

3. *Dryopteris palikuensis* HERAT ex FRAS.-JENK., sp. nov.

Species morphologia *D. wallichianae* similis, sed stipite longioris, base laminae latiora, pinnulis longioris, valde tamen non profunde lobatis, et sporis majoribus differt. Cytotypus praesumptivus triploideus apomicticus.

Holotype: "*Dryopteris palikuensis* sp. nov. prov. det. TISSA R. HERAT 1/1977, Hawai'i, Maui, Paliku, Haleakala, woods. O. Degener, W. Fleming et J. Dawson 27406, 4/6/1959," (C!). Isotypes: US ($\times 2$)!, MICH (seen 10/3/1988)!, B!, L!, NY!

A species similar in morphology to *D. wallichiana* but differing in its longer stipe, wider lamina-base, longer and markedly, yet shallowly lobed pinnules and larger spores.

This species is most probably a triploid apomictic from its rather typically large, irregular spores with a noticeable proportion of abortive ones, a feature contradicted by WAGNER (1993) for a taxon recently described as *D. subbipinnata* WAGNER et HOBODY, which therefore requires further study. I hope Dr. MARY GIBBY can soon investigate my living plants of it to decide this question. WAGNER (pers. comm., 30/9/1992) told me briefly that he had found it to be hexaploid sexual, but on my telling him it was much more likely to be a triploid apomict, he agreed that this possibility had not occurred to him and had not been checked. It should have sufficient 16-celled sporangia to be readily noticeable, if so.

Although a distinctive species it was noticed to be new by Dr. TISSA R. HERAT and was first so determined (as on the type specimen) by him in January 1977 in a number of herbaria including L, B, C, US, NY, MICH and BISH. He gave full details of it in his well-known thesis (HERAT 1979), using the term "provisional" to refer to all his unpublished taxa and combinations, but fully accepting it as a good, new species. The species and his name for it have therefore become well known in Hawai'i, as elsewhere. But there then ensued an unfortunate, long delay during which it remained unpublished as Herat was discouraged from working on it any further after unsuccessfully submitting a paper on it to the American Fern Journal in 1987 (HERAT in litt., 19/5/1993). The paper was reviewed and rejected by WAGNER who took steps to ensure it was most unlikely to be published though it could instead have been recommended to have been altered to comply with the journals' format. In the meantime, WAGNER (1981, 1992 and 1993) wanted to mention this or an allied species, so clearly brought to everyone's notice (some sheets at BISH bear both HERAT's determination as *D. palikuensis* in 1977 and WAGNER's redetermination with his new name in 1982), in his lists etc., but ignored HERAT's name, using a new one of his own and even using two different new nomina nuda on two occasions, while never mentioning HERAT's independent involvement. In my opinion it would seem to constitute an extraordinary breach of courtesy, at the very least, to name it anew in the circumstances of HERAT's having been the first to publicly name and attempt to publish it, even if it is claimed now to have been privately discovered previously or independently by WAGNER, for which I have not yet come across any evidence made publicly available at the time, either when I studied the collections in detail in MICH in 1988, or in any other herbarium and I can only hope that the name given by Herat when the species was first pointed out can be widely brought to attention. But should WAGNER's statements to me (pers. comm.,

30/9/1992) that the possibility for him to work on Hawai'ian *Dryopteris* had to be postponed and was relegated to low priority (so that our formally agreed joint work on it was no longer possible), now turn out to have been an inexactitude, or even some kind of diversion, and should he unfortunately proceed to publish on this genus in advance, after all, and without proper consultation with myself or HERAT, at least the present paper will ensure that the first publicly given name, *D. palikuensis*, will remain sitting in the synonymy as visible a reminder of the true history of the species. In keeping with recommendation 34 A of the Code (GREUTER et al. 1988) I am fortunately discouraged from mentioning any of WAGNER's unpublished names, but instead, HERAT's original name is now formally applied, with his permission and approval, for the interesting discovery attributed to him.

I assume that this species is a neo-endemic derived by hybridisation between the diploid apomictic *D. wallichiana* and some other tripinnate, diploid sexual species in Hawai'i. As such it could also have been placed in section *Remotae* FRAS.-JENK., however in this species, though the lamina is bipinnate, it only becomes rather shallowly lobed again at the base and middle of the frond. It is thus not as highly dissect as members of section *Remotae* and its morphology fits much better in the *Fibrillosae*, where I have placed it. Since both allopolyploid species and basic diploids must be placed within an infrageneric classification, it is rather obvious that the frond-morphology of the species concerned and the definition and cohesion of the section must carry more weight than theoretical origins, as long as it works readily, as here. Doubtless some less practicably minded person could attempt to amuse himself by creating separate sections for all the allopolyploid "nothospecies", but I have only found it necessary to create one such artificial section, *Remotae*, which appears to solve the outstanding problems.

Perhaps because it may be a relatively newly formed species it does not vary much apart from in degree of growth and development, as in all species, and in scale colour. Occasionally a poorly developed or young specimen may be less lobed and approaches slightly lobed-pinnuled forms of *D. wallichiana*, but it is usually easy to distinguish by its longer pinnules and pinnule-teeth and can be confirmed microscopically by its markedly greater spore-size and irregularity. The stipe and rachis scales vary from black to mid-brown, generally being darker than in most Hawai'ian *D. wallichiana*.

List of specimens seen: Maui: Hobdy 2028, 2076 (BISH (×2)); Perlman et al. 10759 (BISH); St. John 21034 (MICH); St. John et Catto 17757 (BISH, MICH); St. John et Mitchell 21034 (BISH, US); Forbes 991-M (BISH (×2)), 991-M (K), 1032-M (BISH); Carlquist 1934 (BISH); Henrickson et Vogl 3530, 3535 (BISH); Degener 22322 (BISH (×3)); Degener et al. 27406 (US (×2)), 27406 (MICH, B, C, L); Wagner 5225 (×2), 5228 (×2), 5435, 65392, 87135 and a further collection (MICH); Bonsey 114, 243a (MICH); Skottsberg 756 (GB); ? Wilkes 8 (K) (?=immature *D. wallichiana*); Fraser-Jenkins field nos. 88/3, 88/158, 88/269, 88/295-88/298.

Section: *Remotae* FRAS.-JENK.

4. *Dryopteris hawaiiensis* (HILLEBR.) ROBINS.

This species is most probably a triploid apomict from its rather typically large, irregular spores with a noticeable proportion of abortive ones. WAGNER (pers. comm.,

30/9/1992) told me briefly that he had found it to be hexaploid sexual, but on my telling him it was much more likely to be a triploid apomict, he agreed that this possibility had not occurred to him and had not been checked. It should have sufficient 16-celled sporangia to be readily noticeable, if so.

I previously (FRASER-JENKINS 1986) referred *D. hawaiiensis* to section *Fibrillosae*. The reason for this obvious error was that at the time my concept of *D. hawaiiensis* actually referred to *D. palikuensis*, which CHRISTENSEN had identified (Maui, Pu'u Kukui. Skottsberg 756, 9/10/1922 (GB)) as *D. hawaiiensis*, but presumably only as part of his very wide concept of that species (see CHRISTENSEN 1925). Unfortunately his determination had influenced and overridden my examination of HILLEBRAND's type material in Berlin in February 1980, especially as both species were included under the name *D. hawaiiensis* in Berlin's general folders (and in NY) and my notes were not clear enough at the time. But as genuine *D. hawaiiensis* belongs in section *Remotae* (along with *D. remota* (A. BR. ex DÖLL) DRUCE, *D. blanfordii* (HOPE) C.CHR., *D. munchii* SMITH (not in Sect. *Cinnamomeae* FRAS.-JENK., as I published) and *D. corleyi* FRAS.-JENK.) this helps to explain why its phloroglucide chemistry, as reported by PATAMA et WIDÉN (1991) using my collections, is, as they stated, so different from members of section *Fibrillosae*. Following my previous publication, they had placed it there though I had discovered my error some four years before and had given them the dried rhizomes under the correct, revised specific name in 1988. Thus their wrong name was merely the result of inadvertent confusion.

D. hawaiiensis is slightly similar to the European *D. remota* in morphology. The deltate lamina becomes tripinnate in the lower pinnae but is markedly less dissect above. It can easily be distinguished from the other wide-fronded species present in the Hawai'ian archipelago by means of its narrow, fibrillose-tipped, lacerate-woolly, rather dense, dark-brown stipe scales which run the whole way up the stipe and rachis. These are quite unlike the all-pale, much more scattered scales of *D. glabra*, with which it could be confused. No confusion is likely with the much larger and exindusiate *D. unidentata*. Occasional plants occur with more scattered scales (or where the scales have been rubbed off), but otherwise its variation is only a normal matter of degree of growth and development, some luxuriant plants being larger and slightly more dissect than others, with wider lamina-bases.

