D. manniana*" differs consistently from true *D. manniana* in its much larger size, wide,



**Fig. 4.** A frond of *Dryopteris manniana* (J.G. Adams 21180, K). Copyright of the Board of Trustees of the Royal Botanic Gardens, Kew; reproduced with permission from the copyright holder.

tripinnatifid fronds, with a more prominent subapical bulbil, the lamina smoother and its pinnae being fully separate throughout most of the frond, wide, rectangular and with slightly asymmetrical bases. It is exindusiate and a tetraploid, sexually-reproducing species from Zimbabwe (Widén et al. 1973).

*Dryopteris bojeri* (Baker) Kuntze. This is a little known Mauritian endemic not collected there recently, and might perhaps now be extinct, though Fraser-Jenkins collected a couple of fronds there on the lip of a small rocky ravine

shortly below the peak top of La Pouce in 1986 and a small living offset from that collection was maintained at Kew for a number of years as a globally highly endangered species, until the fern collection was allowed to run down in the last decade. It is characterised by wide-based, tripinnate fronds that can be up to 1.2 m long, axes that are variously set with capitate glands, up to 62  $\mu\text{m}$  long, and scales that bear very long filiform outgrowths along the margins. The small stomatal and spore sizes [(34–)45(–54)  $\mu\text{m}$  and (32–)34(–44)  $\times$  (18–)20(–22)  $\mu\text{m}$ , respectively]



**Fig. 5.** Holotype of *Dryopteris wideniana* (N.C. Chase 5705, K). Copyright of the Board of Trustees of the Royal Botanic Gardens, Kew; reproduced with permission from the copyright holder.

are within the size range of diploid species in the section.

*Dryopteris comorensis* (Tardieu) Fras.-Jenk (1994: 34). Tardieu-Blot (1956) initially described this species as a variety of *D. inaequalis*, intended in a wide sense, including *D. pentheri* and allies, but it is not related or similar to *D. inaequalis* proper. It has fronds up to 1.9 m long and tripinnate. It can be separated from other species in the region by the rugose stipe scales that bear glands and numerous long outgrowths along the margin. Although similar features occur in *D. pentheri*,

*D. comorensis* does not bear unicellular oblong glands, or 2-celled hairs along the axes and veins as in that species. *Dryopteris comorensis* also has a markedly more glossy upper laminar surface than the rather matt surface of *D. pentheri*. The stomatal and spore sizes [(34–)40(–46)  $\mu\text{m}$  and (34–)37(–44)  $\times$  (20–)23(–26)  $\mu\text{m}$ , respectively] are also significantly smaller than in *D. pentheri*, and are within the range of diploid rather than tetraploid species in the group.

*Dryopteris aquilinoides* (Desv.) C. Chr. The cytology of this very distinctive and

very large species, endemic to La Réunion, is not known, but the small stomatal and spore sizes [(34–)45(–58)  $\mu\text{m}$  and (26–)36(–44)  $\times$  (20–)23(–30)  $\mu\text{m}$ , respectively] are within the range of diploid species. It is characterised by the large rhizome scales and stipe-base scales, the near glabrous dark brown or black-based stipe and glossy frond axes, and the small ovate-caudate scales occurring abaxially along the lamina axes and veins, which bear numerous oblong glands along the margin and on the scale lamina. The similar scale morphology of *D. aquilinoidea* and *D. bernieri* might suggest some affinity, but in other respects they are very different.

*Dryopteris oligodonta* (Desv.) Pic. Serm. This is a diploid, sexually reproducing species (Widén et al. 1973) confined to the Canary Islands (Macaronesia) and nomenclaturally clarified by Pichi Sermolli (1951), now being a well known Canarian endemic species. It is a very large, tripinnate species and diagnostically its frond axes and lamina are variably set with short capitate glands, a feature not observed in any of the African species. It also has characteristic small, ovate scales beneath the costae at the bases of the pinnules. Fraser-Jenkins (1982) suggested that it may be an ancient tertiary African–Mediterranean relict species. *Dryopteris gorgonea* (see above) is obviously closely related to *D. oligodonta*.

More detailed information on the sub-Saharan species appears in Roux' monograph (Roux 2012).

## Material and methods

### Plant material

The following list gives collection data for the material not previously investigated. Collections marked with an asterisk (\*) consist of rhizomes or stipe bases from herbarium specimens, not weighed. *TR* = herbarium of T. Reichstein (now mainly taken to GENT, though said to belong to Z). Voucher specimens are deposited at H if not otherwise indicated; CRFJ's herbarium is mainly at BM and E, with later collections at TAIF, but a voucher specimen of all chemically investigated material is at H. *RBF* = herbarium of R.B. Faden,

now at US, with duplicate specimens in TR. For abbreviations of herbaria, see <http://sciweb.nybg.org/science2/IndexHerbariorum.asp>.

*D. cochleata* (normal dimorphic form). *CRFJ* 8122–8138, 8140–8142, 20 Oct. 1978. N India, Himachal Pradesh, Dehra Dun to Chandigarh, 5 km below Nahana on Paonta Sahib road, road-bank in forest. 11 main rhizomes = 240 g. (H, BM, E). *CRFJ* 9027–9034, 9036, 13 Dec. 1978. S India, Tamil Nadu, W of Madras, NE of Salem, Shevaroy Hills, west of Yercaud, roadside by Botanical Survey of India Orchid Garden, ca. 1400 m. 9 rhizomes = 350 g. (H, BM). — *D. angustifrons*. \*Nepal, “Napalia”, Wallich s.n., 1821 (K). — *D. approximata*. *CRFJ* 9161–9163, 19 Dec. 1978. S India, Tamil Nadu, Western Ghats, North side of Palni Hills, 19 km N of Kodaikanal on Palni road, wooded stream on rocks, 1650 m. 3 rhizomes (H, BM). *CRFJ* 9234–9238, 9241–9242, 21 Dec. 1978, S India, Tamil Nadu, Western Ghats, North side of Palni Hills, 4.5 miles NE of Kodaikanal on Perumal-malai road, dense woods in valley, 1600 m. 7 rhizomes (H, BM). — *D. goeringiana*. \*China, Hopeh (Hebei). Collector no. 884, sub *D. laeta* (PE), collector no. 566, sub *D. laeta* (PE). — *D. carolihopei*. *CRFJ* 8197 (holotype)–8209, 22 Oct. 1976. N India, Uttar Pradesh, N of Dehra Dun, E side of Mussoorie, Landour, St. Paul's Church, in coniferous wood, ca. 2300 m. (H, BM, FR, G). — *D. porosa*. \*China, Kweichow. Collector no. 7858 (PE). — *D. mauiensis*. *CRFJ* with *R.W. Hobdy*, *CRFJ* 14814 (Field no. 52), 26 Feb. 1988. Hawai'ian Islands, East Maui, NE of Haleakala Ranch, on road between Haleakala Ranch and Waikamoi Gulley (and pipeline and Flume), Makawao Forest, above Olinda, E of Pukalani, N slope of Haleakala Mountain, forest, ca. 3500 ft. (1067 m) (H, BM, E, FR). 1 rhizome. *CRFJ* with *R.W. Hobdy*, *CRFJ* 14866 (Field. no. 102), 28 Feb. 1988. Hawai'ian Islands, West Maui, W of Waikapu, forest on S shoulder of Hana'aula mountain, 4000 ft. (1219 m) (H). 1 rhizome. — *D. subcrenulata*. *Mme. F. Rakotonrainibe s.n.*, ca. 21 June 1986, pressed by *CRFJ* 12066, 12068, 12069, 26 June 1986. Madagascar, Tampoketsa d'Ankazobe. (H, K). — *D. subcrenulata* (originally sub *D. mangindranensis*). *CRFJ* 12023–12026, 21 June 1986. Madagascar, SW of Analamazaotra, Andasibe, ca. 975 m. (H, K, E). — *D. schimperiana*. \**I. Kukkonen* 14455, 30 Oct. 1982. Ethiopia, Ethiopia Flora Project Expedition, Welega Adm. Reg., ca. 3 km E of Nekemte, pastured open woodland, epiphytic on solitary trees. Det. R. Viane 31 Oct. 1983, conf. JPR. Sowing (*TR* 5869) made by T. Reichstein, 1. Nov. 1983 in Basel. Spores good, exospore (30–)33–36(–42)  $\mu\text{m}$  long. Diploid,  $2n = ca. 80$  (det. J.J. Scheller, 20 Aug. 1984). (H). — *D. schimperiana* (det. by JPR and confirmed from chemistry by C.-J. Widén). \**J. Kornas* 5211, 9 Jan. 1976. Kenya, Rift Valley Province, Kaijado Distr., Nogong Hills, 1°25'S, 36°38'E, 2400 m. (herb. *TR*, *TR* 5970). — *D. ruwenzoriensis* (conf. J.P. Roux 2012). \**O. Hedberg* 614, 31 March 1948. Uganda, Ruwenzori, Mijusi Valley, 3500 m. (K). — *D. pentheri* (“Northern taxon”). \**T.G. Jefford*, *B.E. Juniper & J. Newbould* 1735, 23 Aug. 1958. Tanzania, W Prov., Kigoma distr., Mahali mountains, Ujambu, 6°13'S, 29°51'E, valley forest, 6000 ft. (1829 m) (K). (det. JPR 2012). \**R.W.J. Keay* 28604, 13 Jan. 1951.

