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Dryopteris (Pteridophyta) of Hawai'i - a monographic study.

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ABSTRACT: Following a previous classification of *Dryopteris* by FRASER-JENKINS (1986), eight of the nine Hawai'ian species are placed in sections within the genus, one still remaining unplaced. The special degree of variation within at least two of the species in the Hawai'ian archipelago is discussed and the taxonomy of the species is rationalised accordingly, mostly bearing out the previous treatment of HERAT (1979). New taxa are: *Dryopteris palikuensis* HERAT ex FRAS.- JENK., *D. fusco-atra* var. *lamoureuxii* FRAS.- JENK. and *D. unidentata* var. *ukelelensis* HERAT ex FRAS. - JENK.; new combinations are: *Dryopteris comorensis* (TARD.- BLOT) FRAS.-JENK., *D. wallichiana* subsp. *madrasensis* (FRAS.- JENK.) FRAS.- JENK., *D. wallichiana* subsp. *coriacea* (FRAS.- JENK.) FRAS.- JENK., *D. glabra* var. *pusilla* (HILLEBR.) FRAS. - JENK., *D. glabra* var. *soripes* (HILLEBR.) HERAT ex FRAS. - JENK., *D. glabra* var. *nuda* (Underw.) FRAS. - JENK., *D. unidentata* var. *paleacea* (HILLEBR.) HERAT ex FRAS. - JENK. and *D. unidentata* var. *acutidens* (HILLEBR.) FRAS. - JENK. Some nomenclatural revision has been necessary as a result of retypification of names which had been misapplied by recent authors, including *D. sandwicensis* (HOOK. et ARN.) C.CHR.

KEYWORDS: *Dryopteris,* Pteridophyta, taxonomy, Hawai'i.

Introduction

Dryopteris on Hawai'i presents a number of special problems compared to other parts of the world because not only are the species highly isolated from other floras and include a number of representatives whose morphology is quite unlike those known from elsewhere, but in addition some of the species present an extraordinary range of variation, considerably greater than that known in any other species of the genus, which has therefore caused considerable controversy as to their treatment.

In 1979 - 1985 when the present author was engaged on a revision and infrageneric classification of the genus world-wide (FRASER-JENKINS 1986), no one had previously attempted to place Hawai'ian *Dryopteris* in any meaningful context within the genus and it became obvious that the genus was still very difficult to understand in Hawai'i despite a number of previous publications treating it (particularly HOOKER and WALKER-ARNOTT 1832, BRACKENRIDGE 1854, MANN 1868, HILLEBRAND 1888, HELLER 1897, ROBINSON 1912, CHRISTENSEN 1925 and HERAT 1979). Of the ten Hawai'ian species I recognized at the time, no less than six were unplaced in the classification (compared with only six others, of which at least one, *D. perrieriana* C. CHR., was a *Ctenitis*, unplaced from the whole of the rest of the world). One of the four placed species, *D. hawaiiensis* (HILLEBR.) ROBINS., had been placed in quite the wrong section due to confusion as to its identity and another, *D. parvula* ROBINS., which I no longer accept as a species distinct from *D. glabra*, had been completely misunderstood and placed not only in the wrong section but also in the wrong subgenus. In fact only two Hawai'ian species were actually placed correctly, whereas there was no such problem on a similar scale when I dealt with other areas of the world. An updated revision of this paper is now being prepared (FRASER - JENKINS, in prep.) to cover all the changes I am aware of.