List of specimens seen: Kauai: sin.coll. 3546, 19/4/1905 (F); Oahu: Lichtentaler s.n. (US); Crosby et Anderson 1322 (MICH); Andersson s.n., 1852 (BM); Baldwin s.n. (BM); other material (NY); Molokai: Higashino et Holt 10102 (BISH); Maui: Woolford 270 (BISH); Hobby 834, 856 (BISH); Hosaka 1688 (US), 1689 (BISH); Topping 3821 (MO); Wagner 87117, 87415 a-e (MICH); Fraser-Jenkins field nos. 88/34-88/36, 88/159-88/193, 88/270, 88/271; Hawai'i: Mann et Brigham 284, 5822 (BISH); Forbes 262-H (BISH), 936-H (BISH, US (×2), K); Russ 28 (BISH); Rock s.n., 1/7/1909 (BISH); C.L. Newell 206, 794, 1041 (BISH); M. Newell s.n., 1910 (BISH); Neal et Hartt 825 (BISH); St. John 25350 (BISH); St. John et al. s.n., 24/12/1949 (BISH); 23942 A (MICH); Woolford s.n., 20/12/1954 (BISH); Hillebrand s.n. (NY), s.n., 1862 (B); Hitchcock 14307, 14311, 14261 (US); Rubtzoff 2666 B (US); Wagner 65426, 87063 (MICH); Macrae s.n., 6/1825 (BM, K); General: sin. coll. s.n. Herb. Rock (BISH); Baldwin 71 (US).

Section: *Marginatae* FRAS.-JENK.

5. *Dryopteris mauiensis* C. CHR.

Synonym: *Polypodium clarkei* BAK.; *D. mauiensis* was a *nomen novum* for *P. clarkei* BAK., non *Dryopteris clarkei* (BAK.) O.KTZE.

The name *D. mauiensis*, though known to me at the time, was inadvertently omitted from my classification (FRASER-JENKINS 1986). Until now the present species has been erroneously referred to as *D. sandwicensis* by almost all workers, including myself, while HELLER (1897) misidentified it as *D. unidentata* (sub *Phegopteris*). However the type of *D. sandwicensis* (K (seen 14/5/1993)!) belongs to the next species, leaving the present name for this one (type K (seen 14/5/1993)!).

D. mauiensis is one of several exindusiate members of Section *Marginatae*, but is otherwise rather typical of the section in its huge size, long stipe, deltate, smooth lamina, wide and usually wide-based, more-or-less obtuse segments and usually relatively few stipe- and rachis-scales. I have no idea why I could not easily place it (sub *D. sandwicensis*) in its section in my 1986 paper, unless its exindusiate sori and rather delicate texture, combined with its being one of the generally rather difficult Hawai'ian species, had me worried! In many aspects it is not unlike *D. chaerophyllifolia* (ZIPP.) C. CHR. from south-east Asia (Sumatra, Java, Sulawesi and North Borneo) and the very similar, but indusiate, *D. macrolepidota* COPEL. (omitted from my classification, FRASER-JENKINS 1986) from Oceania (New Hebrides and Tahiti), but it does not have the stiff, narrow stipe-, rachis- and costal-scales of the two latter.

The species varies in a fairly normal way in the degree of lobing of the pinnules, more highly lobed plants having smaller, narrower segments, occasionally becoming slightly extreme (e.g. Maui, Kaenae Gap, Halehaku, Haleakala. Forbes 1077-M, 7/8/1919. BISH!). It also varies in the degree of scaliness and width of the stipe scales, some plants (e.g. Hawai'i, Kau Forest Reserve, above Kapapala Forest Reserve. Palmer, Wilson, Gustafson et Woodley 625, 19/6/1991. BISH!) showing a considerable density of narrower scales. These extremes connected by intermediates go some way towards the phenomenon of special Hawai'ian variation mentioned above, but are not as well marked as in some other species and do not appear to merit any varietal names.

List of specimens seen: *Kauai*: Palmer 892 (BISH (×2)); Palmer et al. 598 (BISH); Forbes 155-K (BISH); Heller 2838 (US, NY, F, BM, K); *Oahu*: Rock 184, 237, 255, 256 (BISH), s.n., 14 - 21/11/1908 (US); Forbes s.n., 14 - 21/11/1908 (BISH, US), s.n., 3 - 8/5/1909 (BISH); Baldwin 40 (BISH (×2)); Lack s.n., 1880 - 1890 (BISH); W. H[illebrand] s.n., 1/1870 (BM); Hillebrand 45b [? 456] (K); "Panoa, Oahu" (NY); *Molokai*: Forbes 452-Mo (BISH (×2), MO, GB), 467-Mo (BISH (×3), NY, MO); Hillebrand 937 (US); W. H[illebrand] s.n., 6/1870 (BM); Faurie 419 (BM (×2)); *Lanai*: W. H[illebrand] s.n., 30/7/ - (BM); *Maui*: Forbes 439-M (BISH (×2), US, K), 1077-M (BISH, MO); Hobby 2094 (BISH (×2)); Hillebrand 59b [? 596] (K (×2)), s.n., 2/1862 (US, BM); Hitchcock 14939 (US); Wagner 87150 (MICH); Skottsberg 847 (GB, BM); F. L. Clarke, [via] Davenport 1 (K); Fraser-Jenkins field nos. 88/51, 88/52, 88/101 - 88/103; *Hawai'i*: Palmer et al. 625 (BISH); Gifford 9, 32, s.n., 30/6/1927 (×4), s.n., 3/8/1927 (BISH); St. John 25064 (BISH (×3)); M. Newell s.n., 1910 (BISH); Horner s.n., 10/1953 (BISH (×3)); Lichtentaler s.n. (US); Hitchcock 14554 (US); W. H[illebrand] s.n. (BM); Nelson 22 (BM); *General*: Hillebrand et Lydgate s.n. (BISH); "All the islands" [? Baldwin] s.n. (BISH); Baldwin 79 (US); Rogers s.n. (BM).

6. *Dryopteris sandwicensis* (HOOK. et ARN.) C. CHR.

Synonym: *Phegopteris crinalis* var. *tripinnata* HILLEBR.

Lectotype of var. *tripinnata*: "Polypodium (Phegopteris) tripinnatum Sandw. Isl. Ex herb. W. Hillebrand " (B!). A second sheet, labelled "Polypodium crinale β . tripinnatum (etc.)" (B!) is a typical, large, tripinnate *D. crinalis*, but does not comply with HILLEBRAND'S statement, "rachides nearly glabrate", unlike the lectotype, as its axes are well furnished with typical *D. crinalis* scales throughout.

This species was first brought to my attention in February 1988 in west Maui by Mr. BOB HOBODY of the Forestry Division, Wailuku, who was very kindly showing me some of the island's pteridological sites and sights. He was calling it *D. unidentata*, presumably following WAGNER, but I told him that I strongly doubted it was that species as it had virtually no costal scales and might therefore be something new. Later on, when I saw a good deal of herbarium material of it, it became clear to me that it was indeed a distinct species, quite different from *D. unidentata* from which it remains consistently distinct in its virtually glabrous rachis and costae and several other characteristics. I therefore thought that it was an unnamed species and planned to name it after BOB HOBODY, so determining it in various herbaria, particularly in BISH in 1992, pointing out that *D. unidentata*, including its type, has more-or-less prominent, slightly wide, costal scales. However WAGNER has rather surprisingly missapplied the name *D. unidentata* to this species as the bulk of his determinations to this effect in herbaria are this, though he has also included some specimens of the less scaly form of *D. unidentata* var. *unidentata* within his concept, not clearly distinguishing between the two. On 30/9/1992, when I gave him some information at our meeting in Ann Arbor, just before he said he could not continue our work on *Dryopteris*, I told him that he was incorrect in thinking that the type of *D. unidentata* was without prominent costal scales. However when I re-examined the various Hawai'ian *Dryopteris* types at Kew on 14/5/1993, I was very surprised to find that the type of *D. sandwicensis*, a name I misspelled slightly in my 1986 paper, was not, as I had long thought, the previous species, *D. mauiensis*, but clearly belongs to the present one, which is therefore called *D. sandwicensis* here. Evidently when I first investigated these types in 1979 and before, not knowing the present species in the field, I had been unable to recognise it as different from *D. mauiensis* and I had continued in my delusion for many years because virtually all other collectors and workers, including WAGNER, had also missapplied the name *D. sandwicensis* to *D. mauiensis*, which latter was relegated to its synonymy, or ignored.

The present species appears to occupy a position slightly on the edge of Section *Marginatae* towards Section *Aemulae*, the two sections being rather closely adjacent to one another. Although *D. sandwicensis* and *D. mauiensis* could always have diverged from a common ancestor in Hawai'i, it seems more probable to me that *D. sandwicensis* represents a rather more ancient line, long surviving in Hawai'i, coming from nearer the point where the two sections may have diverged from one another. It is thus rather less obviously a member of the *Marginatae*, with some features of segment-shape etc. reminiscent of Section *Aemulae*. But *D. mauiensis* has several other, rather close relatives outside Hawai'i that, like it, are more typical of Section *Marginatae*,

suggesting that it could possibly have come from elsewhere more recently and became recognisably divergent on the islands as a result of this more recent isolation.