Cameroon, Victoria District, Cameroon Mt., SW of Hut no. 2. In gully woodland. Epidermis + spore SEM, deeply folded spores (det. R.L.L. Viane). (BM). \**C.D. Adams 1269*, 1 June 1952. Cameroon, Cameroon Mt., under lava rock in mountain grassland, 9000 ft. (2743 m). Epidermis + spore SEM, 2 kinds of spores, folded (det. R.L.L. Viane). (BM). (det. as *D. glandulosopaleata* by JPR, but chemistry more like that of *D. pentheri* “Northern taxon”). *R.L.L. Viane s.n.*, 3 March 1983. Cameroon, Lake Oku on vertical road side (very dry), ca. 2200 m. (GENT). Living plant (*TR 5803*) planted at Casa Alle Felci, Agarone, Ticino, by TR. (herb. TR). (?*D. pentheri*). *CRFJ & C.D. Fraser Jenkins, CRFJ 11466–11469*, 6 June 1985. Cameroon, NE half of SW Province, ca. 14 km NW of (above) Kumbo on Oku road, E side of Mt. Oku, NE of Bamenda, open roadside bank, ca. 2100 m. (H). (det. JPR). *CRFJ & C.D. Fraser Jenkins, CRFJ 11289*, 26 May 1985. Cameroon, SW half of SW Province, near water pipes of “German Spring”, above “Prison Farm” (“Upper Farm”), near Buea, SE side of Mt. Cameroon, below waterfall and hut, ca. 1100 m. (H). (det. J.P. Roux). Small spores, like a diploid (det. T. Reichstein). \**I. Kukkonen 12373A* (det. JPR), 28 Oct. 1982. Ethiopia, Shewa Adm. Region, 26 km N of Gedo on the road to Fincha, 9°07'N, 37°20'E, ca. 2900 m. Spores (*TR 5971A*) small, good, with exospore ca. (27–)30–33(–36) µm (det. T. Reichstein, 24 May 1984). “Indument of *D. pentheri sensu* Pichi-Sermolli; epidermis + spore SEM” (det. R.L.L. Viane Dec. 1985). (H). — *D. pentheri* (“Southern taxon”). Sub “*D. sp. near pentheri* (“Southern taxon”)”. *CRFJ 12327, 12333–12338*, 27 Oct. 1986. Mascarene Islands, La Réunion, Cirque de Cilaos, Forêt de Grande Matarum, ca. 3 km. above Cilaos, 1700 m. 11 rhizomes. (H, K). (det. JPR). *D. sp. near pentheri* (“Southern taxon”) \**C.D. Fraser Jenkins & A.B. Jenkins s.n.*, 29 Nov. 1974 (*CRFJ 4523*, 25 Dec. 1974). Kenya, Naro Moru River, W side of Mt. Kenya. (E). Propagated from spores by T. Reichstein (*TR 4094–4095*, sown 24 April 1977, *in litt.* 14 Oct. 1981), tetraploid (det. J.J. Schneller). (herb. TR). Sub “*D. sp. near pentheri* (“Southern taxon”)”. *R.B. Faden, M. Githui & C. Smeek, RBF 71/255*, 10 Apr. 1971. Kenya, Taita Hills, Ngangao Forest, 1800–1900 m. (herb. TR). Propagated from spores by T. Reichstein (*TR 3247*) (herb. TR), *see* Widén *et al.* (1973, corrected by Widén *et al.* 1991). Root tip, 2n = 164, tetraploid, det. G. Vida. \**D. sp. near pentheri* (“Southern taxon”) \**E. Bruce 42*, 11 Jan. 1935. Tanzania, Ulugurus, Bunduki, in planted *Cupressus* forest, frequent (3–4 ft., upright rootstock), 4125 ft. (1257 m) (BM). (det. as *D. tricellularis* by JPR, but chemistry does not fit that). \**D. sp. near pentheri* (“Southern taxon”) \**M. Richards 6533*, 16 Oct. 1956. Tanzania, Ngozi, Mbeya, Poroto mountain, 7000 ft. (2134 m) (fronds to 3 ft. tall) (BM). (det. as *D. fadenii* by JPR but chemistry does not fit that). Sub “*D. sp. near pentheri* (“Southern taxon”)” *CRFJ 11910–11912*, 13 June 1986. Madagascar, Antananarivo, Park de Tsimbazaza. (H, K, E). (det. JPR). *D. sp. near pentheri* (“Southern taxon”) *CRFJ 12091*, 28 June 1986. Madagascar, ca. 5 km. S of Anjozorobe, remnant patch of forest, ca. 1200 m. (H, K). *D. sp. near pentheri* (chemistry same as *D. pentheri*, Southern taxon) \**D.S. Mitchell 572*, 20 Jan. 1960, *sub D. athamantica*. Zimbabwe, Goromonzi District, Chikawasha, on forest floor, closed canopy, 4700 ft. (1433 m) (BM). Epidermis + spore SEM. Deeply folded spores, no warts or spines. Very different from all other spore SEMs (det. R.L.L. Viane). \**E.A.C.L.E. Schelpe 5368*, 25 June 1955. Zimbabwe, Umtali District, “Cloudlands”, Vumba Mts., 5200 ft. (BM). Epidermis + spore SEM. Folded spores (det. R.L.L. Viane). (det. JPR 2012). *W.B.G. Jacobsen s.n.*, 27 Oct. 1981. South Africa, Natal, 1590 m. (J). Propagated from spores by T. Reichstein (*TR 5601*). Not cytologically verified but probably diploid, as spores small (det. T. Reichstein) (herb. TR). \**H.B. Rycroft 505*, 20 Oct. 1941. S Africa, Howick, near Umgeni River. (BM). Epidermis and spore SEM. Folded and papillose spores (det. R.L.L. Viane). (det. as *D. athamantica* by JPR, but chemistry does not fit that, and its morphology is markedly different and clearly not *D. athamantica*, det. CRFJ, 2013). — *D. filipaleata*. *RBF 71/885* (first det. by JPR (2012) as *D. tricellularis*, but now reidentified as *D. filipaleata* with slightly different chemistry). Kenya (herb. TR). Progeny from spores (*TR 3305*) tetraploid, sexual (herb. TR). Probably an allotetraploid from *D. fadenii* [e.g. *RBF 71/68* (= *TR 3224*)] and *D. spec. unknown* [e.g. *RBF 71/468* (= *TR 3248*)], *see* Widén *et al.* (1991). The latter is now reidentified as *D. tricellularis* (Roux 2012). \**R.L.L. Viane 75/3301*, 24 Oct. 1975. Kenya, K4, Nyeri district, Aberdare mountains, Kindorongo mountains, Kindorongo Track above Tucha (Tusha), crossing a small tributary of the Chania River, 0°29'S, 36°45'E, 2920 m. (GENT; det. by JPR and confirmed from chemistry by CJW). Progeny from spores (*TR 5644*) tetraploid 2n = ca. 160 (det. J.J. Schneller, 14 July 1982). (herb. TR). \**K. Otten & R.L.L. Viane 75/3297* (= *TR 5645*), 23 July 1975. Kenya, Mt. Kenya, N side near Sirimon track, slopes around waterfall, ca. 2700 m. (GENT) (herb. TR). (det. from chemistry by CJW). \**R.B. Faden & A. Evans, RBF 70/66*, 14 Feb. 1970. Kenya, K4, Murung'a distr., Kimakia Forest Station to Gatara Road crossing of Kimakia? River, 0°46'S, 36°45'E, 2470 m. (K). (det. as *D. fadenii* by JPR 2012, but chemistry does not fit that and is similar to *D. filipaleata*) \**M. Richards 24073*, 17 Nov. 1969. Tanzania, Arusha distr., Mt. Meru, Ngare Nanyuki Forest, 2560 m. (K). (tentatively det. by JPR 2013 as *D. fadenii*, but chemistry does not fit it). — *D. tricellularis*. *RBF 71/468*, 13 June 1971 (det. JPR). Kenya. Progeny from spores (*TR 3248*) diploid, 2n = ca. 82 (det. G. Vida), sexual. “Probably a new species” (det. T. Reichstein), published as “*D. schimperiana*” by Widén *et al.* 1973 and corrected to “*D. sp. unknown*” by Widén *et al.* 1991. (herb. TR). *D. tricellularis*, *sub “Dryopteris inaequalis”* (det. by JPR and confirmed from chemistry by CJW): \**Mlle. R. Bonnefille A/212*, 24 Nov. 1968. Ethiopia, Zurquala Volcano, 8°32'N, 38°57'E, forest 2500 m. (EA). Progeny from spores (*TR 3193*) diploid 2n = ca. 82 (det. G. Vida) (herb. TR). — *D. glandulosopaleata*. *CRFJ & C.D. Fraser Jenkins, CRFJ 11373, 11386, 11388, 11395*, 2 June 1985. Cameroon, SW half of SW Province, gully above hut 1 (Johannes Albrecht Hut), above Upper (Prison) Farm, above Buea, E side of Mt. Cameroon, among uppermost trees, ca. 1950 m. (K, H). (det. JPR). — *D. occidentalis*. Sub “*D. athamantica* towards *D. pentheri*”. *CRFJ & C.D. Fraser Jenkins, CRFJ 11447–11448*, 6 June 1985. Cameroon, NE half of SW Province, 5 km SW of Kumbo, NE of Bamenda, road banks, ca. 1700 m. (H). (det. JPR). Spores large (det. TR). — *D. caperata*. \**J. Viégas da Graça Espírito Santo 5052*, 13 Feb. 1973. São Tomé and Príncipe, São Tomé, S Nikolau, 870 m. (LISC). (det. JPR). \**A. Möller s.n.*, Aug.