The second major problem concerns variation within the species. While one species, *D. wallichiana* (SPRENG.) HYL., hardly varies at all except in its scale colour, which also occurs elsewhere in the range of this pan-subtropical montane species (see FRASER-JENKINS 1989a and others), the rest of the species are more variable, some very markedly so, in important features such as degree of dissection, segment-size, width and acuteness of segment-apex, frond-size, soral position and density and width of scales. Yet the variants are all fully connected by intermediate forms that are not sterile hybrids. One species in particular, *D. unidentata* (HOOK. et ARN.) C. CHR., shows more variability than any other known *Dryopteris* species; it is followed by the only slightly less variable species, *D. glabra* (BRACKENR.) O. KTZE. The phenomenon of remarkable infraspecific variability in Hawai'i has been pointed out by many authors and applies to Angiosperms as well as to ferns. Even some of the earlier authors on ferns (particularly HILLEBRAND 1888) appear to have been well aware of it, but it is difficult to distinguish between genuine recognition of the phenomenon and the tendency of earlier authors to have much broader species concepts, treating good, but related species as mere varieties of what would be a "super species" by today's standards. Thus while CHRISTENSEN (1925) called this problem of variation plus intermediates to attention and specifically referred to *D. unidentata* and *D. glabra*, he was unable to carry his reasoning through to successfully sorting out the species themselves in his somewhat preliminary, generically revised list. He was unable to separate *D. fusco-atra* (HILLEBR.) ROBINS. from *D. wallichiana*, or even *D. hawaiiensis* (including *D. palikuensis* HERAT ex FRAS.-JENK.) from *D. wallichiana,* and, incredibly, also *D. marginata* (WALL. ex CLARKE) CHRIST and *D. xanthomelas* (CHRIST) C.CHR. (sub *D. fibrillosa* (CLARKE) HAND.-MAZZ.) from *D. filix-mas*! These absurd and even at the time out of date comments make it impossible to make much sense of his species concepts, especially when he ended up suggesting that *D. glabra*, *D. crinalis* (HOOK. et ARN.) C.CHR. and *D. unidentata* could all be one species. But his more specific and definite statements that *D. nuda* UNDERW. is a synonym of *D. glabra* and *D. acutidens* C.CHR. (including var. *ukelelensis* HERAT ex FRAS.-JENK.) was probably a form of *D. unidentata*, seem to suggest he had some understanding of the unusual variability in Hawai'i. It was not until an excellent and detailed, but, sadly, unpublished, study by HERAT (1979) in his Ph.D. thesis, that anyone was able to deal realistically with the genus. His work was generally most successful and shows a great deal of taxonomic insight often not displayed by later workers. In essence, although the present author's concepts were developed quite independently of HERAT's, whose thesis I did not see until late 1992, there are few major points of difference presented here apart from that I do not accept *D. nuda* as a species, I accept an extra species, *D. mauiensis* C. CHR., having redefined *D. sandwicensis* (HOOK. et ARN.) C. CHR., and I include *D. crinalis* within the genus. I have also made a few minor adjustments to the varieties of *D. glabra* and *D. unidentata*. There is no doubt that HERAT really came to understand Hawai'ian *Dryopteris* as no other workers have done and has been the only person to "understand the range of variations within and between infraspecific taxa before trying to understand the limits of the group" (HERAT 1979 : 34), or, one might add for clarification, of the species. It is a pity that HERAT's work remained unpublished as, since then, the most recently circulated list of provisional taxa by WAGNER (1992) has shown less understanding of relative taxonomic weighting of the taxa and has merely divided them into a large number of mythical new species. He had evidently been selecting certain extremes of the variation but ignoring the continuity of the variants, which amounts to a kind of regression to a post - Victorian, "Komarovian" stamp-collecting taxonomy, the varieties being placed as species, which somewhat debases that rank.

The reason why variation has such a prominent place in the Hawai'ian flora has been outlined by a number of authorities (e.g., recently, CARLQUIST 1965 and GILLETT 1972), but in simple terms it appears to have been caused by the temporary isolation of populations on each island, which itself only exists relatively temporarily, and the reinvasion of populations at an early stage of speciation onto other islands to coexist with different, sometimes perhaps "original" populations, which are less differentiated, or have otherwise differentiated in a different direction. The islands themselves are thought to arise from a particular point of upwelling of magma below the ocean floor, which remains still while the crust-plate slowly migrates west-north-westwards over it. Each time a weaker area in the crust passes over the point a new island forms, while the older islands gradually erode away and finally disappear to the west (ZIMMERMAN 1948, WILSON 1963a and b). The beginnings of speciation through selection of variants occur in isolation in different morphological (or chemical) directions on different islands and proceed to different degrees, but do not continue any further on that island as it disappears. However spores are from time to time successfully blown between islands so that introgression begins to occur when the new variants are not sufficiently separated by genomic sterility barriers, while other populations never happened to evolve separately as far as the extremes in the first place. Thus at any one time one can find a range between the most extreme forms developed in isolation, those less well separated and those which have merged into one another, all forming an extensive series with fertile intermediates. However not all speciating populations have become reunited in this way and a number of groups of fully distinct species have evolved on the islands. In *Dryopteris* it is probable that *D. unidentata* may have evolved in situ in Hawai'i from *D. glabra* or a common ancestor; whereas other species such as *D. mauiensis* and *D. sandwicensis* had a separate origin (as surmised by HERAT 1979) from a different section, *Marginatae* FRAS.-JENK., at least the former perhaps in Oceania. Others may have evolved immediately in situ by allopolyploidy, for example the apomictic triploid, *D. palikuensis*, which must presumably have had *D. wallichiana* as one ancestor and a tripinnate diploid sexual species as the other.