D. sandwicensis has smaller fronds than *D. unidentata*, though they are larger than in *D. glabra* and are markedly deltate; the stipe is clothed with long, brown or dark-brown, twisted, very narrow or linear scales at its very base and bears some scattered, ovate, pale-brown scales at mid-stipe, while the upper stipe and rachis are glossy, without scales, or bearing small, black, very narrow and very scattered ones. The pinnacostae are mostly glossy and naked, but if a very few scales are present, they are small, black, very narrow, hair-like and very scattered. The ultimate segments are more-or-less rounded-rectangular and are usually rather wide and obtuse, though they can become narrower in some specimens, but are not as pointed or as toothed as in *D. glabra* and are usually more-or-less without teeth unless sterile or slightly juvenile in morphology. The exindusiate sori are characteristically marginal on the segments.

D. sandwicensis varies somewhat in the length, colour and prominence of the stipe-base scales, in whether or not the costae bear a few hair-like black scales and in the degree of lobing of the ultimate segments, which often become more lobed in the larger specimens when the lower lamina just becomes quadripinnate. But this variation is not worthy of nomenclatural recognition.

List of specimens seen: *Kauai*: Flynn et Harder 2945 (BISH, MO); Flynn et al. 2738 (BISH (x2), MO); Heller 2587 (BISH (x3), BM); Forbes 718-K (BISH, US), 723-K (BISH (x2), US), Wiebke s.n., 19/6/1926 (BISH); Smith et al. s.n. (US), s.n., 1/5/1929 (K); Wood 1237 (US); Hitchcock 15248 (US); Wagner 65354 (MICH); Detappe et Wagner 87190 (MICH); Faurie 386 (MICH); Skottsberg 1044 (GB); *Oahu*: Higgins 63 (BISH); Takeuchi et Paquin 3500 (x2), "Waianae 987" (BISH); Mann et Brigham 185 (BISH); Stone 3169 (BISH, K); Herbst 420 (BISH); Garber et Forbes 160 (BISH); G.W.R. s.n., 5/1930 (BISH); Degener 11983 (US, MO), 17534 (MO), 17563 (F, MO), 17691 (MO), 21090 (MO, MICH), 21091 (US, BM); Degener et al. 12351 (BISH, K); St. John 13134 (BISH); Grant 7230 (BISH); Wilkes 28 (BISH); Fosberg 9508 (BISH); Hathaway 390 (BISH); Palmer et al. 765 (BISH); Topping 3556 (BISH), 3611 (US, MO), 3732 (US), 3852 (MO); Safford 909 (US); Baldwin s.n. (US); Boyd 2224 (MO); Wagner 5459, 5739 (x2), 9618, 9618 c, 9629 (x2) (sub "*D. glabra* x *crinalis*", det. Wagner, but spores good and not hybrid) (MICH); Faurie 376, 465 (MICH); Andrews s.n., (MICH), "Oahu" (C); Skottsberg 282 (GB); Beechey s.n., herb. Hook. (K), Hillebrand 45 (K), 941 (US), s.n., rec. 6/1862 p.p. (K); *Molokai*: Lorence et al. 5617 (BISH); St. John et al. 12735, 23452 (x2), 23474 (BISH); Wagner 9548 (x2), 9564 (MICH); Faurie 385 (BM); *Lanai*: St. John et Eames 18757 (BISH, MICH); St. John et Hosaka 18865 (BISH (x2), US, MICH); St. John et al. 18881 (MICH); Forbes 59-L (BISH), 81-L (MICH); Munro 56 (BISH (x2), MO, MICH, GB), 90, 167 (x2), 411, 477, 532 (x2) (BISH); Degener 22017 (BISH), 35262 (K); *Maui*: Hobby 356, 765, 855, 2093, 3039 (x2) (BISH); Nagata 1914 (BISH); Forbes 1077-M (BISH), 1618-M, 1839-M (US), 1967-M (US, K), 2357-M (BISH), 2422-M (BISH, US), 2427 a - M (US); Mann 592 (BISH); Mann et Brigham 592 (BISH (x3)); Wilkes 28 (US); Wagner 5205, 65437 (MICH); Faurie 467 (MICH); W.H [Hillebrand] s.n. (B, BM (x2)); Fraser-Jenkins field nos. 88/84-88/94, 88/272, 88/273; *Hawaii*: Lyons s.n., 1860 (BISH (x3), MO); Whitney s.n. (BISH); Flynn 2757 (BISH); Rock 3625, 3631 (BISH); Russ 19, 22, 23, 24 (BISH); Eggler 231 (US); Wagner 65408 (MICH); Nelson 12 p.p. (BM); *General*: Baldwin 14 (BISH), 76 p.p. (US), s.n. 1879 (BISH); "Sandwich Isles". sin. coll. 880 (BISH); "All the Islands" [? Baldwin] (BISH); Lack s.n., 1880-1890; Lyons s.n. (MICH); [Hillebrand] 45 (B); W.H [Hillebrand] s.n. (BM); Hillebrand et Lydgate s.n. (BISH (x3)).

Section: *Aemulae* FRAS.-JENK.

CHRISTENSEN (1925) placed *D. unidentata* and *D. acutidens* in Section *Parapolystichum* (KEYS.) C. CHR. (see CHRISTENSEN 1920) in error as that name is a synonym of *Lastreopsis* CHING.

The exindusiate members of this section, along with other exindusiate *Dryopteris* species, were placed by earlier authors (e.g. HILLEBRAND 1888, HELLER 1897 etc.) into the separate genus, *Phegopteris* (C. PRESL) FÉE, following the Hookerian over-reliance on indusial characteristics without allowing exceptions in defining genera, which was prevalent at the time. At least HILLEBRAND may have had some disquiet about this when he observed the similarity of one form of "*Phegopteris unidentata*" (HOOK. et ARN.) J. SMITH to some larger "*Aspidium glabrum*" (BRACKENR.) METT.

7. *Dryopteris unidentata* (HOOK. et ARN.) C. CHR.

This large, exindusiate species usually shows the characteristic acute-pointed, often narrow-based and acutely toothed segments of this section and, at least in its medium-acute segmented variants shows a distant similarity to *D. glabra* though much larger and with dark, instead of pale or reddish-yellow scales. After careful consideration I am now confident that it is a member of this section, a relationship much obscured by its extraordinary range of variation, it being the most variable of all the Hawai'ian *Dryopteris* and becoming markedly dissimilar to *D. glabra* in its extreme forms. WAGNER has confused the nomenclature and misapplied the name *D. unidentata* to *D. sandwicensis*, as can be seen from the large bulk of his determinations, at BISH, MICH, US and elsewhere, though he has also included some true *D. unidentata* together with it under the name.

The variation in this species is exceptional, but nevertheless the variants are all connected by fertile intermediates and have evidently failed to speciate completely. HERAT (1979) has been the only person to make sense of this, having realised that its variants are not species in any acceptable sense of the term, in contrast to WAGNER (1992), who has raised a veritable cluster of mythical and unworkable, unpublished "species." But HERAT already dealt with them most successfully as varieties, including a new variety of his own, the most extreme and remarkable variant, var. *ukelelensis* HERAT ex FRAS.-JENK., which was subsequently taken up by WAGNER (1988, 1992) and turned into a species again with his own new name.

In this species the density and width of the characteristic stiff, lanceolate stipe-, rachis- and costal scales varies considerably, a few populations of intermediate laminar morphology (see below sub var. *unidentata*) having few costal scales, though all plants have more-or-less prominent and numerous stipe- and rachis-scales. The width and degree of lobing and toothing of the ultimate segments varies spectacularly from tripinnate-fronded populations with wide, obtuse, tightly contiguous, toothless and shallowly crenate segments to remarkable quadripinnate (and a fifth time pinnatifid), very finely dissect, acute-segmented and acute-toothed plants. In any one locality the population may be consistent and can appear quite distinct, the same form also being recognisable elsewhere, but examining different localities the complete range of intermediates can be found. I have nevertheless decided here to name the main variants

in some Hawai'ian species, not a practice I would normally find necessary when they overlap in this way, because in these cases some populations are recognisable and so extreme; it is also useful to relate them to the names by which they have been referred to in the past.

The varieties are as follows:

A. Dryopteris unidentata var. *paleacea* (HILLEBR.) HERAT ex FRAS.-JENK., **comb.nov.**

Basionym: *Phegopteris unidentata* var. *paleacea* HILLEBR., Flor. Hawaiian Isl.: 564-565 (1888).

Lectotype: "Phegopteris unidentata Mann β. var. paleacea Hillebr. Maui; Sandw. Isles. coll. Baldwin. Ex Herb. W. Hillebrand" (B!).

HILLEBRAND's herbarium in B contains a number of specimens varying from acute-segmented var. *unidentata* to the present variety, sensu stricto, all labelled as var. *paleacea* due mainly to their scaliness. But some specimens can be rejected as types because their prominent segment-teeth do not fit the protologue, or because they came from an island he did not cite. The type selected here most nearly fits the description and is the most obtusely lobed and toothless of his specimens.