1985. São Tomé and Príncipe, São Tomé, Encosta do Pico, 1950 m. (COL). (det. JPR). — *D. fadenii*. Isotype: *R.B. Faden*, *A. Evans*, *J.B.C.* & *S. Cameron*, *RBF 71/68* (= TR 3224), 24 Jan. 1971 (for details see Widén et al. 1973, 1991, Roux (2012) and Synopsis above). Kenya, K3, Nyandarna District, Sasumur Dam, just below outlet, 2460 m. (herb. TR, H). Propagated from spores by T. Reichstein (TR 3224). Root apex was diploid sexual,  $2n = ca. 82$  (det. G. Vida). \**R.B. Faden*, *A.J. Faden*, *J.B.C.* & *S. Cameron*, *RBF 74/1348*, 18 Aug. 1974 (chemistry identical to *RBF 71/68*). Kenya, Kikuyu Escarpment Forest (S Aberdare Forest), Ndiara Waterfall on Ndiara River along Sasumna pipeline road,  $0^{\circ}48' S$ ,  $36^{\circ}42' E$ , bamboo forest with *Arundinaria* dominant, 2370–2400 m a.s.l. Rhizome woody, ascending, fronds tufted ca. 1.2 m. tall, costules with small bullate scales on the underside; common (herb. TR). — *D. lewalleana* (“Northern taxon”). \**A.A. Bullock* 2567, 24 Feb. 1950. Tanzania, Nanyangwe, 6000 ft. (1829 m) (K). (det. JPR 2012). \**R. Mkarira* for *E Milne-Redhead* & *P. Taylor* 8276, 19 Jan. 1956. Tanzania, Colonial Office East African Expedition 1955–1956, Songea District, about 32 km E of Songea, 930 m. (K). (det. JPR 2012). \**R.M. Harley* 9531, 6 Sep. 1959. Tanzania, Tanganyika Expedition 1959, Mpanda District, Kungwe-Mahali Peninsula, ca.  $6^{\circ} S$ ,  $30^{\circ} E$  (K). (det. JPR 2012). \**F. de A. Mendonça* 1321, 8 Nov. 1942. Moçambique, Zambesia, Serra de Gúruí, encostas dos morros Maipi. (BM). (det. JPR 2012). — *D. lewalleana* (“Southern taxon”). *Sub* “*D. sp. near pentheri*”. \**D.R. Tweedie* 4236, March 1972. Kenya, S Kulal, Northern Province, Top of Kulal, in montane forest, growing in a roadside bank, 7000 ft. (2134 m) (to 3 ft. tall). (K). (det. JPR 2012). \**F. White* 2725, 6 May 1952. Zambia, Eastern Province, Lundazi District, 7000 ft. (2134 m) (BM). (det. JPR 2012). Epidermis + spore SEM. Folded and papillose spores (det. R.L.L. Viane). *D. lewalleana* (det. JPR 2012) (“Southern taxon”): \**D. Johnstone* 297, 23. Jan. 1950. S Africa, Natal, Htildoane Mtota forest. (BM). Epidermis + spore SEM. Deeply folded and papillose spores, small spines (det. R.L.L. Viane). \**E.A.C.L.E. Schelpe* 5012, 8 Jan. 1955. S Africa, Cape Province, Hogsback, S side, Middel Drift Div., 3700 feet (1128 m). Spores to Kew Oct. 1959, Rhizome creeping. (BM). (det. JPR 2012). — *D. athamantica*. *R.B. Faden* 71/476. Kenya. (= TR 3249), (herb. TR). (det. JPR 2012). Root apex was diploid,  $2n = ca. 80$  (det. G. Vida) (Widén et al. 1973). \**I. Kukkonen* 12558, 5 Nov. 1982. Ethiopia, Ethiopian Flora Project Expedition, Kefa Adm. Reg., 86 km E of Jima on road to Welkite. (H). \**I. Kukkonen* 12417, 28 Oct. 1982. Ethiopia, Ethiopian Flora Project Expedition, Welega Adm. Reg., Amarti Valley, ca. 20 km along road from Fincha to Shambu, ca. 2750 m. (H). *CRFJ* & *C.D. Fraser Jenkins*, *CRFJ 11441–11443*, 6 July 1985. Cameroon, NE half of SW Province, pass E of Bamenda on road to Kumbo, banks of road, ca. 1700 m. (K, H). *CRFJ* & *C.D. Fraser Jenkins*, *CRFJ 11460–11461*, 6 July 1985. Cameroon, NE half of SW Province, ca. 14 km NW of and above Kumbo on Oku road, NE of Bamenda, open roadside bank near Eucalyptus wood, ca. 2100 m. (H, K). *CRFJ* & *C.D. Fraser Jenkins*, *CRFJ 11436*, 5 July 1985. Cameroon, NE half of SW Province, ca. 4 km. W of Bali, W of Bamenda, grassy roadside bank, ca. 1000 m. (H). *CRFJ 11462*, *11463*, 6 July 1985. Cameroon, NE half of SW Province, ca. 14 km NW of and above Kumbo on Oku

road, NE of Bamenda, open roadside bank near Eucalyptus wood, ca. 2100 m. (H, K). (slightly intermediate towards *D. pentheri*, det. CRFJ). *I. Kukkonen* 13266, 20 Feb. 1986. Zambia, Prov. Kopperbelt, Distr. Kitwe, Ndola, Dola Hill National Forest. (H). — *D. inaequalis*. \**C.L.P. Zeyher s.n.*, 1845, herb. J. Smith 1966. S Africa, Cape of Good Hope. (BM). (det. JPR; det. on sheet as *D. inaequalis*, but not typical by CRFJ 1981). Spore SEM. Folded and papillose spores, small spines (det. R.L.L. Viane). \**I. Kukkonen* & *M. Lassig*, *IK 11651*, 29 Jan. 1982. S Africa, Cape Province, on NE slope of Table Mt., Skeleton Gorge above Kirstenbosch Bot. Garden, in shade under trees. (H). (conf. CRFJ). — *D. bernieri*. *CRFJ 12281*, *12283–12284*, *12286–12289*, *12291–12292*, 25 July 1986. Mascarene Islands, La Réunion, La Fournaise, on path from the Gite to Fonds de la Rivière d’Est, low forest, ca. 1950 m. (H, K). — *D. manniana*. *CRFJ* & *C.D. Fraser Jenkins*, *CRFJ 11327–11333*, *11335–11337*, 1 July 1985. Cameroon, SW half of SW Province, ca. 0.5 km SW of “German Spring” waterfall and pipes, SW from “Prison Farm” (Upper Farm), above Buea, E side of Mt. Cameroon, on rocks in gully, 1200 m. (K, H). (det. CRFJ, conf. JPR). 10 rhizomes. Tetraploid sexual (det. M. Gibby). \**J.G. Adams* 21180, 18 March 1965. Liberia. Mt. Nimba Expedition. (K). (det. CRFJ, conf. JPR). — *D. wideniana*. \**E.J. Newman* & *T.C. Whitmore* 477, 17 Aug. 1956. Malawi, Iter Zambesiicum, Nyasaland, Mt. Mlanje, L Ruo Plateau, 5800 ft. (1768 m) (BM). (det. CRFJ; *D. manniana* det. JPR). \**R.B. Faden*, *E. Evans*, *M. Githui*, *R. Osborn* & *C. Smeenk*, *RBF 71/219*, 9 April 1971, Kenya, K 7, Taita District, Taita Hills, Mbololo Hill (Mruru Ridge), lower part of main forest, 1450–1525 m. (herb. TR). (det. CRFJ; *D. manniana* det. JPR). Propagated from spores by T. Reichstein (TR 3246) (herb. TR). Root apex tetraploid,  $2n = ca. 164$  (det. G. Vida) (Widén et al. 1973). \**Revd. W Deans Cowan s.n.*, 1881. Madagascar. (BM). (det. CRFJ; *D. manniana* det. JPR). Holotype: \**N.C. Chase* 5705, 5 Aug. 1955. Zimbabwe, Umtali District, Vumba Mts., 1590 m. (K). (det. CRFJ; *D. manniana* det. JPR). \**E.A.C.L.E. Schelpe* 2394, 24 July 1949. Kenya, Thuchi River, Mt Kenya, 4900 ft. (1494 m). (BM). (det. CRFJ; *D. manniana* det. JPR). — *D. comorensis*. *CRFJ 12190–12192*, 15 Aug. 1986. Comoro Islands, Grande Comore, Nioumbadjou, ca. 800 m. (H, K, E). (det. CRFJ and JPR). — *D. aquilinoïdes*. *CRFJ 12340–12342*, 28 July 1986. Mascarene Islands, La Réunion, S of St. Denis, Plaine des Chicots, above Le Brûle, below La Roche Ecrite, dense forest, 1500 m. (H, K). — *D. oligodonta*. *TR 1939*. Gran Canaria, canyon Northern Valsendero, western Valleseco, 800 m, Laurel wood. *P.R.O. Bally*, *G. Kunkel*, *H.L. Reichstein* & *T. Reichstein*, 23 March 1967. Diploid  $2n = 82$  (det. G. Vida, 3 June 1969 from root apex).

## Extraction procedure and analysis of rhizomes

For the preparation of crude extractives and isolation of pure compounds, both the old standard method and the new improved methods



were used (see von Euw *et al.* 1980, 1985, Patama & Widén 1991, Widén 1998, Widén *et al.* 1996, 1999, 2001). In the present paper only *D. approximata*, *D. cochleata* and *D. carolihopei* were preparatively separated by column chromatography on silicagel.

For final identification of individual phloroglucinols a complete set of pure reference substances was available. For structure and numbering see table 4 in Widén *et al.* (1991) and Widén *et al.* (1993, 1996, 1997, 1998, 1999, 2001) and references therein.

## Results and discussion

Previous and new analytical results from the various taxa studied are summarised in Tables 1–5. As in Widén *et al.* (1999), the homologues of the individual phloroglucinols were not separately listed in order to facilitate the reading of the tables. Compounds not present in the section *Marginatae* are omitted from Tables 1 and 2.

As in Widén *et al.* (1996, 1999, 2001) the main purpose of the present work was to find out how chemical composition reflects taxonomic relationships in the species of *Dryopteris* investigated. The results of some previous investigations are also included in the tables for comparison (Widén *et al.* 1971, 1973, 1978, 1991, 1997, Puri & Widén 1978, Patama & Widén 1991). The results presented in Tables 1–3 indicated that there is huge variation in the phloroglucinol content and patterns of the extensive material from Asia, the Hawai'ian Islands and Africa that we studied. Surprisingly two species even appear to lack phloroglucinols entirely. In all we now studied 29 species out of 42 species listed by Fraser-Jenkins (1986, 1994, and present work) in the section *Marginatae* and the results are discussed below.