The species that have not "succeeded" in separating fully into a new group of distinct species present a particular problem taxonomically and nomenclaturally as it can be difficult to see what rank they should be placed at when the extremes are so recognisably distinct but there is no real cut off point from all the rest. The definition and choice of ranks is naturally left up to the individual by the Code (GREUTER et al. 1988) and indeed any rank can quite properly and desirably have more than one different type of application by the same or different authors, depending on and reflecting the infinitely variable situations that actually exist from group to group. An interesting attempt to summarise recent usages of ranks has been made by HAMILTON and REICHARD (1992), though part of the impression given, to my mind rather misguidedly and too simplistically, is that different applications of the same rank are in some way undesirable and to be rationalised by tightening up the meanings of the ranks. Perhaps as a reflection of the current North American lack of traditional taxonomic insight and emphasis, reading between the lines, they appear almost to harbour some judgemental dislike of infraspecific ranks, which are "still" widely used, and even seem to want to reduce them to only one infraspecific rank instead of subspecies and variety etc. This general failing of North American systematic botany to reflect the situation in nature may result from the same philosophy that WAGNER and his followers' work displays in their tendency to apply only two ranks, the genus and the species, which sometimes leads to some most inappropriate treatments. However few nowadays would be likely to want to make a case for treating variants such as some of the Hawai'ian *Dryopteris* varieties as species, though unfortunately such appears to have been the case in WAGNER's (1992) most recent proposed list. Clearly they are not species in any accepted sense of the rank and his treatment must either have been the result of failure to observe or appreciate the significance of the spectrum of intermediates, or of an unnecessarily restricted usage of the taxonomic hierarchy of ranks, or both. However, most workers would apply the specific rank once the taxa could actually be thought to have speciated, rather than before that point, and it is hardly controversial to state that in the two main species concerned in Hawai'ian *Dryopteris* the variants have not yet speciated and indeed are probably on the whole no longer heading towards doing so, at least on the existing islands. An infrageneric rank is obviously more appropriate. My own practice, probably in keeping with most, is that I find the subspecific rank generally preferable for a closely related group of taxa that are biologically separated (different cytotypes in a polyploid critical complex, for example), or geographically well separated if vicariants, but though stable in their separation, are sufficiently close morphologically that they overlap somewhat impracticably or are separated only by very minor, or microcharacteristics. I would use the rank of variety when the taxa are not so well separated biologically and geographically, including for many slightly overlapping ecotypes and I would use the rank of forma for impermanent morphological conditons, or those affecting only a few individuals within the populations. The most appropriate rank for the *Dryopteris* variants concerned, as aptly chosen by HERAT, would appear therefore to be that of variety, which is used here accordingly. Had the specific rank been chosen, as WAGNER had intended, it would have been impossible to name any of the intermediates with a binomial since one would continually have to say that a particular specimen was between one species and another, a position normally applicable to genuine hybrids, which these are not. But with the infraspecific rank of variety such a situation is implied and understood. They are indeed not species, both in nature and in their nomenclature, which reflects this; it is only to be expected that some individuals will fall between one variety and another and there is no problem to say so as it does not affect the essential binomial nomenclature. Indeed for those who do not wish to consider the varieties, for one reason or another, the answer is simple, they can simply be omitted as the description and concept of the species concerned should include them anyway.