This variant was first shown to me in the field by BOB HOBODY (under the name *D. acutidens*) near Hana'aula, western Maui*, in February 1988, where it reaches an extreme obtuse-lobed and contiguous-segmented form. It was again named by WAGNER (1992) as an unpublished "new species." The wide, obtuse and crenate, shallowly rounded-, or rectangularly lobed, more-or-less toothless segments vary from closely contiguous to separate (as in the present lectotype); the frond is tripinnate, becoming quadripinnate or quadripinnatifid below and the stipe and rachis scales are prominent, dense and somewhat wide, with numerous, rather wide costal and costular scales. Some plants also develop tall, elongated soral receptacles sticking out of the lower surface of the lamina and have been named as a further unpublished "new species" by WAGNER (1992), though this feature is of no taxonomic consequence and also occurs in some *D. glabra*.

List of specimens seen: *Kauai*: Flynn et al. 2111 (BISH); Palmer et Flynn 1026, 1031 (BISH); Rock s.n., 10/1916 (BISH); *Oahu*: Hillebrand s.n., rec. 6/1862 (K); *Molokai*: Higashino et Holt 10094 p.p. (BISH (x2)); Forbes 338-Mo p.p. (MICH, K); Wagner 9566 (MICH); *Maui*: Hobdy 2095 (BISH); Palmer et Obata 678 (BISH); Mann 591 (BISH); Mann et Brigham 591 (BISH (x2)); Forbes 1077-M (x2), 2166-M (BISH); Hitchcock 14780 (US); Perlman et al. 10598 (US); Wagner 87168 (MICH); Faurie 408 (MICH); Baldwin s.n. (B); Skottsberg 2680 (BM); Fraser-Jenkins field nos. 88/104-88/110; *Hawai'i*: St. John et al. 18590 p.p. (BISH (x2)); Giffard s.n., 30/6/1927 (BISH); Wagner 87062 (MICH); *General*: Baldwin s.n., 1879 (BISH).

*It occurs amongst a large population of a common Hawai'ian *Sphenomeris* reported by WAGNER (1988 and 1992) and MONTGOMERY et al. (1992) as being "*Odontosoria chinensis*" (L.) J. SMITH, or its synonym *Sphenomeris chusana* (L.) COPEL. But the well-known *S. chinensis* (L.) MAXON, from Asia, is quite a distinct species, as I pointed out to BOB HOBODY at the time. I have now found that the Hawai'ian plant is the Chinese, Japanese and south-east Asian *S. biflora* (KAULF.) AKAS., which has a deltate, not lanceolate lamina and thicker and wider segments, and is newly reported from Hawai'i here.

B. *Dryopteris unidentata* var. *unidentata*

In this variety the ultimate segments are more-or-less acute-tipped, as are the pinnulets, but are obtusely lobed at the sides, slightly toothed, with small, often insignificant teeth, and not contiguous; they are not as wide as in the more extreme forms of var. *paleacea*. The frond is quadripinnate and the stipe- and rachis-scales are markedly less dense than in the other varieties, nor as wide as in var. *paleacea*, often becoming only scattered on the rachis. The costal scales (as in the holotype (K!)), which consists of two large pinnae with scattered, slightly wide scales on the costae) are also more scattered than in the other varieties, but are still fairly numerous in most specimens and, though narrower than in the other varieties, are not hair-like as in *D. sandwicensis*. Occasional plants, particularly when younger, or when growing in well-shaded, conditions may have rather few costal scales and if small and stipe-less can be confused with *D. glabra* or *D. sandwicensis*, but the scales are much darker and costal ones are never entirely absent.

List of specimens seen: *Kauai*: Forbes s.n. (BISH); Heller 2874 (US, NY, MO); Skottsberg 996 (GB); [Hillebrand] 67 (B); Wagner 87200 (MICH); *Oahu*: Forbes 2013-0 (BISH); Judd s.n., c. 1888 (BISH); St. John 14034 (BISH, MICH); Smith et Whiting 8 (BISH); Skottsberg 148 (BISH, GB, BM); Garber 160 (BISH); Wagner 9617 a et b (MICH); Beechey [Lay] s.n., [19-30/5/1826, or 2/1827], herb. Hook. (K); *Molokai*: Higashino et Holt 10094 p.p. (BISH); St. John et al. 12596 (BISH), 13287 (BISH, MICH); Forbes 338-Mo p.p. (BISH, US, MICH, MO); Hitchcock 15035 (US); Skottsberg 2532 (GB); W. H [illebrand] s.n. (BM); Hillebrand s.n. (NY); *Lanai*: Forbes 59-L (BISH (x2), MO); *Maui*: Forbes 1735-M (BISH, US, K), 2427b-M(K); Mann 502 (BISH); Mann et Brigham 502 (BISH (x2)); Hobdy 531, 822, 2082, 3039 (BISH); Cranwell et al. 2532 (BISH); "P. spinulosa. Maui" *sin. coll.* s.n. (BISH); Fraser-Jenkins field nos. 88/37, 88/274; *Hawaii*: U.S. South Pacific Exploring Expedition [Wilkes] s.n. (BISH); Wilkes 26 (BISH, US), 29 (BISH (x2)); Forbes 152-H (BISH); M. Newell s.n., 1910 (BISH); W.H[illebrand] s.n., 1862 (BM); Hillebrand s.n. (NY); Nelson 5, 12 p.p., 13, s.n. (BM); *General*: Baldwin 76 p.p. (US); J.D. Smith 631 (US); herb. C. Chr. s.n. (BM); Hillebrand s.n. 1863, herb. J. Smith (BM).

C. *Dryopteris unidentata* var. *acutidens* (HILLEBR.) FRAS.-JENK., **comb.nov.**

Basionym: *Dryopteris acutidens* C. CHR., Ind. Fil. I: 250 (1905), nom. nov. for *Phegopteris spinulosa* HILLEBR., non *Dryopteris spinulosa* (SW.) O. Ktze.

Lectotype: "Phegopteris spinulosa Hillebr., Hawaii, Hama Kua, Sandw. Islds. coll. W.H [illebrand]. Ex herb. W. Hillebrand" (B!). In merely mentioning a type locality and not citing any specimen or collector, ROBINSON (1912) was not selecting a lectotype.

This variety has more long-toothy segments than var. *paleacea*, but is otherwise similar in having wide, obtuse, but slightly more deeply lobed, more-or-less rectangular segments. The frond becomes quadripinnate below and the stipe- and rachis-scales are somewhat less prominent and dense than in var. *paleacea*, but remain somewhat wide. The costal and costular scales are more-or-less dense, but not quite as much so as in var. *paleacea*, though similar in width.

There is some variation in the width of the ultimate segments which in some specimens approach the narrowness of those in var. *ukelelensis* and show a transition towards it while not quite reaching the extremes of that variety.

List of specimens seen: *Kauai*: Rock 3 (BISH); Wagner 65350 (towards var. *ukelelensis*), 87202 (MICH); Faurie 413 (towards var. *ukelelensis*)(MICH, BM); Hitchcock 15411 (towards var. *ukelelensis*)(US, NY); *Oahu*: Oahu College s.n., 2/1889. (MICH); *Molokai*: Faurie 412 (towards var. *ukelelensis*) (MICH); [Hillebrand](towards var. *ukelelensis*) (B); *Maui*: Wagner 65472 (MICH); Bonsey 176 b (towards var. *ukelelensis*)(MICH), 187 (towards var. *ukelelensis*)(MICH); W. H [illebrand] s.n., 1870 (towards var. *ukelelensis*)(BM); Hillebrand s.n. (NY); *Hawai'i*: Lyons s.n., ? 1860 (BISH, MICH); Horner "1940-55" (MICH); Faurie 415 (MICH); W. H [illebrand] s.n. (B); Hillebrand s.n. (NY); St. John et al. 18590 p.p. (towards var. *ukelelensis*)(BISH (x2)); Rock et Lindsay 6 (towards var. *ukelelensis*)(BISH (x2), US, K); "Puu Makaala," Wagner s.n., 27/2/1987 (towards var. *ukelelensis*)(MICH); *General*: "All the Islands" [? Baldwin](BISH); Baldwin, 1879 (BISH), s.n., 28/10/1896 (F); Lyons s.n., 1877 (MICH); Strickland s.n., 1850 (BM); Hillebrand s.n., 1863 (BM); Hillebrand et Lydgate s.n. (towards var. *ukelelensis*) (BISH); Gaudichaud s.n., 5/1839 p.p. (K (x2)).

D. Dryopteris unidentata var. *ukelelensis* HERAT ex FRAS.-JENK., var. nov.

A var. *unidentata* frondibus maximis quadri- vel quinque-pinnatis, segmentibus ultimis angustissimus acutis, dentes acutos ferrentibus, axibus frondium paleis vestitis, paleis stipitis longioris et angustioris quam in var. *paleacea*, differt.