As pointed out in the Introduction, we investigated two kinds of fern material, (1) larger quantities of rhizome material collected and carefully dried at room temperature by CRFJ and others in the 1970s and 1980s, and also (2) small pieces of petiolar (stipe) bases from herbarium specimens of various ages. The oldest herbarium-collections were ca. 105–180 years old (see Material and methods). Although we

had previously found out that phloroglucinol composition has remained quite stable in similarly old material (e.g. see Widén *et al.* 1976), we cannot exclude the existence of decomposition reactions of the individual phloroglucinols, such as para-aspidin (7) and margaspidin (13) and the formation of artefacts like aspidinol (2) (see Discussions in Widén *et al.* 1991, 1999). Moreover in connection with the present work it was also observed that flavaspidic acid (5) and trisflavaspidic acid (23), for example, may decompose, apparently by autoxidation, during long storage in various conditions, due to their having many reactive phenolic hydroxyles present in their molecules. For this reason we had to be careful in the interpretation of old material in comparison with that more recently collected.

## Asian species

Of the 15 Asian and Oceanian species (11 being from mainland Asia) in the section, we studied 10 species. Of these *D. approximata*, *D. carolihopei*, *D. angustifrons*, *D. porosa* and *D. mauiensis* were investigated for the first time.

*Dryopteris cochleata* from N India differed from material of the same species investigated previously from the Philippines in the complete absence of desaspidin (8) and containing only traces of albaspidin (10). Thus two geographically separated, chemical races appear to be present in this species, though the S Indian material we investigated contained trace amounts of albaspidin (10) and is thus slightly intermediate. However, we do not think the chemical difference is of taxonomic significance given the close morphological similarity between the Indian and Philippine plants. Furthermore we did not sample material from other intermediate areas of its wide geographical range.

Of the little known *D. angustifrons* from “Nepal” (see Synopsis above) more likely provenance from Myanmar (Burma)], only one small, ca. 180 year old petiolar base was available for our chromatographic studies due to its great rarity and the few collections of it. Although we cannot exclude autoxidative or other changes in the phenolics of such an old herbarium-specimen (see above), we are nevertheless able to state

**Table 1.** Semi-quantitative results showing the phloroglucinol composition in Asian and Hawaiian taxa of *Dryopteris* subgenus *Dryopteris* section *Marginatae*. 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 <sup>1)</sup> Collection number or lit. ref. <sup>2)</sup>	Origin <sup>3)</sup>	Aspidinol-B (2 <sup>4)</sup> )	Flavaspidic acid (5)	Aspidin (6)	Para-aspidin (7)	Desaspidin (8)	Albaspidin (10)	Phloraspin (11)	Phloraspidinol (12)	Margaspidin (13)	Methylene-bis-aspidinol (18)	Fillicic acid (19)	Trispara-aspidin (20)	Triflavaspidic acid (23)	Fraginol (3)
<b>Asian taxa</b>															
<i>D. cochleata</i>	Widén et al. (1978)	–	+++	–	+	++	+++	–	–	–	–	–	–	–	–
2x, s	CRFJ 8122–38, 8140–42	(+)	+++	–	+	–	+++	–	–	–	–	–	–	–	–
	CRFJ 9027–34, 9036	(+)	+++	–	+	–	+++	–	–	–	–	–	–	–	–
<i>D. angustifrons</i> <sup>8)</sup>	Wallich (1821)	–	++	+	–	++	–	–	–	–	–	–	–	–	–
<i>D. subimpressa</i> <sup>7)</sup>	Widén et al. (1997)	–	++	+	–	++	–	–	–	–	–	–	–	–	–
2x, s		–	++	+	–	++	–	–	–	–	–	–	–	–	–
<i>D. approximata</i>	CRFJ 9161–63	–	–	–	+	–	+++	–	–	–	–	–	–	–	–
2x, s	CRFJ 9234–38, 9241–42	–	++	–	+	–	+++	–	–	–	–	–	–	–	–
<i>D. goeringiana</i> <sup>8)</sup>	PE 884, 566	–	+	–	–	–	+	–	–	–	–	+++	–	–	–
<i>D. ramosa</i> <sup>8)</sup>	Widén et al. (1991)	(+)	+++	–	++	–	+	–	–	–	–	+++	+	(+)	+
2x, s		(+)	++	–	+++	–	+	–	–	–	–	+++	+	(+)	(+)
<i>D. carollhopei</i>	CRFJ 8197–8209	(+)	(+)	–	+	–	(+)	++	–	+++	–	+	–	(+)	–
2x, s	Puri et al. (1978) <sup>9)</sup>	+	++	–	+	–	–	+	+	+++	–	+	–	(+)	–
<i>D. marginata</i> <sup>8)</sup>	Widén et al. (1991)	–	+++	–	–	–	+	–	–	–	–	+	–	(+)	++
2x, s		–	+++	–	–	–	+	–	–	–	–	+	–	(+)	++
<i>D. porosa</i>	PE 7858	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2x, s		–	–	–	–	–	–	–	–	–	–	–	–	–	–
<b>Hawaiian taxa</b>															
<i>D. mauiensis</i>	CRFJ 14814, 14866	–	–	–	–	–	–	–	–	–	–	–	–	–	–

<sup>1)</sup> 2x = diploid, 3x = triploid, 4x = tetraploid, a = apomictic, s = sexual. <sup>2)</sup> CRFJ = C.R. Fraser-Jenkins; PE = collector's number in herb. Beijing. <sup>3)</sup> Phil = Philippines. <sup>4)</sup> Aspidinol (2) is mostly an artefact. <sup>5)</sup> In addition to the compounds listed in the table the North Indian taxon contains minute amounts of tetra-albaspidin-ABBA (25-ABBA). <sup>6)</sup> The spot identified as aspidin (6) may also be due to substance TR-1579 of unknown structure with similar chromatographic properties (see von Euw et al. 1985). <sup>7)</sup> In addition to the phloroglucinols listed, trisedaspidin (27) was detected. <sup>8)</sup> In addition *D. goeringiana*, *D. ramosa* and *D. marginata* contain trace amounts of abbreviatin (30). <sup>9)</sup> This material from near Simla was first identified by Puri as *D. marginata*, but that species does not occur in the W. Himalaya, where it has been confused with *D. carollhopei*. According to its characteristic phloroglucinol composition it must also be *D. carollhopei*.

**Table 2.** Semiquantitative results showing the phloroglucinol composition in African taxa of *Dryopteris* subgenus *Dryopteris* section *Marginatae*. Estimated from intensity of spots in TLC and yield in preparative column chromatography. +++ = 20% or more of the crude filixin mixture, ++ = 10%–20%, + = 5%–10%, (+) = 1%–5%, – = < 1%.

Taxon and ploidy, reproduction <sup>1)</sup> Collection number or lit. ref. <sup>2)</sup>	Origin <sup>3)</sup>	Aspidinol (2) <sup>4)</sup>	Flavaspidic acid (5)	Para-aspidin (7)	Desaspidin (8)	Albaspidin (10)	Phloraspidin (11)	Phloraspidin (12)	Margaspidin (13)	Methylene-bis-aspidinol (18)	Filixic acid (19)	Trispara-aspidin (20)	Tristavaspidic acid (23)	Pentherin I (brown unknown)	Pentherin II (yellow unknown)
<i>D. subcrenulata</i>	Madg	+	++	–	–	+	–	–	–	–	++	–	+	–	–
	CRFJ 12066, 12068, 12069	–	++	–	–	+	–	–	–	–	++	–	+	–	–
<i>D. schimperiana</i> 2x, s	Madg Ethiopia Kenya	–	++ ++ ++	– ++ –	– – –	++ ++ ++	++ ++ ++	– – –	++ ++ –	– – –	++ ++ +	– – –	++ ++ ++	++ ++ ++	– – –
	IK 14455 JK 5211	–	++	–	–	++	++	–	–	–	++	–	++	++	–
<i>D. ruwenzoriensis</i> 4x, s?	Uganda	–	+	–	–	–	–	–	–	–	++	–	+	++	–
	OH 614	–	+	–	–	–	–	–	–	–	++	–	+	++	–
<i>D. pentheri</i> 4x, s	Tanzania	–	++	–	–	++	–	–	–	–	++	–	+	++	–
	TJ 1735	–	++	–	–	++	–	–	–	–	++	–	+	++	–
	RK 28604	–	++	–	–	++	–	–	–	–	++	–	+	++	–
	CA 1269	–	++	–	–	++	–	–	–	–	++	–	+	++	–
"Northern albaspidin/ filixic acid chem. race"	?RV s.n. Cam Cam Cam	–	++ ++ ++	– – –	– – –	++ ++ ++	– – –	– – –	– – –	– – –	++ ++ ++	– – –	++ ++ ++	++ ++ ++	– – –
	CRFJ 11466–69 CRFJ 11289	–	++ ++	– –	– –	++ ++	– –	– –	– –	– –	++ ++	– –	++ ++	++ ++	– –
	IK 12373	–	++	–	–	–	–	–	–	–	++	–	++	++	–
"Southern aromatic chem. race"	Ethiopia Reunion	–	+	++	–	–	–	++	++	–	++	+	++	–	–
	CRFJ 12327, 12333–38	–	+	++	–	–	–	++	++	–	++	+	++	–	–
	CRFJ 4523	+	+	++	–	–	+	++	++	–	++	+	–	–	–
	Kenya	–	+	++	–	–	+	++	++	–	++	+	–	–	–
	RBF 71/255 <sup>5)</sup>	–	+	++	–	–	+	++	++	–	++	+	–	–	–
	?EB 42	–	–	–	–	–	+	++	++	–	++	+	–	–	–
	Tanzania	–	–	–	–	–	+	++	++	–	++	+	–	–	–
	?EMR 6533	+	–	–	–	–	+	++	++	–	++	+	–	–	–
	CRFJ 11910, 11912, 11913	–	+++	+++	–	–	+	++	++	–	++	+	–	–	–
	Madg	–	+++	+++	–	–	+	++	++	–	++	+	–	–	–
	CRFJ 12091	–	+++	+++	–	–	+	++	++	–	++	+	–	–	–
	DSM 572	–	+++	+++	–	–	+	++	++	–	++	+	–	–	–
	Zim	–	+++	+++	–	–	+	++	++	–	++	+	–	–	–
	ES 5368	–	(+)	–	–	–	(+)	++	++	–	++	+	–	–	–
	WJ s.n.	–	++	–	–	–	–	++	++	–	++	+	–	–	–
	S Africa	–	++	–	–	–	–	++	++	–	++	+	–	–	–
	HR 505	–	+	–	–	–	+	++	++	–	++	+	–	–	–

continued

Table 2. Continued.