Although many of the presumably more ancient endemic species are now so distinct that they can hardly be related to any mainland continental or other Oceanian species and their origin is obscure, it seems apparent from looking at the fern-flora that a considerable proportion of species is related distantly, or sometimes more closely, to the Sino-Japanese (i.e. E. China, Japan), or Sino-Himalayan (i. e. Himalaya, W. and S. China, Taiwan) floras. It is indeed difficult to understand the Hawai'ian species properly without a substantial knowledge of the corresponding genera in Asia, which rather evidently appears to be largely absent from the current North American work in Hawai'i. Some good examples of such connections occur in *Polystichum*, where *P. haleakalense* BRACKENR. appears to be related to the Sino-Himalayan *P. wilsonii* CHRIST and *P. hillebrandii* CARUTH. is close to the Sino-Himalayan and Sino-Japanese *P. neolobatum* KURATA, while the possible new species, *P. bonseyi* WAGNER et HOBDY, is very closed to the Japanese *P. tagawanum* KURATA and its group. Some of them may even be part-ancestral to the mainland allopolyploids. It is also well known that there exist smaller but nevertheless significant connections with other floristic regions. *Dryopteris*, as chance would have it, does not include any such close relationships to other species except for the occurrence of the widespread *D. wallichiana*, though whether the Hawai'ian populations of it originated in Asia or the New World (or both) is at present impossible to say, but I rather suspect from its paler or browner scale-colour that it could have come from the New World. There also exists a quite extraordinary, almost unprecedented connection between *D. glabra* and Atlantic European *D. aemula* (AIT.) O. KTZE., which will be discussed further below.

Taxonomic treatment

The following summarised treatment is now put forward for Hawai'ian *Dryopteris*. Details are given where appropriate; the sections have been outlined by FRASER - JENKINS (1986). Some representative specimens are cited from some major herbaria.

Subgenus: *Dryopteris*
Section: *Fibrillosae* CHING

1. ***Dryopteris fusco-atra*** **(HILLEBR.) ROBINS.**

Although (FRASER-JENKINS 1989a) gave *Lastrea truncata* BRACKENR., non *Dryopteris truncata* (POIR.) O. KTZE., as a synonym of *D. fusco-atra* on the basis of a poor quality isotype at Kew (K!), the type collection seems to have been mixed and isotypes at US (!) and BISH(!) are both *D. wallichiana*. The one at US is evidently the specimen from which the plate was drawn and corresponds well with the rest of the protologue. It is therefore selected here as lectotype ("*Lastrea truncata* BRACKR. sp. nov. Margin of forest, Bullock Plains, Mouna Kea, Hawaii. Wilkes 8.") and I now agree with ROBINSON'S (1912) synonymising of the name with *D. wallichiana*. The Kew specimen consists of a small, sterile, juvenile specimen with a wide lamina-base and long pinnules. It is probably a juvenile *D. palikuensis*, rather than *D. wallichiana*, and is not *D. fusco-atra* as I had originally thought, but it is a difficult specimen to identify for certain.

This species is most probably a triploid apomict from its rather typical, large, irregular spores with a noticeable proportion of abortive ones. I hope Dr. MARY GIBBY can soon investigate my living plants of it to decide this question. The rather widely basally joined pinna-lobes and very dark scales suggest that it is somewhat intermediate between sections *Hirtipedes* FRAS.-JENK. and *Fibrillosae*, though obviously referable to the latter. It is morphologically intermediate between *D. wallichiana* and the diploid sexual *D. hirtipes* (DC.) O. KTZE. and if its origin came about by hybridisation between them, it might either have been formed in situ in the archipelago, with *D. hirtipes* later becoming extinct there, or elsewhere in Oceania, *D. fusco-atra* itself becoming extinct everywhere else except in Hawai'i. Although it is easily distinguishable from *D. wallichiana* (as pointed out by ROBINSON (1912) and in contrast to CHRISTENSEN'S (1925: 23) less critical comments) by its dark fuscous or black scales, long stipe and larger, differently shaped pinna-lobes, it has surprised me to see the number of specimens of it misdetermined as *D. wallichiana*, or its synonyms, by recent workers. Even the very occasional plants with browner scales are readily separable from *D. wallichiana*. The phloroglucide chemistry of *D. fusco-atra* has been investigated utilising my collections by PATAMA and WIDÉN (1991) and found to be distinct from *D. wallichiana*, though it should be born in mind that phloroglucide chemistry is sometimes so specific that alone it cannot always decide whether a taxon is necessarily a good species or not.