Holotype: Hawai'ian Islands, E. Maui, gulley N.E. of Haleakala Ranch on road between ranch and Waikamoi Gulley and Flume, Makawao Forest, above Olinda, E. of Pukalani, N. slope of Haleakala Mountain, c. 1250 m. C.R. Fraser-Jenkins et R.W. Hobdy Field no. 88/57, 26/2/1988 (BM); paratypes: Ditto: 88/53 (NMW, FR, BISH), 88/54 (H), 88/55 (US); 88/56 (H).

Differs from var. *unidentata* by the very large quadri- or five-times pinnate fronds, the very narrow, acute ultimate segments bearing acute teeth, the axes of the fronds well clothed with scales and the stipe-scales longer and narrower than in var. *paleacea*. Although I had seen herbarium specimens before, sometimes labelled *D. acutidens*, including by CHRISTENSEN, it was first shown me in the field by BOB HOBODY in February 1988 and was overwhelming in its magnificence! Apart from a comment by DAVENPORT in 1882 on a specimen at Kew, informing BAKER that he thought it was a new species, it was first recognized as distinct from var. *acutidens* by HERAT (1979), who named it var. *ukelelensis* both in his thesis and in many herbarium determinations (including in BISH, BM, K, MICH, MO, US etc.), so that the name became well known in Hawai'i and elsewhere, though unfortunately he did not publish it. The plant was then listed by WAGNER (1988 and 1992), who inevitably made a species of it and used his own new name (even applying more than one name at different times in his herbarium determinations); it was also mentioned by MONTGOMERY et al. (1992). I also pointed it out (FRASER-JENKINS 1989 b) as a variant of what I then thought should be called *D. acutidens*, mentioning as well the coarser fronded plants now called var. *paleacea*. It was not until shortly afterwards that I realised *D. acutidens* (and its variety) and *D. unidentata* are conspecific. Although connected to var. *acutidens* by some intermediates the pure form of this variety has the most remarkable, very finely dissect and narrow, non-contiguous segments, matched in the rest of the genus only by the completely unrelated East Himalayan endemic species, *D. sikkimensis* (BEDD.) O. KTZE.

This taxon is undoubtedly the most splendid *Dryopteris* I have ever seen and is very nearly the largest, along with *D. comorensis* (TARD.-BLOT) FRAS.-JENK., **comb. nov.**; (basonym: *Dryopteris inaequalis* var. *comorensis* TARD.-BLOT, Not. Syst. (Paris) 15 (2): 161 (1956)), a species I inexplicably left out of my classification of the genus (FRASER-JENKINS 1986), though it was well known to me at the time, *D. oligodonta* (Desv.) PICH.-SERM. and *D. aquilinoides* (Desv.) C. CHR. The sight of these four ferns growing side-by-side in our unheated greenhouse in my father's garden at Bridgend (South Wales) is perhaps the most spectacular the genus, or a lot of other genera too, has to offer! Unfortunately, I have recently lost the Hawai'ian plant, which requires very damp, luxuriant conditions that I could not supervise while abroad.

List of specimens seen: *Mauui*: Munro 777, 789, "cultivated in Lanai", 478 (BISH); Forbes 742-M (BISH (x2)), 915-M (BISH (x4), US, MICH, K), 2166-M (BISH); Hobdy 738, 842 (x2), 883 (BISH); Degener 18160 (BISH, F), 18160 d (US), 28073 (MICH (x2)); Lyon "B" (BISH (x4)); Baldwin s.n. (F); Noe 34 (F); Andrews s.n. (MICH); Oahu College s.n. "Akele", 1/1890 (MICH); Bonsey 1780 (MICH); Wagner 9525, 65464, 87148, 87149, 87161 (MICH); W.H [illebrand] s.n. (B); Hillebrand 597 (K (x2)); Skottsberg 1088 (BM); F.L. Clarke, [via] Davenport 2 (K); Fraser-Jenkins field nos. 88/53-88/57.

8. *Dryopteris glabra* (BRACKENR.) O. KTZE.

Lectotype: "L. *glabra* Brk. in forest above saw-mill, Hawaii. Capt. Wilkes Exped. 17" (US!); isolectotype: Wilkes 17 (US-type collection!). Other specimens of Wilkes 17, but from different localities are in US and BISH.

Synonyms: *D. nuda* Underw., *D. parvula* Robins., *D. tenebrosa* Wagner.

This is the second of the two species of Hawai'ian *Dryopteris* in this section which shows a high degree of variation. It has therefore caused a considerable amount of confusion and a number of taxa have been named at varietal or even specific level which belong to it. In addition there is also the most interesting question of its near vicariance with the European *D. aemula* (AIT.) O. KTZE., mentioned below.

It varies markedly in size, with plants of all varieties capable of becoming precociously fertile even when very small and some small local populations consisting mostly of dwarf plants which never achieved normal size. It also varies in the degree of dissection, width and acuteness of its segments, from wide, obtuse, hardly lobed segments to acute, narrow, highly lobed or dissect segments. The width of the lamina-base, the angle of the lower and mid-pinnac (from acute to right angles) and their dromy (from anadromous to catadromous) are all quite highly variable, as is the degree of glandularity of the frond, axes and indusia (from densely glandular to virtually eglandular). The sori, too, vary in position from subcostal to marginal, or even extra-marginal on exserted teeth in some plants, while some populations develop long receptacles so that the sori stick out from the lower surface of the lamina. A few populations are even exindusiate, which would have had the earlier authors generically tongue-tied! All these parameters vary together in different morphological directions and appear to be partially genetically fixed within local populations, which are often mixed as well, to add to the confusion. Thus in some areas no two populations look alike, while in others exactly the same form can be recognised in widely different

localities. To attempt to name some of these variants as species would be utter folly, as hardly needs to be emphasised to those whose eyes are open when in the field. Yet this is exactly what has happened, even nowadays. It was certainly what WAGNER (1993) has done and also happened some time ago in the case of *D. nuda*, which was described anew without reference to *D. glabra*, perhaps because Underwood thought it of less interest, being a common species, while HELLER himself had given it the same number as his *D. nuda* specimens and apparently did not recognise it as distinct. Whatever the reason, its maintenance as a species by later authors, including WAGNER, is untenable. In reality it does not differ consistently in any feature from *D. glabra* and, as I told Dr. DAN PALMER, who was working with WAGNER, in December 1992, it is evidently merely another variant, well connected by intermediates.

Based on HILLEBRAND's (1888) partly successful and detailed account, HERAT (1979) has undoubtedly again achieved the most competent treatment for these taxa at the varietal level, though he was not far-reaching enough in accepting *D. nuda* as a species.

Though the varieties often overlap somewhat they can usually be recognised and are thus accepted as of some taxonomic significance and are outlined here:

A. Dryopteris glabra var. *pusilla* (HILLEBR.) FRAS.-JENK., **comb. nov.**

Basionym: *Aspidium glabrum* var. *pusillum* HILLEBR., Flor. Hawaiian Isl.: 577 (1888).

Lectotype: "*Aspidium glabrum* Mett. var. γ . *pusillum*. Kauai. Mr. E. Johnson. Ex herb. W. Hillebrand" (B!).

Synonyms: *Dryopteris parvula* ROBINS., nom. nov. for var. *pusillum*; *D. parvula* f. *minuta* SKOTTSB.; *D. tenebrosa* WAGNER.

WAGNER's *D. tenebrosa* (1992 and 1993) was yet another new specific name for this minor variety and he had produced another one again for it (written on "Kauai. Wagner 87186". MICH, (seen 10/3/1988)!) at an earlier stage which has remained unpublished. He had previously illustrated it as a "new species" (WAGNER 1988) and though I referred it (FRASER-JENKINS 1989 b: 258) to *D. parvula*, which I mistakenly accepted as a species at the time, this was evidently ignored. However his taxon does not differ in any respect from *D. parvula* (i.e. the present variety) except in being eglandular and, as I pointed out to him in 1988, this is of such random variability in *D. glabra* (as in many other species) as to be of no taxonomic significance at all, whether one adheres to one-characteristic taxonomy or not! Indeed HERAT (1979) was much nearer the situation when he sank *D. parvula* and var. *pusilla* into var. *soripes*, as the two varieties are very close, probably no less so than larger specimens of var. *soripes* are to more finely dissect specimens of var. *glabra*. Previously (FRASER-JENKINS 1986) I had referred *D. parvula* to section *Purpurascentes* FRAS.-JENK, due to a superficial resemblance to some members of that section, but this was a complete misinterpretation which I later corrected (FRASER-JENKINS 1989 b).

Var. *pusilla* is a very small, precociously fertile form of *D. glabra* and usually has submarginal or marginal sori, a small, sometimes vestigial indusium and variable glandularity. Intermediate sized plants are easy to find (e.g. Kauai. Wagner 5536. MICH (seen 10/3/1988)!) and on Maui there some very small, precociously fertile var. *soripes*, as at Waikamoi Flume, but so far no true, extreme var. *pusilla*.