Taxon and ploidy, reproduction <sup>1)</sup> Collection number or lit. ref. <sup>2)</sup>	Origin <sup>3)</sup>	Aspidinol (2) <sup>4)</sup>	Flavaspidic acid (5)	Para-aspidin (7)	Desaspidin (8)	Albaspidin (10)	Phloraspin (11)	Phloraspidin (12)	Margaspidin (13)	Methylene-bis-aspidinol (18)	Filixic acid (19)	Trispara-aspidin (20)	Trisflavaspidic acid (23)	Pentherin I (brown unknown)	Pentherin II (yellow unknown)
<i>D. filipaleata</i> 4x?, s	RBF 71/885 <sup>5)</sup>	Kenya	++			(+)					+			‡	
	RV 75-3301	Kenya	++			+					(+)			+	
	RV 75-3297	Kenya	++			+					(+)			+	
	RBF 70/66	Kenya	++								+			+	
	MR 24073	Tanzania	++			(+)					+			+	
<i>D. tricellularis</i> 2x, s	RBF 71/468 <sup>5)</sup>	Kenya	+++			++					+				
	RB A212	Ethiopia	+++												
<i>D. glanduloso-paleata</i> 4x?, s	CRFJ 11373	Cam	+++			+					+				
	CRFJ 11386, 11388	Cam	+++			+					+				
	CRFJ 11395	Cam	+++			+					+				
	CRFJ 11447, 11448	Cam	++			+					+				
<i>D. occidentalis</i> 4x?, s	JV 5052	Sa To	+++			++					++				
	AM s.n.	Sa To	+			+++								+	
<i>D. fadenii</i> 2x, s	RBF 71/68 <sup>5)</sup>	Kenya	+++											+	
	RBF 74/1348	Kenya	+++											+	
<i>D. lewalleana</i> 2x, s?	AB 2567	Tanzania	++								++			+	
	EMR 8276	Tanzania	+			++					++			+	
"Northern albaspidin/ filixic acid chem. race" "Southern aromatic chem. race"	RH 9531	Tanzania	+			++					+			+	
	FM 1321	Moz	+++			++					+			+	
	DT 4236	Kenya	++								+			+	
	FW 2725	Zambia	-								+			+	
DJ 297	S Africa	+								+			+		
ES 5012	S Africa	-			(+)					+			+		

<i>D. athamantica</i>																					
2x, s	RBF 71/476 <sup>5)</sup>	Kenya	+	+++	-	(+)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	IK 12558	Ethiopia	+	+++	-	(+)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	IK 12417	Ethiopia	+	+++	-	(+)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	CRFJ 11441, 11443	Cam	+	+++	-	(+)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	CRFJ 11460, 11461	Cam	+	+++	-	(+)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	CRFJ 11436	Cam	+	+++	-	(+)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	CRFJ 11462, 11463	Cam	+	+++	-	(+)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	IK 13266	Zambia	+	+++	-	(+)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Widén et al. (1971)	S Africa	+	+++	-	(+)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. inaequalis</i>	CZ 1845	S Africa	-	-	-	(+)	++	++	-	-	-	-	-	-	-	-	-	-	-	-	-
2x?, s	IK 11651	S Africa	-	+++	-	+++	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. bernieri</i>	CRFJ 12281,	Reunion	-	+++	-	+++	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	12283, 12284																				
	12286-89,																				
	12291, 12292	Reunion	-	+++	-	+++	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. manniana</i>																					
4x, s	CRFJ 11327-33,	Cam	+	+++	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
"Para-aspidin chem. race"	11335-37																				
"Chem. race lacking para-aspidin"	JA 21180	Liberia	-	++	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. wideniana</i>	EJN 477	Madg	-	+++	-	+++	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4x, s	RBF 71/219 <sup>5)</sup>	Kenya	-	+++	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
"Chem. race lacking para-aspidin"	DC s.n.	Madg	-	+++	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	NCC 5705	Zim	-	+++	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	ES 2394	Kenya	-	+++	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. comorensis</i>	CRFJ 12190-92	Com	-	+++	-	++	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2x?, s																					
<i>D. aquilinoidea</i>	CRFJ 12340-42	Reunion	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2x?, s																					
<i>D. oligodonta</i>	Widén et al. (1973)	Can Isl	+	+++	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2x, s																					

<sup>1)</sup> 2x = diploid, 4x = tetraploid, s = sexual, s.n. = sine numero (without number). <sup>2)</sup> CRFJ = C.R. Fraser-Jenkins, IK = I. Kukkonen, RB = R. Bonnefille, AM = A. Möller, MR = M. Richards, RBF = R.B. Faden, TR = T. Reichstein, RV = R.L.L. Viane, JK = J. Korman, OH = O. Hedberg, AB = A.A. Bullock, TJ = T.G. Jefford, EMF = E. Milne-Redhead, RH = R.M. Harley, JV = J. Viégas da Graça Espírito Santo, RK = R.W.J. Keay, CA = C.D. Adams, FM = F. de A. Mendonça, DT = D.R. Tweedie, EB = E. Bruce, DSM = D.S. Mitchell, FW = F. White, ES = E.A.C.L.E. Schelpe, WJ = W.B.G. Jacobsen, HR = H.B. Rycroft, DJ = D. Johnstone, CZ = C.L.P. Zeyher, EJN = E.J. Newman, DC = W. Deans Cowan, NCC = N.C. Chase, JA = J.G. Adams. <sup>3)</sup> Sa To = São Tomé, Cam = Cameroun, Moz = Mozambique, Reunion = La Réunion, Mascarene Islands, Madg = Madagascar, Zim = Zimbabwe, Can Isl = Canary Islands, Com = Comoro Islands, East Africa, Zam = Zambia. <sup>4)</sup> Aspidinol (2) is mostly an artefact. <sup>5)</sup> See also previous results in Widén et al. (1973) and correction of provisional names in Widén et al. (1991).

**Table 3.** Amounts of crude extractives in the *Dryopteris* material investigated. Those not listed here were from stipe bases, not weighed. For abbreviations and other data see Tables 1–2. n.m. = not measurable.

Taxon	Collection number or lit. ref.	Origin	Dry rhizome (g)	Ether extract		Crude filicin	
				crude (g) [%]	cation free (g) [%]	MgO (g) [%]	Ba(OH) <sub>2</sub> (g) [%]
<b>Asian taxa</b>							
<i>D. cochleata</i>	Widén et al. (1978)	Phil	10	0.250 [2.51]	n.m.	0.126 [1.26]	n.m.
	CRFJ 8122–38, 8140–42	N India	205	2.815 [1.37]	n.m.	1.057 [0.52]	0.212 [0.10]
	CRFJ 9027–34, 9036	N India	302	3.227 [1.07]	n.m.	1.244 [0.41]	0.094 [0.03]
<i>D. subimpressa</i>	Widén et al. (1997)	N India	257	5.46 [2.12]	4.75 [1.85]	n.m.	n.m.
	Widén et al. (1997)	N India	10.6	0.411 [3.88]	n.m.	0.072 [0.75]	0.096 [1.01]
<i>D. approximata</i>	CRFJ 9161–63	S India	11.1	0.237 [2.13]	n.m.	n.m.	n.m.
	CRFJ 9234–38	S India	22.2	0.801 [3.61]	n.m.	0.267 [1.31]	0.040 [0.19]
<i>D. goeringiana</i>	CRFJ 9241, 9242	S India	34.7	1.67 [0.48]	1.36 [0.39]	n.m.	n.m.
	PE 884, 566	China	3.3	0.21 [6.36]	n.m.	n.m.	n.m.
<i>D. ramosa</i>	Widén et al. (1991)	Pakistan	29	1.2 [4.14]	n.m.	0.63 [2.17]	0.16 [0.45]
	Widén et al. (1991)	N India	33.5	1.87 [5.58]	n.m.	0.38 [1.13]	0.45 [1.34]
<i>D. carolinhopei</i>	CRFJ 8197–8209	N India	24.6	0.75 [3.06]	n.m.	0.199 [0.84]	0.024 [0.10]
	CRFJ 8197–8209	N India	191.6	4.86 [2.54]	4.50 [2.50]	n.m.	n.m.
<i>D. marginata</i>	Puri et al. (1978)	N India	200	6.43 [3.23]	n.m.	n.m.	n.m.
	Widén et al. (1991)	N India	27.8	3.15 [11.32]	n.m.	0.256 [0.95]	0.311 [1.16]
<i>D. porosa</i>	Widén et al. (1991)	N India	101	6.62 [6.62]	5.78 [5.78]	n.m.	n.m.
	PE 7858	China	2	0.098 [4.91]	n.m.	–	–
<b>Hawaiian taxa</b>							
<i>D. mauiensis</i>	CRFJ 14814, 14866	Hawai'i	2.9	0.011 [0.38]	n.m.	–	–
<b>African taxa</b>							
<i>D. subcrenulata</i>	CRFJ 12066, 12068, 12069	Madg	6.5	0.43 [6.6]	n.m.	n.m.	n.m.
	CRFJ 12023, 12026	Madg	32.8	1.74 [5.3]	n.m.	n.m.	n.m.
<i>D. pentheri</i>	?RV s.n.	Cam	6.7	0.38 [5.6]	0.26 [3.8]	n.m.	n.m.
	CRFJ 11466–69	Cam	49.2	5.7 [11.6]	4.9 [9.9]	n.m.	n.s
"Northern albaspidin/ filixic acid chem. race"	CRFJ 11289	Cam	6.0	0.7 [12.0]	0.6 [10.0]	n.m.	n.m.
	CRFJ 12327, 12333–38	Reunion	177.4	n.m.	6.4 [3.6]	n.m.	n.m.
"Southern aromatic race"	RBF 71/255 (Widén et al. 1973)	Kenya	335	13.0 [3.89]	n.m.	2.89 [0.89]	n.s
	CRFJ 11910, 11912, 11913	Madg	22.5	1.37 [6.1]	n.m.	n.m.	n.m.
<i>D. filipaleata</i>	CRFJ 12091	Madg	3.3	0.16 [4.8]	n.m.	n.m.	n.m.
	WJ s.n.	S. Africa	12.4	0.31 [2.5]	n.m.	n.m.	n.m.
	RBF 71/885 (Widén et al. 1973)	Kenya	345	16.51 [4.8]	n.m.	5.53 [1.60]	n.m.