D. fusco-atra shows one piece of variation beyond what would normally be expected. In February 1988 I discovered a variant that has seldom been collected before and has not been referred to in the literature, growing at the well-known Makawao forest reserve on Maui. A local population I found there contained a mixture of the normal plant with more-or-less truncate pinna-lobes rather widely joined together at their bases and some remarkable plants that I at first suspected of being a new species. They had fully separate pinnules which became much longer just above the middle of the pinna and were elongate-lanceolate in shape with long, acute-pointed apices and shallow, acute side-lobes. In other respects it was exactly the same as *D. fusco-atra* and the spores too are similar in size and in the proportion of abortive spores; though a plant of it, still growing well in my father's garden at Bridgend, South Wales, in an unheated greenhouse, has not yet been investigated cytologically. Although unknown to Wagner when I showed it to him in 1988, on further study in a number of herbaria I found that my plant was only an extreme, linked by intermediates to normal *D. fusco-atra*, and I am now convinced that it is merely the normal Hawai'ian phenomenon of variation within the species. It may be relevant that some approach towards a similar type of variation can occur in *D. hirtipes* in south-east Asia and particularly in Oceania. In Samoa, the Cook Islands and Marquesas Islands a taxon named *D. fatuhivensis* E. BROWN occurs. Some fresh material was kindly shown me in 1992 by Dr. JOHN GAME of Berkeley, California, who recently discovered it in the Cook Islands. Although (FRASER-JENKINS 1986 and 1989a) I had long thought it probably distinct, I now find that it shows a range of variation from the normal, but more extreme, lobed plants to only shallowly lobed plants which are identical to *D. hirtipes*, with which it shares the same fragile texture etc. In agreement with SLEDGE (1973: 7), who reported Samoan *D. hirtipes*, I am now able to synonymise this "species" with *D. hirtipes* (which can also become similarly lobed occasionally), but perhaps in its extreme form when the lobe-apices are extended and long it is doing a similar thing to what happens in the new variant of *D. fusco-atra*. This variant is now formally named below, but it is hoped that it will not therefore be made into a "new species", especially not with a new specific epithet, contrary to recommendation 61 A.4. of the Code (GREUTER et al. 1988).

A. *Dryopteris fusco-atra* var. *fusco-atra*.

Pinna-lobes joined at their bases, usually rather widely (up to nearly half their length), slightly narrower, but obviously truncate at their apices. Some plants develop obtusely rounded pinna-lobe apices and less widely joined pinna-lobes, thus slightly approaching var. *lamoureuxii*.