List of specimens seen: Kauai: Palmer 902 p.p. (BISH); Palmer et al. 933 (BISH); Cranwell et al. 2991 (BISH), s.n., 19/8/1938 (GB); Wagner 5574, 87186 p.p. (MICH); Skottsberg 2991 (C); Johnson s.n. (B); [Hillebrand] 63 p.p. (B); [Hillebrand] 63 p.p. (B); General: Hillebrand s.n. (NY).

B. Dryopteris glabra var. *soripes* (HILLEBR.) HERAT ex FRAS.-JENK., **comb. nov.**

Basionym: *Aspidium glabrum* var. *soripes* HILLEBR., Flor. Hawaiian Isl.: 577 (1888).

Lectotype: "*Aspidium glabrum* Mett. δ . var. *soripes* Hillebr. *Lastrea glabra* var. *soripes*. Pali of Waikola (Maunahui) Molokai. Coll. Dr. W. Hillebrand Ex herb. W. Hillebrand" (B!).

This variety consists of small to medium-sized plants with thin, fragile stipes, a delicate lamina, long pinnae with the lower and middle ones often at right angles to the rachis and with extended tips, the pinnae more-or-less narrow and symmetrical about their axes (i.e. the basicopic pinnules not usually much or at all longer than the acroscopic ones, except in the lowest pinnae) and the segments acute, narrow, at 90° to their axes and finely dissect. The sori are sometimes submarginal, often more-or-less raised up on an elongated receptacle, clearly visible in the living state, although other plants with an identical frond-morphology and belonging here have normal receptacles. This feature can sometimes occur in other varieties or even species on Hawai'i. The fronds are usually quite glandular, but may sometimes be almost eglandular. Occasionally plants are exindusiate or have vestigial indusia, but the indusia are more usually normal-sized.

List of specimens seen: Kauai: Vitale 48 (BISH); Wagner 5536, 87186 p.p. (seen in 1988)(MICH); Molokai: Palmer et al. s.n., 14/1/1990 (BISH (x3)); W.H [illebrand] s.n. (BM); Hillebrand s.n., s.n., 7/1870 (B); Wagner 9548 (MICH); Mauai: St. John et Catto 17943 (BISH); St. John et al. 25727 (BISH (x2)); Skottsberg 846 (BISH, BM); Hobdy 854 (BISH); McAlpin 504 (US); Lyon s.n., 7/2/1929 (sub "Hybrid *Dryopteris* abortive spores", det. Wagner, but spores good and not hybrid) (BISH), s.n., 7/2/1929 (K); Fraser-Jenkins field nos. 88/39, 88/68-88/80; Hawai'i: Giffard 1 (BISH (x4)).

C. Dryopteris glabra var. *glabra*

Synonyms: *Nephrodium rubiginosum* var. *nudicaule* HOOK., *Spec. Fil.* 4: 143 (1862); (lectotype of var. *nudicaule*: "an *L. rubiginosa* var. *nudicaulis* Hook. Oahu. J. Diel" (K!)); *Aspidium glabrum* var. *ambiguum* HILLEBR., *Aspidium glabrum* var. *quadripinnatum* HILLEBR.

This variety consists of medium-sized or large plants with acute segments, varying from tripinnate to quadripinnate (and even again pinnatifidly lobed) below and the plants usually have highly glandular axes and lamina. In many plants the ultimate segments curve upwards and, as noticed by HILLEBRAND (1888: 576), the plants can then be indistinguishable in every respect, including scale- and stipe-colour, segment-shape, toothing and glandularity, from European *D. aemula*, which has the same upward curving of the segments. I published some details of this remarkable incidence of vicariance (FRASER-JENKINS 1989 b), not having noticed HILLEBRAND's comment, and a year later I even received an ingenious, if intentionally legendary explanation for it (GRAHAM 1991), which provided a most original competition-winner! But the

resemblance can be so close, even in detail, that, as HILLEBRAND so aptly said, were it not for the other variants (particularly the much larger plants), the two species would surely have been synonymised. I recently sent back to Britain a living frond I collected at the top of Pu'u Konahua'nui on Oahu in 1992 which was identical to *D. aemula*, though HILLEBRAND says that the glands are more elongated (less globose) and thus taller in *D. glabra*, but I have found specimens that have globose glands. Some plants also have some of the characteristic scent of dried hay when the fronds have been recently pressed and dried, though not as strongly as in the European plant. Having analysed my Hawai'ian material from 1988, Dr. C.-J. Widén has found that the basic phloroglucide chemistry of *D. glabra* is similar to that of *D. aemula* and it is only the more distinctive and derived fully aromatic compounds of *D. aemula* that are absent in *D. glabra*, though even one of these, a compound similar to, or the same as trisaemulin, is present (see WIDÉN and FRASER-JENKINS, in prep.). How this quite extraordinary case of near vicariance came about defies logical explanation at present, but is surely of great interest as it is unlikely to have been mere chance long-distance dispersal with such a restricted species.

List of specimens seen: *Kauai*: Crosby et Anderson 2018 (BISH); Flynn et al. 2757, 3069 (BISH); Smith et al. s.n., 30/4/1929 (BISH (x3), US), s.n., 1/5/1929 (US); Forbes 135-K (US, K), 196-K (BISH), 374-K (US, K); Swezey s.n., 14/7/1992 (BISH); Hobdy et al. 3372 (x3), 3374, 3375 (BISH); Higgins 109, 137 (BISH); Cranwell et Skottsberg 3744 (BISH (x2), GB); Heller 2750 p.p. (BISH (x4), NY, F, L); Palmer 902 p.p. (BISH); Vitale 49 (BISH); Rock 1439 (BISH); Hitchcock 15444 (US); Croat 44968, 44990 (MO); Wagner 5543 (MICH (x2)), 87185, 87188 (MICH); Knudsen 156 (BM); [Hillebrand] 63 p.p. (B); *Oahu*: Lamoureux et Smith 2558 (BISH); Whittier et Young 1765 (BISH); Herbst 446 (BISH); Grant 7415 (BISH); Char et Buelow "NARS-29" (BISH); Garber 313 (x2), 314 (BISH); Hosaka 1133 (BISH); Herat et Herat 528 (BISH); Wilkes 17 p.p. (BISH); Fosberg s.n., 30/4/1933 (US); Topping 2724, 3852 (US); Degener 11983 (F); Degener et Salucops 12033 (US); Meebold s.n., 3/1930 (F); Grant 7230 (MO); Wagner 9617b (MICH); Barclay 1220 (BM); Hillebrand s.n., rec. 6/1862 (K); Diel s.n. (K); Beechey s.n., herb. Hook. (K); Fraser-Jenkins s.n., 17/12/1992; *Molokai*: Krajina s.n. 12/6/1962 (BISH); Imada 112 (BISH); St. John et al. 12578 (BISH); Munro 395, 561 (BISH); Vitale 45 (BISH); Hitchcock 15015, 15101 (US); *Lanai*: Munro 91 (BISH); St. John et Hosaka 18881, 18900 (BISH); *Mau'i*: Forbes 167-M (BISH, US), 904-M (x2), 1022-M (BISH); 1147-M (BISH, K), 1166-M (BISH (x2)), 1200-M, 1201-M (BISH), 1223-M (BISH, US, K), 1239-M (K), 2390-M (US), 2641-M (BISH, US); St. John et Catto 17747, 17772 (BISH); St. John et Mitchell 21003 (BISH); Henrickson et Vogl 3480, 3529b, 3586 (BISH), 3594 (US); Woolford 140 (BISH); Palmer et Obata 658, 685 (BISH); Higashino 754 (BISH, US); Higashino et al. 9715 (BISH); Skottsberg 757 (GB, BM), 846 (GB); Cranwell et Skottsberg 2644 (BISH, GB); Cranwell et al. 2741 (BISH, GB); Crosby et Anderson 1809 (BISH); Munro 766, 767 (BISH), s.n., 18/12/1928 (US); Nagata 1929 (BISH); Hobdy 243, 724, 820, 2097 (BISH); Neal et Hartt s.n., 14/8/1933 (BISH); Meebold 17543 (US); Ewart s.n., 21/10/1928 (US); Montgomery 81-135 (US); McAlpin 509 (US); Hitchcock 14768 (US); Wagner 87113, 87144 (MICH); Hillebrand s.n. (B); W. H [illebrand] s.n. (BM); Bailey s.n. (NY); Lindley s.n. (NY); Fraser-Jenkins field nos. 88/38, 88/58-88/65, 88/111-88/112, 88/194-88/236, 88/299; *Hawai'i*: Whitney s.n. (BISH); St. John 25367, 25373 (BISH); St. John et al. 11407 (BISH), 18434 (BISH (x2), US), 18595, 24024 (BISH); Russ 20, 30 (BISH); Forbes 813-H (BISH (x2), US), 891-H (BISH (x2), US, K); Forbes et al. s.n. 9/1908 (BISH, US); Rock s.n., 29/11/1957 (BISH); Neal s.n., 5/8/1929 (US), s.n., 13/8/1929 (BISH (x2), K); Neal et Hartt 824 (BISH); M. Newell s.n., 1910 (BISH); C.L. Newell 517, 518, 803 (BISH); Mann et Brigham 266 (BISH); Lyons s.n., ? 1860 (BISH (x3)); Woolford

s.n., 20/12/1954 (BISH); Morley 149-H (BISH); Wilkes 17 p.p. (BISH, US (x2)); Hitchcock 14330, 14334, 14392 (US); Rubtzoff 2655 (US); Wagner 65397 (MICH (x2)), 87055, 87060 (MICH); Hillebrand s.n., 1862 (B); Macrae s.n., 6/1825 (K); Lindley s.n. (K (x2)); General: Hillebrand 40 (F), 791 (BISH), s.n. (K); Lack s.n., 1880-1890 (BISH); "All the Islands" [? Baldwin] (BISH (x2)); "All the Islands." Baldwin s.n. (F); Baldwin s.n. (F); Lyons s.n., 1877 (US); Church s.n., herb. Mohr (US); Gaudichaud s.n. (US), s.n., herb. Webb (K); J.D. Smith 584 (US); "Panama [err.]." Barclay, herb. J. Smith (BM); Douglas 40 (K (x2)). Some of the above specimens may belong to var. *soripes* as a result of my being unable to recheck my earlier notes, either in places I could not yet revisit (GB), or when I was prevented from seeing material by WAGNER in 1992 (MICH).