<i>D. triculularis</i>	RBF 71/468 (Widén et al. 1973)	Kenya	53.6	3.83 [7.15]	n.m.	1.06 [1.98]	n.m.
<i>D. glandulosopaleata</i>	CRFJ 11373, 11386, 11388, 11395	Cam	22.2	3.2 [14.4]	2.8 [12.2]	n.m.	n.m.
<i>D. occidentalis</i>	CRFJ 11447, 11448	Cam	16.9	1.02 [6.0]	0.86 [5.1]	n.m.	n.m.
<i>D. fadenii</i>	RBF 71/68 (Widén et al. 1973)	Kenya	9.30	14.13 [1.52]	n.m.	6.31 [0.67]	4.29 [0.45]
<i>D. athamanica</i>	RBF 71/476 (Widén et al. 1973)	Kenya	426.5	15.6 [3.65]	n.m.	3.92 [0.94]	4.29 [1.01]
	CRFJ 11441–43	Cam	23.9	1.33 [5.56]	1.09 [4.5]	n.m.	n.m.
	CRFJ 11460, 11461	Cam	13.5	0.67 [5.0]	0.52 [3.8]	n.m.	n.m.
	CRFJ 11436	Cam	36.4	1.38 [3.8]	1.14 [3.1]	n.m.	n.m.
	CRFJ 11462	Cam	17.3	1.05 [6.1]	0.87 [5.0]	n.m.	n.m.
	CRFJ 11463	Cam	14.4	0.68 [4.7]	0.55 [3.8]	n.m.	n.m.
	IK 13266	Zambia	5.9	n.m.	0.21 [3.5]	n.m.	n.m.
<i>D. bernieri</i>	CRFJ 12281, 12283, 12284	Reunion	30.5	2.31 [7.6]	n.m.	n.m.	n.m.
	CRFJ 12286–89, 12291, 12292	Reunion	247.6	n.m.	10.85 [4.4]	n.m.	n.m.
<i>D. manniana</i>	CRFJ 11327–33, 11335–37	Cam	5.3	0.3 [5.7]	n.m.	n.m.	n.m.
<i>D. wideniana</i>	RBF 71/219 (Widén et al. 1973)	Kenya	410	20.1 [4.9]	n.m.	6.42 [1.57]	2.79 [0.68]
<i>D. comorensis</i>	CRFJ 12190–92	Comores	32.5	1.07 [3.3]	n.m.	n.m.	n.m.
<i>D. aquiloides</i>	CRFJ 12340–42	Reunion	44.2	0.34 [0.77]	n.m.	n.m.	n.m.
<i>D. oligodonta</i>	Widén et al. 1973	Can Isl	160	4.0 [2.5]	n.m.	n.m.	n.m.

that its phenolics are significantly different from those of the other probably related species we investigated. It contained aspidin (6) or the substance *TR 1579* of unknown structure (von Euw *et al.* 1985), filixic acid (19) and desaspidin (8). This important finding distinguishes it at once from the closely similar *D. carolihopei*, with which it could otherwise conceivably have been considered conspecific, as it is similar to a narrow and erect-fronded (possibly abnormal) plant of the latter with an attenuated rhizome. Unfortunately we were not been able to obtain material of the tetraploid *D. camusiae*, which looks as if it might be partly derived from *D. angustifrons*.

In the N Indian species, *D. subimpressa*, flavaspidic acid (5), aspidin (6) and desaspidin (8), mainly consisting of propionyl homologues (Table 4), were detected. The presence of desaspidin (8), among other differences, distinguishes it at once from *D. marginata* or *D. carolihopei*, which might be among its closest relatives.

The S Indian species, *D. approximata*, contains albaspidin (10) as its main compound as well as some flavaspidic acid (5), trisflavaspidic acid (23), and para-aspidin (7). Noteworthy, however, is the absence of the ubiquitous substances 5 and 23 in one of the two samples, *CRFJ 9161–9163*, from the same area and with typical *D. approximata* morphology, not different from the other sample. It thus displays some chemical variation even locally and study of material from Sri Lanka would be of value. The presence of large amounts of albaspidin (10) distinguishes it immediately from the related N Indian species of the section with which it had previously been confused prior to its recognition by Sledge (1973).

*Dryopteris goeringiana* from China showed only flavaspidic acid (5), albaspidin (10) and much filixic acid (19) and is thus rather similar to what appears from morphology to be a related species, *D. ramosa*, though that also has a number of additional compounds, such as para-aspidin (7) and some other traces. A specimen (China, Honan no. 2643, PE) identified as *D. sublaeta*, a name which had been misplaced by Fraser-Jenkins (1986) as a synonym of *D. goeringiana*, has considerably larger spores (det. CRFJ) than that; its type (China, Honan. 5662)

is a similar specimen. This name was omitted by Wu (2000).

Of the W Himalayan species, *D. ramosa*, we had material from Pakistan and India. Both samples investigated proved to be rather uniform and contained some albaspidin (10) and fraginol (3) and considerable amounts of flavaspidic acid (5), para-apidin (7), trispara-aspidin (20), and filixic acids (19) (Widén et al. 1991). Thus the apparently related species, *D. goeringiana* differs from *D. ramosa* in not containing para-aspidin (7), fraginol (3) as well as trispara-aspidin (20) and trisflavaspidic acid (23). Unfortunately we were not been able to obtain material of the more closely related *D. shiromensis* to compare with *D. ramosa* and *D. goeringiana*.

#### The Sino-Himalayan *D. marginata* assemblage

*Dryopteris carolihopei* from N India was always included within *D. marginata*, but following its taxonomic recognition from its distinctive

morphology, we can now confirm that the two are also chemically very different. *Dryopteris carolihopei* contained only minute amounts of the common phloroglucides, flavaspidic acid (5), para-aspidin (7), albaspidin (10), filixic acids (19) and trisflavaspidic acid (23). Its main compounds proved to be phloraspidin (11) and margaspidin (13), as well as some abbreviatin (30) and methylene-bis-aspidinol (18), none of which are present in *D. marginata*, which may not be so closely related to it as might be thought. These fully aromatic phloroglucinols were lacking in the other Asiatic species of the section. It seems likely that the biosynthesis of desaspidin (8) from its putative precursor phloraspidin (11) is totally blocked, and that of para-aspidin (7) can only occur in part from its putative precursor margaspidin (13) (see fig. 2 in Widén et al. 1999 and discussion). The material reported as *D. marginata* from Simla, NW India, by Puri and Widén (1978) was wrongly identified and in fact belongs to *D. carolihopei* (det. CRFJ) although slight differences are seen in comparing with the new material investigated.

**Table 4.** The semiquantitative composition of the acylfilicinic acids (36) and homologues (see Widén et al. 1991) after reductive cleavage of the crude filicins. For abbreviations and further data see Tables 1–2.

Taxon	Collection no. or lit.ref.	Origin	Acylfilicinic acid (%) in total amount			
			valeryl	butyryl	propionyl	acetyl
<b>Asian taxa</b>						
<i>D. cochleata</i>	CRFJ 8122–38, 8140–42	N India	–	40	20	20
	CRFJ 9027–34, 9036	N India	–	40	40	20
<i>D. subimpresca</i>	Widén et al. (1997)	N India	–	5	85	10
<i>D. approximata</i>	CRFJ 9234–38, 9241, 9242	S India	–	20	70	10
<i>D. ramosa</i>	Widén et al. (1991)	Pakistan	–	40	40	20
	Widén et al. (1991)	N India	–	53	30	20
<i>D. carolihopei</i>	CRFJ 8197–8209	N India	–	–	–	–
<i>D. marginata</i>	Widén et al. (1991)	N India	–	90	8	2
<b>African taxa</b>						
<i>D. pentheri</i>	RBF 71/255 Widén et al. (1973)	Kenya	–	35	35	30
"Southern aromatic race"						
<i>D. filipaleata</i>	RBF 71/885 Widén et al. (1973)	Kenya	–	98	1	1
<i>D. tricellularis</i>	RBF 71/468 Widén et al. (1973)	Kenya	47	30	21	2
<i>D. fadenii</i>	RBF 71/68 Widén et al. (1973)	Kenya	–	95	–	5
<i>D. athamantica</i>	Widén et al. (1971)	S Africa	–	45	45	10
	RBF 71/476 Widén et al. (1973)	Kenya	–	46	46	8
<i>D. wideniana</i>	RBF 71/219 Widén et al. (1973)	Kenya	–	43	22	35
<i>D. oligodonta</i>	Widén et al. (1973)	Can Isl	–	76	18	6



**Table 5.** Pure crystalline compounds isolated from the analysed taxa. For abbreviations and additional data see Tables 1–2. In mixed crystallisates the main homologues are underlined. For compounds isolated from the Asian taxa *D. ramosa* and *D. marginata*, see Widén *et al.* (1991).