List of specimens seen: Kauai: Higgins 131 (BISH, US); Hitchcock 15224 (US); Degener et Hathaway 21094 (US, MO) Heller 2587 (F), 2589 (BISH(x3), US, MO, BM, K), s. n., 21/8/1895 (towards var. *lamoureuxii*) (F), 2746 (towards var. *lamoureuxii*) (US, MO); Wagner 87206 (sub "*D. fusco-atra x wallichiana*" , det. Wagner, but spores good and not hybrid) (MICH); Forbes 1083-K (BISH, GB); Rock 1345,1482,2238,2258 (BISH), 2238 (towards var. *lamoureuxii*) (BISH); Flynn et al. 3414 (BISH); Takeuchi et Paquin "Alakai 77" (BISH), Brodie s.n., 15/11/1903 (BISH (X5)), s.n., 2/10/1904 (K); Oahu : Wilson et Palmer 1731 (BISH); Pyle et Pyle 3792 (BISH); Stone 3168 (BISH); St. John 11610 (BISH); St. John et Fosberg 12142 (BISH); G.W.R. s. n., 5/1933 (BISH); Forbes 15940 (BISH, MO), s.n., 12-19/2/1909 (BISH); Degener et al. 9271 (K), 9932 (MO), 12300 (US), 20793 (BISH); Hathaway et Degener 265 (US,GB); Judd 29(BISH); Selling 3579 (BISH, GB); Nagata 1330 (BISH); Takeuchi et al. "Waianae 109" (BISH); Grether et Wagner 3406 (US); Topping 3488 (US, MO), 3514, 3735 (MO), 3793 (US); Skottsberg s.n., 23/8/1922, s.n., 30/8/1922 (GB); Hillebrand s.n., rec. 6/1862 (BM,K); Molokai: Forbes 35-Mo (BISH (x2),MO)582-Mo (BISH,MO); Kondo et Kondo s.n., 18/6/1962 (BISH); Degener 9274 (MO, NY, F, K); Lanai: [Forbes] s.n., 6/1913(BISH), Forbes 25-L, 49-L (BISH, K), 96-L (BISH, K, MO), 533 (BISH);Munro 89(x2), 361 (BISH); Degener 35750 (BISH, GB); Degener et Degener 35750 (BM); Maui: St. John et Catto 17934 (BISH, US); St. John et al. 25725 (BISH); Crosby et Anderson 1810 (BISH, US, MO); Lamoureux et de Wreede 3957, 4018 (BISH); Hobdy 1055 (BISH); Forbes 735-M, 1726-M (x3), 1920 (BISH), 2317-M (BISH, MO); Higashino et Mizuno 2692, 2777, 2964, 3043, 3128 (BISH); Higashino et Allen 10188 (BISH), Baldwin 36 (BISH(x2)); Mann et Brigham 255 p.p. (BISH, US, MO); Hitchcock 14856,14873 (US); Wagner 65460 (MICH); Degener 22114 (BISH); Aborn s.n., 31/3/1962 (BM); Fraser-Jenkins field nos. 88/2, 88/3 (towards var. *lamoureuxii*), 88/5, 88/136 - 88/143, 88/144 (towards var. *lamoureuxii*), 88/145, 88/146, 88/153 (towards var. *lamoureuxii*); Hawai'i: Lyons s.n., ? 1860 (BISH(x6)); Rock 3893,3894 (x2) (BISH); Rock et Lindsay 10 (BISH); M. Newell s.n., 1910 (BISH); C. L. Newell 1040 (BISH); St. John 25062 (BISH, MICH); St. John et al. 11292 (BISH), 11304 (BISH, K), 11400, 18500, 18573 (BISH), 11303 (towards var. *lamoureuxii*) (BISH, US); Forbes 862-H (towards var. *lamoureuxii*)(BISH, K); Takeuchi 5762 (BISH (x2)); Higashino 6221 (BISH); Higashino et Meyer 6005 (BISH); Hosaka 1523 (BISH); Giffard s.n. 9/3/1927 (BISH); Russ 27 (BISH); Neal s.n., 5/8/1929 (BISH); Smith et Whiting 48 (BISH); Perlman et al. 10689 (US); Hitchcock 14309 (US); Noe 43(F); Degener 9274 (F); Nelson 6 p.p., 9 (BM); General: [?Rock] 2258 (BISH); Hillebrand s.n., 1863 (BISH), s.n. (MICH, B (×2)), 1(BM), 24 (B); Hillebrand et Lydgate s.n. (BISH); Gaudichaud s.n., 9-10/1836 p.p. (US, F, BM), s.n., 6/9/1836 (US), 7 (herb. Webb, 1844) (K); Strickland s.n., 1850 (BM); Baldwin s.n. (B).

B. *Dryopteris fusco-atra* var. *lamoureuxii** FRAS.-JENK., **var. nov**.

A var. *fusco-atra* pinnis pinnatis, pinnulis, prasertim iis breviter super medium pinnae, valde elongatis acutis, marginibus leviter lobatis differt.

Holotype: Hawai'ian Islands, E. Maui, Makawao Forest, c. 1 1/2 miles above bottom gate into Haleakala Ranch on road to Waikamoi Gulley and Flume (pipeline), above Olinda, E. of Pukalani, N. slope of Haleakala Mountain, 1250 m. C.R.Fraser - Jenkins** field no. 88/151, 1/3/1988 (BM). Paratypes: Ditto: 88/147 (H), 88/148 (K,G), 88/149 (NMW), 88/150 (BISH, FR), 88/152 (US).

Differs from var. *fusco-atra* in its pinnate pinnae and the pinnules being markedly elongated, acute and with the margins slightly lobed, especially those shortly above the middle of the pinnae which are often the longest.

List of specimens seen: Kauai: Rock 2233 (BISH); Wiebke s.n., 2/1984 (BISH); Maui: St. John et al. 25724 (BISH); Wagner 5178 (MICH); Fraser-Jenkins (as above); Hawai'i: Nelson s.n. (BM).