D. Dryopteris glabra var. *nuda* (UNDERW.) FRAS.-JENK., **comb. nov.**

Basionym: *Dryopteris nuda* UNDERW. in HELLER, Minnesota Bot. Stud. 1 (48): 780 (1897).

Lectotype: "*Dryopteris nuda* Underw., n.sp. Plants of the Hawai'ian Islands collected on the island of Kauai, on the ridge west of the Hanapepe river by A.A. Heller 2750, August 22, 1895" (BISH (sheet 498201)!); isolectotypes: Ditto (BISH (sheet 498208)!, US!, F!, MO!, UC!, BM (x2)!, K!). Four other sheets of the same number in BISH belong to two slightly different forms of *D. glabra* var. *glabra*, two (498200 and 05552) are intermediate towards var. *nuda* and the other two (498199 and 498602) are more normal var. *glabra*. It should be noted that some of HELLER's numbers, including 2750, consist of collections from more than one locality. Other "duplicates" are in F (!) and L (!) and are both normal var. *glabra*.

It has been possible to select a lectotype with confidence here because although all the rest of the protologue applies equally to var. *glabra* and var. *nuda* just one key-word shows unequivocally which he most intended. The frond is described as tripinnatifid and one can see that Underwood really intended the precise modern usage of the word (i.e. not quite tripinnate/tripinatisect) from his description of *Gymnogramma sadlerioides* UNDERW. (= *Saddleria squarrosa* (GAUD.) MAXON) on the same page. For this reason I have superceded ROBINSON's (1912) citation of the specimen of var. *glabra* in NY, apparently the only one she saw, as "the type," since that is easily tripinnate, nearly quadripinnatifid.

Var. *nuda* is at its most characteristic and extreme, with obtuse, wide, opposite segments in some populations in the Waianae mountains of western Oahu, but also occurs elsewhere. It is connected by a complete range of intermediates to var. *glabra* and is impossible to maintain as a species, especially when the majority of specimens are slightly intermediate between the more obtuse-segmented and less dissect "*D. nuda*" and the more acute-segmented and more dissect *D. glabra* var. *glabra*. Even within the more obtuse-segmented forms of var. *nuda* there is considerable variation in the degree of dissection and size of the segments, some larger plants becoming tripinnate and developing a wider lamina-base, with the pinnae at right angles to the rachis. Typical plants of var. *nuda* often have darker tipped scales at the very base of the stipe and on the rhizome apex (an organ confused by some North Americans, for irrelevant anatomical reasons, with the term stem, perhaps also because it does not sound sufficiently like the many, usually superfluous technological jargon-words they prefer to invent!), but such scales can also occur in normal var. *glabra*.

List of specimens seen: Kauai: Forbes 142, 247-K (BISH); Heller 2750 (BISH (x2), US, F, UC, BM (x2), K, MO); Doty et Chock 17 B (BISH); Rock 2217 (BISH); Brodie s.n., 3/10/1904 (BISH (x4)); Croat 44886 (US); Stone 3361 (US); Faurie 380, 390 (MICH); Wagner 5555 (MICH); Wagner et Lorence 6331 (US); Oahu: Baldwin 31 p.p. (BISH); Hillebrand et Lydgate s.n. (BISH); Takeuchi et Pyle "Waianae 1001/3522" (BISH); G.W.R. s.n., 18/5/1933 (BISH); Rock s.n., 8/1908 (MICH); Forbes 2564-0 (x2), s.n., 28/7/1908 (BISH, US), s.n., 12-19/12/1909 (BISH); Degener 17531 (BISH (x2), US (x2), F, MO), s.n., 23/8/1939 (MO); Degener et al. 10171 (MO); Mann et Brigham 185 (BISH, MO (x2)); Judd 31 (BISH); St. John 13335 (BISH); Skottsberg 282 (BISH), 282b (BM); Meebold s.n., 6/1932 (BISH (x2)); Egler 37-226 (BISH); Grant 7394 (BISH, MO); Fosberg 8727 (MICH), 8729 (US), 9003, 9078 (BISH), 13800 (US); Herbst 450 (BISH); Selling 3743 (BISH); Topping 2724 (MO), 3556 (US), 3750 (US, MO), s.n., 10/1927 (MICH); Bartsch 30 (US); Taylor 6370 (US); Safford 890 (US); Wagner 3261 (US), 9616 (x2), 65237, 65238, 87104 (MICH); Faurie 388 (MICH); Hillebrand s.n. (BM); Lea s.n., 2-3/1887 (BM); Barclay s.n., 9-23/7/1837 (BM); Halermann s.n. (B); Maui: Palmer et Obata 686 (BISH); Baldwin 31 p.p. (BISH); Hawai'i: Hitchcock 14312 (US (x2)); General: Lack s.n., 1880-1890 (BISH); E.C. Smith s.n. (MO).

Unplaced species.

9. *Dryopteris crinalis* (HOOK. et ARN.) C. CHR.

Lectotype: "Polypodium (Phegopteris) crinale, Hook. et Arn. Oahu. B. Beechey." (K!); the top specimen on the sheet which contains another specimen of *D. crinalis* and one of *D. unidentata* var. *paleacea*.

Although the name *Polypodium crinale* var. *tripinnatum* HILLEBR., sometimes sub *Dryopteris*, has quite frequently been applied to the larger fronds of this species this is a misapplication of a name which properly applies to *D. sandwicensis* (see under that species). The type of *D. crinalis* is itself the larger, tripinnate form.

This strange and presumably very ancient species is unlike all other *Dryopteris* species and has no obvious close relatives. It is possible that it could be related very distantly to *D. unidentata*, or even to some members of the subgenus *Erythro-varia* (H. ITÔ) FRAS.-JENK. (inadvertently misspelt as "*Erythrovariae*" in my classification (FRASER-JENKINS 1986)), as I previously suggested (FRASER-JENKINS 1989b), but I still remain unable to recognize its true affinities and place it. I am not even entirely confident (as with *D. ascensionis* (HOOK.) O. KTZE. and *D. cognata* (C. PRESL) O. KTZE.) that it is a true *Dryopteris*, though it fits the genus by definition. In some respects, notably its stiff, exserted, bristle-like stipe and rachis scales and its strangely brittle laminar texture, dark colour and expanded vein endings, lying just within the margin, it is very similar indeed to *Nothoperanema*, but it lacks columnar upper laminar-surface scales, which appear to be diagnostic for that genus.

The placing of *Nothoperanema* itself also requires looking into as it may be better placed as a fifth subgenus of *Dryopteris*, depending on whether or not the laminar scales are of genuine significance and might indicate other affinities. The laminar scales seem to be variable in prominence within the genus (as in the Asian *N. hendersonii* (BEDD.) CHING, where though clearly present, they are somewhat less developed than in other species) and the bristle-like stipe-scales are also variable, becoming rather wider and more *Dryopteris*-like in *N. hendersonii*. If *Nothoperanema* were actually better placed as a subgenus of *Dryopteris*, a further Hawai'ian fern species,

Dryopteris rubiginosa (BRACK.) O. KTZE., would have to be added to the list of Hawai'ian *Dryopteris*. HOLTUM had annotated specimens of it at Kew and BM in 1982 and 1983 as a *Stenolepia* or *Nothoperanema*, rather than a *Ctenitis* as it was known to North American botanists working on Hawai'i, and in November 1992 Dr. ALAN R. SMITH at Berkeley, who is about to make the necessary new combination, pointed out to me that he believed it to be a *Nothoperanema*. As I know Asian *Nothoperanema* well, I was able to support his conclusion fully and told him that it appears rather closely allied to *N. squamiseta* (HOOK.) CHING. But I have not yet come to a final clear decision about the status of *Nothoperanema* beyond strong suspicions mentioned above that it might belong to *Dryopteris*. If so, it could be the case that *D. crinalis* were some kind of borderline species between the two, in which case I would be tempted to place it as an exception within a subgenus *Nothoperanema*, merely being a species without upper laminar-surface scales.