Taxon	Collection no. or lit.ref.	Origin	Compounds isolated in crystals (mg)
<b>Asian taxa</b>			
<i>D. cochleata</i> <sup>1)</sup>	CRFJ 8122–38, 8140–42	N India	albaspidin BB, PB = 10-BB, PB (0.2)
<i>D. subimpressa</i>	Widén <i>et al.</i> (1997)	N India	aspidin PB, BP, PP, AA = 6-PB, BP, PP, AA (30.3); desaspidin PB, BP, PP = 8-PB, BP, PP (193.2); desaspidin AP, PA = 8-AP, PA (0.5); trisdesaspidin PBP = 21-PBP (2.9)
<i>D. approximata</i> <sup>1)</sup>	CRFJ 9234–38, 9241, 9242	S India	albaspidin PB, PP, AB, AP = 10-PB, PP, AB, AP (12.9); trisflavaspidic acid = 23 (4.6, not studied in detail)
<i>D. carolilhopei</i> <sup>1)</sup>	CRFJ 8197–8209	N India	margaspidin-BV, BB, BP = 13-BV, BB, BP (298); margaspidin-BB = 13-BB (4.8)
<b>African taxa</b>			
<i>D. pentheri</i>	RBFB 71/255, Widén <i>et al.</i> (1973, 1991)	Kenya	methylene-bis-aspidinol-BB, PB, PP = 18-BB, PB, PP(1); albaspidin-BB, PB = 10-BB, PB(1); filixic acid-PBB, PBP, 19-BBB, PBB, PBP (1); para-aspidin BB, PB, BP, PP = 7-BB, PB, BP, PP(10); trispara-aspidin, BBB, PBB, PBP = 20-BBB, PBB, PBP (11) <sup>2)</sup> ; phloraspin-BB = 11-BB (16, not quite pure)
<i>D. filipaleata</i>	RBFB 71/885 Widén <i>et al.</i> (1973)	Kenya	albaspidin-BB = 10-BB (4.1); flavaspidic acid-BB = 5-BB (1227)
<i>D. tricellularis</i>	RBFB 71/468 Widén <i>et al.</i> (1973)	Kenya	filixic acid-VV, VB, VBB, BBB, PBB = 19-VV, VB, VBB, BBB, PBB (3.3); flavaspidic acid-VV, VB, BB = 5-VV, VB, BV, BB = 5-VV, VB, BV, BB (188)
<i>D. fadenii</i>	RBFB 71/68 Widén <i>et al.</i> (1973)	Kenya	pentherin I (22.9, not quite pure); pentherin II (32.1, not quite pure); flavaspidic acid BB = 5-BB(21); albaspidin-BB = 10-BB(6.4)
<i>D. athamantica</i>	RBFB 71/476 Widén <i>et al.</i> (1971)	Kenya	para-aspidin-BB, PB, BP = 7-BB, PB, BP(317); para-aspidin-BB, PB, BP, PP = 7-BB, PB, BP, PP(404); aspidinol-B, P, A = 2-B, P, A(104); aspidinol-B, P, A = 2-B, P, A(26)
<i>D. wideniana</i>	RBFB 71/219 Widén <i>et al.</i> (1973)	Kenya	albaspidin-BB, PB, PP = 10-BB, PB, PP(13); filixic acid-BBB, PBB, PBP, ABB, ABP, ABA = 19-BBB, PBB, PBP, ABA, ABP, ABA(4); filixic acid-BB, PBP, ABB, ABP = 19-BBB, PBB, PBP, ABP (100); flavaspidic acid-BB = 5-BB(52); flavaspidic acid-BB, PB = 5-BB, PB(492)
<i>D. oligadonta</i>	Widén <i>et al.</i> (1973)	Can Isl	filixic acid-BBB, PBB, PBP = 19-BBB, PBB, PBP(7)

<sup>1)</sup> *D. approximata* and *D. carolilhopei* were extracted using the new, improved method and *D. cochleata* with the classic standard method (see von Euw *et al.* 1980, 1985, Widén *et al.* 1991). However, this has no adverse effect on the semiquantitative results in Tables 1 and 2 as both methods can be used in parallel. <sup>2)</sup> It was first identified as trisaspidinol, but was later corrected to trispara-aspidin (20), cf. Widén *et al.* (1973, 1976).

In *D. marginata* from NE India the above mentioned compounds (11), (13) and (18) as well as para-aspidin (7), are lacking. The species containing instead flavaspidic acid (5) (main compound) and fraginol (3) as well as trace amounts of (10), (19) and (23). It thus shows a completely different phloroglucinol spectrum from *D. carolihopei*, as mentioned above. It is also different from the other species investigated.

*Dryopteris porosa* from China apparently differs from nearly all other related species in the section in our finding of a complete absence of phloroglucinols in its rhizome. However, its frond morphology shows that it is very closely related to *D. marginata* and we feel that this species should be investigated further, utilising more and fresher material before concluding that it is definitely without phloroglucinols.

### Hawai'ian species

Many of the Hawai'ian *Dryopteris* species (see Fraser-Jenkins 1994) show relationships to the Asian species more than to any other area and this is generally true of the majority of Hawai'ian pteridophytes (Palmer 2003). A new study by Geiger and Ranker (2005) supports this view.

In the present paper, only *D. mauiensis* concerns us as a member of the section *Marginatae*, with its frond morphology typical of the section and perhaps indicating a relationship to *D. marginata* itself. Two other species, namely *D. sandwicensis* and *D. unidentata* also show some morphological characteristics that somewhat approach the section *Marginatae* (Fraser-Jenkins 1994), but from their morphology we do not think they actually belong in the section and they have so far been treated, though with some uncertainty, in the section *Aemulae* (Part II, Widén et al. 1999). In our opinion they are clearly not related to *D. mauiensis*, even though we also found them to contain only traces of phloroglucinols, or to be lacking in them. It could be surmised that *D. mauiensis* merely imitates the section *Marginatae* as a case of parallelism, but this seems unlikely given its very strong resemblance in all its morphological features, and it is more likely that the complete absence of phloroglucides does not indicate a major taxonomic disjunction.

However Geiger and Ranker (2005) placed both *D. mauiensis* and a yet more distinct Hawai'ian species, *D. crinalis* as belonging to an "exindusiate group", including *D. sandwicensis* and *D. unidentata*, though rather weakly supported there. The group contains species with a number of quite different morphologies and being exindusiate is not in itself normally associated with any particular section in *Dryopteris*. CRFJ is of the opinion that until we understand more of the significance of such studies including the functional role of the genetic sequences concerned, and are no longer required to interpret molecular polyphyly and monophyly as absolute diagnostic deciding factors in taxonomy and systematics, it is not possible to place full reliance on this idea. The real relationships and origins of some of the species they placed together in their Hawai'ian "exindusiate group" (and of *Nothoperanema rubiginosa*) are not yet clear and we continue to interpret the obvious *Marginatae*-type morphology of *D. mauiensis* as indicating that it must indeed belong to *Marginatae*, though we are undecided about the position of the other exindusiate species.

### African species

Of the 27 African, or African-related species we accept in the section *Marginatae*, we investigated 19 species. It is clear that the taxonomic situation is highly complicated with a large, partly cryptic complex of critical and confused, closely related species, a number of which have only recently become known to science. Some of these correspond with taxa first proposed, though not validated, by our late colleagues, T. Reichstein and J. Sarvela, on cytological and chemical grounds. In the present paper we took steps to relate these taxa with the modern species recently described by JPR and feel we have now reached as clear a taxonomic understanding as possible at the present time due to our joint cooperation.

In *D. subcrenulata* from Madagascar the following phenolics were found: flavaspidic acid (5) and filixic acid (19) were the main compounds together with minute amounts of albaspidin (10) and trisflavaspidic acid (23).

*Dryopteris schimperiana* is from Ethiopia and Kenya. For our investigation only two properly documented specimens were available. The Ethiopian fern contained considerable amounts of flavaspidic acid (5), para-aspidin (7) and margaspidin (13) as well as some aspidinol (2, artefact) albaspidin (10), trisflavaspidic acid (23) and pentherin I. On the other hand, the Kenyan fern differed from the Ethiopian one by its lack of para-aspidin (7) and margaspidin (13), but in containing great percentages of phloraspin (12), which is structurally related to (13). Noteworthy, also is the high percentage of pentherin I and the occurrence of filixic acid (19) not present in the Ethiopian fern.

*Dryopteris ruwenzoriensis* from Uganda exhibits a phloroglucinol spectrum similar to that of *D. subcrenulata* and of *D. pentheri* "Northern albaspidin/filixic acid chemical race". Roux also stated that it is related to *D. pentheri*, which is now verified from the chemistry.

The phloroglucinol pattern of the species complex identified as *D. pentheri*, including *D. lewalleana*, is most interesting. It consists of at least two geographically separated chemical races: (1) a "Northern albaspidin/filixic acid chemical race" containing albaspidin (10) and often filixic acid (19), but lacking the aromatic compounds phloraspin (12), phloraspidinol (14), margaspidin (13) and methylene-bis-aspidinol (18); and (2) a "Southern aromatic chemical race" containing the aromatic compounds (12), (13), (11) (main compound) and (18) as well as varying amounts of para-aspidin (7), again pointing to the existence of a partial biosynthetic block in the bioformation of para-aspidin (7) (see under *D. carolihopei*, above). Pentherin I is almost always present. In the latter chemical race albaspidin (10) and filixic acid (19) are present only in traces or are lacking, as well as pentherin I. Interestingly the same chemical races were found in the closely related *D. lewalleana* and in *D. inaequalis* (see below), indicating the close relationships of these three taxa.