2. *Dryopteris wallichiana* (Spreng.) Hyl. subsp. *wallichiana*.

For a detailed synonymy, range and discussion see FRASER-JENKINS (1989: 354 - 359). Since then this subspecies has now come to my notice from south India (Kodaikand, Palni Hills. S. M. Vasudeva 1133, 25/1/1975. PUN!), from where I had previously seen only the triploid taxon, *D. wallichiana* subsp. *madrasensis* (FRAS.-JENK.) FRAS.-JENK., **comb. nov.** (basionym: *Dryopteris madrasensis* FRAS.-JENK., Bull. Brit. Mus. Nat. Hist., Bot., 18(5): 359 - 360 (1989)).

This subspecies is diploid, presumably apomictic, from Hawai'i as elsewhere (Maui, Waipoli Road, Kula, Fraser-Jenkins field no. 88/16, 25/2/1988, diploid at mitosis, M. GIBBY (pers. comm., 2/6/1990)). WAGNER (pers. comm.,30/9/1992) told me briefly that he had found it to be tetraploid sexual, but on my telling him it is normally an apomictic diploid, he agreed that he had not checked the possibility. It has few 16-celled sporangia and has therefore occasionally been mistaken for a tetraploid sexual species on observing 82 bivalents at meiosis as I have already pointed out (FRASER-JENKINS 1989a: 356).

D. wallichiana is hardly variable in Hawai'i except in scale colour, which is usually mid-brown but can often be very pale, occasionally reddish-brown and rarely very dark brown (e.g. Maui, Haleakala, Paliku. Henrickson et Vogl 3530, 18/6/1969. BISH!). This range of colour is more similar to the central American populations of the species rather than to the Sino-Himalayan and Japanese plant which has a greater preponderance of dark-brown or black scaled forms, though all such colour forms can

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* Named after Professor CHARLES H. LAMOUREUX of the Lyon Arboretum, Honolulu, who was Herat's supervisor at the University of Hawai'i and is himself a most competent pteridologist studying Hawai'ian ferns.

** Fraser-Jenkins herbarium is at present at BM, but will be partly diseminated to FR, H, NMW and elsewhere in future, as well as to BM; on two dates I collected with Mr. R. W. Hobdy on Maui, but the other collections were made by me alone.

occur in all parts of its world range. There is also some variation in the degree of lobing of pinna-lobes, from unlobed to the lower ones shallowly lobed (e.g. Maui, Waipoli Road, Kula. Fraser-Jenkins field no. 88/267, 3/3/1988 (BM)). However it does not become as lobed or as long-pinnuled as *D. palikuensis.*

In the European-type flora of far-western Asia, the species is represented by a triploid taxon, *D. wallichiana* subsp. *coriacea* (Fras.-Jenk.) Fras.-Jenk., **comb. nov.** (basionym: *Dryopteris affinis* subsp. *coriacea* Fras.-Jenk., Willdenowia 10(1): 112-113 (1980)), which I had originally thought belonged to *D. affinis* (Lowe) Fras.-Jenk., but its long, very dense, exserted scales, stiffer frond and more widely basally linked, more rectangular pinna-lobes clearly place it within *D. wallichiana*. Fraser-Jenkins (1988) has discussed the ranks and taxonomic treatment of both *D. wallichiana* and *D. affinis*, contrasting with some recent North American suggestions.