So far we were not been able to correlate chemical characters with morphology for the *D. pentheri* subgroup. *Dryopteris pentheri* and *D. lewalleana* clearly contain considerable morphological and chemical variation, suggesting the subgroup consists of a critical species com-

plex, which needs further study and identification (see also Widén *et al.* 1973, 1991, Schelpe & Anthony 1986).

*D. filipaleata* (4x = *D. "species nova"*) is chemically somewhat variable and contains flavaspidic acid (5), mostly albaspidin (10), filixic acid (19), trisflavaspidic acid (23) and always pentherin I. In fact the phloroglucinol spectrum is close to that of the *D. pentheri/D. lewalleana* "Northern albaspidin/filixic acid chemical race", supporting the opinion of Roux (2012) that these species are closely related. From *D. tricellularis*, *D. filipaleata* mainly differs through occurrence of pentherin I not present in *D. tricellularis*.

Two diploid ferns from Kenya (RBF 74/468) and Ethiopia (RB A212) were determined as *D. tricellularis* by JPR. The specimen from Kenya contained much (5) as well as only traces of (10), (19) and (23) but was lacking pentherin I. The Ethiopian fern differed from the Kenyan fern by the occurrence of great percentages of albaspidin (5) but in lacking filixic acid (19). As suggested by JPR, the morphology of *D. tricellularis* indicates that it should be related to *D. fadenii*, but this could not be verified by chemistry. However a relationship with *D. pentheri/D. lewalleana* "Northern albaspidin/filixic acid race" seems evident.

In *D. glandulosopaleata* from Cameroon, a great percentage of flavaspidic acid (5) as well as small amounts of albaspidin (10), trisflavaspidic acid (23) and filixic acid (19) were observed. Thus a relationship to the *D. pentheri* aggregate "Northern albaspidin/filixic acid chemical race", is obvious.

In *D. occidentalis* from Cameroon the same phloroglucinols as those in *D. glandulosopaleata* could be detected, but filixic acid (19) was absent. However as in the former species a relation to *D. pentheri*, "Northern albaspidin filixic acid race", seems possible.

Of *D. caperata* from São Thomé two old herbarium vouchers were investigated. Some variability of the phenolics was observed in line with some morphological variation. Both samples contained huge amounts of albaspidin (10), varying amounts of flavaspidic acid (5), trisflavaspidic acid (23) and also pentherin I in traces. However filixic acid (19) found in JV 5052 was lacking in AM s.n. As only two old collections

were investigated it is perhaps not possible to talk of any different chemotypes/chemical races. Its very different phloroglucinol spectrum supports JPR's conclusion that it is a species distinct from *D. pentheri*.

*Dryopteris fadenii* differed somewhat from the other African taxa here discussed in its phloroglucinol spectrum. Flavaspidic acid (5) was the main compound, accompanied by some trisflavaspidic acid (23). Pentherin I also occurs in considerable quantity as well as minor amounts of the unique substance pentherin II, not present in any other species investigated.

We investigated quite a large collection of *D. athamantica* from different parts of Africa, finding that it is remarkably similar throughout in its phloroglucinol spectrum: para-aspidin (7) is always the main compound followed by minute amounts of aspidinol (2, artefact), flavaspidic acid (5), albaspidin (10), trispara-aspidin (20) and trisflavaspidic acid (23) (see Widén et al. 1973). In *IK 12417* pentherin I was also observed.

Of *D. inaequalis* from South Africa only one typical specimen (*IK 11651*) from S Africa was available for our investigations. Its phloroglucinol spectrum was rather similar to the "Northern albaspidin/filixic acid chemical race" of *D. pentheri/D. lewalleana*. But filixic acid (19) was absent. Another 170 years old atypically wide and large herbarium specimen from S Africa (*CZ-1845*) exhibited quite a different phloroglucinol pattern in containing the aromatic compounds phloraspin (11), phloraspidinol (12), margaspidin (13) and methylene-bis-aspidinol (18) as well as some albaspidin (10). In fact it was similar to the "Southern aromatic race" of *D. pentheri/D. lewalleana*. But this might be explained by the fact that the morphology of this specimen differed considerably from the other, typical *D. inaequalis* specimen.

The taxonomy of *D. inaequalis* and the *D. pentheri* agg. was treated in various different ways during the last century (Schelpe & Anthony 1986, Kornaš et al. 1993) but often both under the name *D. inaequalis*. But more recently these two had been treated as rather clearly separate species (Pichi-Sermolli 1984, 1985, Fraser-Jenkins 1986) and they have now been further divided into several species by Roux (2002,

2003, 2004a, 2004b, 2004c, 2004d, 2005, 2012).

In *D. bernieri* from La Réunion large amounts of flavaspidic acid (5), albaspidin (10) and pentherin I were observed as well as minute amounts of trisflavaspidic acid (23).

The *D. manniana* aggregate, of which we analysed quite extensive material of different origins, varies considerably in morphology as well as chemistry. Flavaspidic acid (5) is usually present in great percentage, accompanied by varying amounts of albaspidin (10) (not present in every specimen), filixic acid (19) (not present in every specimen) and trisflavaspidic acid (23); desaspidin (8) and pentherin I were also present only in *RBF-71/219* from Kenya (see also Widén et al. 1973). *CRFJ 11327-11333* and *11335-11337* from Cameroon differed considerably from the other specimens investigated in the occurrence of much para-aspidin (7), rather less flavaspidic acid (5) and some margaspidin (28). Pentherin I was observed only in the rhizome material from Kenya. The Cameroon plant is identified here as true *D. manniana s. stricto* "para-aspidin chemical race". Another "chemical race lacking in para-aspidin" was detected from Kenya, Zimbabwe and Madagascar. It contained greater percentages of 5 as in the former race and as the chemical difference corresponds with its considerably distinctive morphology, it has been separated and described here as *D. wideniana*. However a specimen from Liberia is somewhat problematical. Its morphology is closer to *D. manniana*, but its chemistry is like that of *D. wideniana*, in lacking (7). In the present work we placed it below *D. manniana* as "chemical race lacking para-aspidin (7)".

*Dryopteris comorensis* from the Comoro Islands is close to the *D. pentheri* aggregate, "Northern albaspidin/filixic acid chemical race", in its chemistry and to other taxa discussed above, but its frond morphology is somewhat different.

The very distinct species, *D. aquilinooides*, endemic to La Réunion, differed from *D. subcrenulata* in containing only small amounts of flavaspidic acid (5). However no relationship could possibly be indicated by this as the two species are at opposite ends of the spectrum morphologically and cannot have anything to do with each other.

*Dryopteris oligodonta* from the Canary Islands differs from the above taxa in containing a high percentage of para-aspidin (7) and filixic acid (19), accompanied by minute percentages of flavaspidic acid (5) and trispara-aspidin (20) (Widén *et al.* 1973).

## Conclusions

Considerable amounts of ether extract (oleoresin) and phloroglucinols (crude filicin) are usually present in the species of subgenus *Dryopteris*, sect. *Marginatae*. There are, however, two apparent exceptions, *D. porosa* from China and *D. mauiensis* from Hawai'i, which completely lack these phenolics, though *D. porosa* perhaps needs reinvestigation.

In most cases flavaspidic acids (5), albaspidin and/or filixic acids (19), triflavaspidic acids (23) and often para-aspidin (7) are present. It is noteworthy that the fully aromatic compounds phloraspidin (11) and margaspidin (13) occur in *D. carolihopei* from India and in *D. pentheri* and *D. lewalleana* "Southern aromatic chemical race" as well as in *D. inaequalis* from Africa. Thus these putative biosynthetic intermediates in the biosynthesis of desaspidin (8) and para-aspidin (7) seem to be relatively frequently distributed in *Dryopteris* species worldwide (see Widén *et al.* 1996, 1999 and 2001). As pointed out by Widén *et al.* (1999) in most species the occurrence of albaspidin (10) seldom coincides with that of filixic acid (19). However, in the present work it was observed that 10 and 19 occur together rather often, especially in the "Northern albaspidin/filixic acid chemical race" of *D. pentheri* and in *D. lewalleana*, *D. glandulosopalata* and *D. comorensis*. Pentherin I ("brown unknown") occurs in several African *Dryopteris* species, whereas the related pentherin II ("yellow unknown") has been detected solely in *D. fadenii*. Aspidin (6) was detected only in *D. subimpressa* and probably in *D. angustifrons* in the ferns of this section.

From our work, together with that of Japanese investigators (see Widén *et al.* 2001), ca. 160 *Dryopteris* species from Eurasia, Africa and America have now been studied, with the result that as far as we know only seven spe-

cies are completely devoid of phloroglucinols (though reinvestigation of some of these is desirable). In addition to the two species mentioned above these are: *D. polita* from SE Asia (subgenus *Erythrovaria*, sect. *Erythrovariae*, into which CRFJ now sinks the section *Politae*), *D. kilemensis* from Africa (subgenus *Nephrocystis*, sect. *Purpurascetes*), *D. sabae* from Japan and *D. macrochlamys* from Sri Lanka (both in subgenus *Nephrocystis*, sect. *Diclisodon*, into which CRFJ has now sunk sect. *Nephrocysti*) and *D. diffracta* from China (which might be in the section *Diclisodon*, or more probably represents a good genus, *Acrorumohra*, related to *Diclisodon* as well as, perhaps more closely to *Arachniodes*). Moreover *D. unidentata* from Hawai'i (subgenus *Dryopteris*, sect. ?*Aemulae*), *D. sparsa* and subspecies from Japan and India and *D. subexaltata* from Japan (both in subgenus *Nephrocystis*, sect. *Diclisodon*) also lack phloroglucinols (see Widén *et al.* 1999, 2001). Some of the populations from eastern N America of the circumboreal species, *D. expansa* (subgenus *Dryopteris*, sect. *Lophodium*), are interesting in having a chemical race that is completely devoid of phloroglucinols, but which is not recognisable morphologically or taxonomically.

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