List of specimens seen: *Kauai*: St. John et al. 10725 (BISH), 13801 (BISH, K); Flynn et al. 3062 (BISH); Smith et al. 8 (BISH); Rock 1366, 1464, 2216, 2219 (BISH); Chock 976 (BISH); Stone 1554 (BISH), 951-K (BISH, US, K); Heller 2749 (BISH, NY, F, MO, BM, K); Brodie s.n., 4/10/1903, s.n., 2/9/1904 (BISH); M.R. s.n., 8/10/1908 (BISH); Wiebke s.n., 30/6/1926 (BISH); Kusche 160 (US); *Oahu:* Lichtentaler s.n. (US); various material (MICH); *Molokai*: Lorence 5643 (BISH); St. John et al. 12391 (BISH); St. John et Williams 19930 (BISH); Cranwell et Skottsberg 2573 (BISH, GB); *Maui*: Wilbur et Webster 956 (BISH); Lamoureux et De Wreede 4020, 4027 (BISH); Hobdy 256, 367, 2029 (BISH); St. John et Catto 17731 (BISH, US) 17745, 17965 (BISH); St. John et Mitchell 21002 (BISH); Forbes 445-M, 725-M (BISH), 782-M (×2) (BISH), 782-M, 782 (K), 990-M, 998-M, 1831-M, 1871-M, 2134-M (BISH); Munro 751 (BISH); Olson 101 (BISH); Henrickson 3785 (US); Henrickson et Vogl 3507 (BISH), 3530 (BISH, US); Higashino 606 (BISH, US), 755, 774 (US), 851 (BISH); Higashino et Mizuno 1701, 2067, 2970, 2992, 3064, 3094, 3114, 3157 (BISH); Perlman et al. 10559 (BISH, US); Hosaka 1688 (BISH), 2476 (BISH, US);Tanabe 62 (BISH); Neal et Hartt s.n., 14/8/1933 (BISH); Neal s.n., 16/8/1933 (BISH); Harrison s.n. (BISH); Ishikawa 335 (BISH, US); Baldwin 37 (BISH); Bonsey et al. H.459 (BISH); Degener 9276 (BISH), 9277 (US, MO, K), 22324 (BISH); Degener et al. 25318a (BISH); Mc Alpin 638 (F); Mann et Brigham 255 p.p. (BISH, MO); Wagner 65459, 87136 (MICH); Piggott 3224 (BM); Bulow 204a (K); Bailey (NY); Fraser-Jenkins field nos. 88/6 - 88/32, 88/154 - 88/157, 88/267, 88/268; *Hawai'i*: Higashino 6220, 7089 (BISH); Higashino et Croft 6077, 6329 (BISH); Neal et Hartt 670, 810, 821 (BISH); Neal s.n., 1/8/1929, s.n., 5/8/1929 (BISH); Degener 3794, 35752 (BISH); C. L. Newell 524, 525, 807, 1042 (BISH); Christ s.n., 15/8/1958 (BISH); Fosberg 10242 (BISH, US); Lyon A (BISH); St. John s.n., 24994, 25356, 26793 (BISH); St. John et al. 11388 (BISH), 18444 (BISH, US), 18546 (BISH), 18601 (BISH, US), 22386, 23937, 24018 (BISH); Cowan et Frederick 22538 (BISH); Forbes 314-H, 707-H, 722-H (BISH), 808-H (BISH, US, F, K); Morley s.n., 6/1934, 165 (BISH); Kondo s.n., 10/7/1946 (BISH); Perlman et al. 10472 (US), 10726 (BISH, US, F); Hosaka 1525 (BISH, US), 2215 (BISH), s.n., 12/7/1946 (BISH, GB), s.n., 13/7/1946, s.n., 14/7/1946 (BISH); Higgins 108 (BISH); Herbst 923 (BISH (×2)), 9231 (US (×2)); Topping 3626 (BISH, US); Herat et al. 735 (BISH); Mc El Downey 23 A (BISH); Giffard 15 (BISH); Woolford s.n., 29/12/1954 (BISH); Iltis et Iltis H-169 (BISH); Meebold s.n., 5/1932 (BISH); Russ 29 (BISH); Fagerlund et Mitchell 774 (BISH); Degener 3794, 9272 (K), 35752 (BISH); Degener et Degener 30700 (US (×3)), 33643 (BM); Degener et al. 3911 (MO); Greenwell (in Degener)19381 (BISH); Bryan s.n., 24/1/1957 (US); Wood et Zevin 1532 (US); Hitchcock 14257, 15567 (US); Wilkes 8 (BISH, US); Flynn et Lorence 2296 (F); Skottsberg 562, 658, 695,1887 (GB); Nelson s.n., s.n. p.p. (BM); *General*: Lack s.n., 1880-1890 (BISH); Hillebrand et Lydgate s.n. (BISH); Whitney s.n. (BISH); Gaudichaud s.n. (B), s.n., 6/9/1836 (US), s.n. p.p. 9-10/1836 (F,BM); Baldwin s.n. (B), 65 (US, NY); Challenger Expedition s.n., 8/1875 (K); sin. coll. s.n., Herb. Moore, 1876 (K).