D. crinalis does not vary much except in a way that mirrors growth and development forms. On Kauai (especially), Oahu and Maui it can develop into a larger, tripinnate form, matching the type, but it is otherwise only bipinnate becoming almost tripinnatifid at the base of the lamina. This variation does not seem to be of much taxonomic or nomenclatural significance.

List of specimens seen: Kauai: Forbes 269-K (BISH), 289-K (BISH, US), s.n., 8/1909 (BISH (x2)); Flynn et al. 3038 (BISH); Heller 2587 (MO, NY); Johnson s.n. (B); Oahu: Judd 63 (BISH); Rock s.n., 8/1908 (BISH); Forbes 1609-0 (BISH), s.n., 11-14/4/1908 (US), s.n., 14-21/11/1908 (BISH); Baldwin s.n., 1879 (BISH); Hillebrand s.n., 6/1862 p.p. (K); Hillebrand et Lydgate s.n. (BISH); Faurie 383 (MICH); Lichtentaler s.n. (US); Boyd 2223 (MO); Topping 2789 (MO); Beechey s.n. (K); sin. coll., s.n., herb. C. Chr. (BM); Molokai: Faurie 446 (MICH); Hillebrand s.n. (B); Maui: Hobby 573, 737, 2025 (BISH); Wagner 5098, 9532, 65455, 87162 (MICH); Forbes 857-M, 889-M (BISH), 1273-M (BISH, MICH, K), 1757-M (BISH); Rock 8570 (BISH); Baldwin s.n., 12/8/1979, s.n., 1879 (BISH); Skottsberg [? no.] (GB), 1100 (BM); Hawai'i: Lyons s.n., ? 1860 (BISH, MICH); Hillebrand s.n. (B, MICH); General: Baldwin 75 (US, NY), s.n. (F, B); Hillebrand s.n. (B); Hillebrand et Lydgate s.n. (BISH); Lack s.n., 1880-1890 (BISH); Andrews s.n., 8/1889 (MICH); Rock s.n. (BISH), sin. coll. Hook. et Arn. 44, herb. Hook. (K).

Further research

So far only one Hawai'ian species, the diploid apomictic *D. wallichiana* has had its cytology correctly published, though WAGNER appears to have made some preliminary counts on other species. However these may not yet be reliable, except with sexual species, as he has apparently not distinguished between apomicts and sexual species. Since my advice to him on doing this (in September 1992), I notice that he has not stated the cytotype of his *D. subbipinnata*, which he had previously thought to be hexaploid, which indicates that his cytological investigation done so far needs to be re-investigated for any taxon with more than $n=41$ before altering for publication. From examining the spore-size and regularity (apparently misinterpreted by WAGNER 1993) one can guess that *D. fusco-atra*, *D. palikuensis* and *D. hawaiiensis* should be triploid apomictic, while *D. mauiensis*, *D. sandwicensis*, *D. unidentata*, *D. glabra* and *D. crinalis* are probably all diploid sexual. But these "pseudocount" estimates, though probably correct, urgently need to be tested and checked cytologically. Fixations I have

prepared from my living plants of most of the taxa growing at Bridgend, Wales, or in MARTIN RICKARD's fine fern-garden at Kyre Park, Tenbury Wells, Worcesterstershire, England, are being studied by Dr. MARY GIBBY at the BM, London.

A comprehensive programme of chemical analysis of the phloroglucide content of dried rhizomes I collected in the Hawai'ian Islands (including *D. rubiginosa*, which also has phloroglucides) has been carried out by Dr. C.-J. WIDÉN of Helsinki and we now have results on nearly all the taxa. These are intended to be published by WIDÉN et FRASER-JENKINS (in prep.) in the near future.

Some further careful study of the spores of Hawai'ian *Dryopteris* would be advisable, particularly in the search for hybrids, not so far reported from the area, but which could cast important new light on the relationships between taxa. Several specimens I have cited in the text were claimed to have abortive spores and therefore to be hybrids by WAGNER in determinations at BISH and MICH, but on examination I found they did not have abortive spores at all. This seems to have been due to lack of experience in the examination and interpretation of spore-samples as some of them do not even have partly immature spores, which is the condition that most often leads to erroneous claims of hybrid-type spore-abortion. An unreported case of a hybrid between two probable apomictic species has also been claimed by him (pers. comm., 1988), which, so far as is known, is impossible since all the apomicts investigated to date produce only one sex, for reasons not yet understood but perhaps connected with the development of sexes in spore-bearing plants. Such a case obviously requires a full investigation of the cytological status of the proposed parents (of which some indication should be obtainable from spore-examination, if collected in good state, as in this case), as well as of the spores and cytology of the plant concerned. I have also found and cultivated a plant (Maui, Makawao forest. Fraser-Jenkins field no. 88/135, 1/3/1988) which appears to be exactly what one would expect from the same proposed parentage (*D. fusco-atra* var. *fusco-atra* and *D. wallichiana*), but has unfortunately consistently refused to become fertile, including the original collection. At present I suspect it could merely be an aberrant individual of *D. fusco-atra* with *D. wallichiana* tendencies such as brown scales (but a long stipe and wider lamina-base) and narrower, deeper-cut pinna-lobes. I have as yet found no evidence of a sexual form of either of the two potential parent-species from the locality (or elsewhere), along with the normal forms, but I hope the plant may soon feel like taking more of an interest in reproduction given the comfortable bed it now finds itself in! A detailed study of Hawai'ian *Dryopteris* spores, combined with cytology and preferably carried out locally, could well turn up some interesting findings.

Acknowledgements

I am truly grateful for the most friendly help given to me during my visit to Hawai'i in 1988 by BOB HOBODY of Wailuku, Maui, who accompanied, me on two fascinating excursions (to Makawao Forest and Hana'aula), showing me varieties of *D. unidentata* and other species. I especially appreciated his help in this bastion of American-style private property, where "trespass" has long been a major crime, unlike in the freer lands of Asia, and merely visiting the country can end one up in prison, being shot (without redress), or both! I am also most grateful to Dr. JANE MEDLAR of Bishop Museum, Honolulu and Dr. DAN PALMER of Honolulu for their help during my visits to Oahu. Many thanks, too, to Dr. MICHAEL G. PRICE of the University of

Michigan, Ann Arbor, Professor CHARLES H. LAMOUREUX of the Lyon Arboretum, University of Hawai'i, Honolulu, Dr. TISSA R. HERAT of the Open University, Nugegoda, Sri Lanka and Dr. JOHN C. GAME of Berkeley, California, for their encouragement, advice, permission and help. I am most grateful to Professor TADEUS REICHISTEIN of Basel for his most generous financial sponsorship, enabling me to go to Hawai'i. I would also like to thank the curators and pteridologists of the various herbaria I visited and mostly drew on for this study: B, C, GB, BM, K, NY, US, F, MICH (in part only), MO and BISH.

Finally I must thank Dr. HERB WAGNER and his wife, of Ann Arbor, U.S.A., for advising me that I was free to go ahead and publish my work on Hawai'ian *Dryopteris* when I visited then at Ann Arbor in September 1992. Although I have always worked independently on this subject I was invited by him at his initiation to collaborate in joint research (WAGNER in litt., 26/1/1988; accepted by me, in litt., 19/2/1988 and confirmed by him, in litt., 1/8/1989); from time to time I therefore let him know of my findings and had pointed out difficult or interesting specimens in my determinations at MICH, BISH etc. I then waited for some five years, during which he was unable to offer any information in return and was apparently not ready to go ahead with preparing for our publication. On meeting the WAGNERS on 30/9/1992 during my recent stay, I continued to give him some brief but important information to help clear up mistakes they had made in both cytology and typification as well as to point out the existence of intermediates connecting the present varieties of *D. unidentata* etc. But he then finally told me that due to his recent unfortunate ill health he had had to abandon his plans to work further on Hawai'ian *Dryopteris*, which now had to take a very low priority, and he would therefore no longer be able to continue with our proposed "joint" work or publication on it, which he had had to put aside. Though this actually turned out to be not entirely the case, with his subsequent rapid, almost immediate publication in May 1993 of a paper including two new Hawai'ian *Dryopteris*, doubtless this must have been merely coincidental and I have to presume that he still has the intention to comply with what he said while opting out. Indeed, I suppose I am sure that he must also have intended the same when he first invited me to join him after I had told him I was on my way to Hawai'i to look at the genus there as part of my world-wide study of it. However, be that as it may, he has now agreed that I should go ahead alone with my findings and it was clear that my long overdue work no longer needed to be delayed apart from fitting in with my ongoing programme of Asian work.

Taking him at his word about his withdrawal from the subject I have therefore produced the present paper as an independent presentation of my study, indeed one often not in agreement with WAGNER's less realistic ideas, due to his not having joined in discussion with me. As it turned out, my independence was perhaps fortuitously, if rather surprisingly maintained during my recent visit to Ann Arbor because though I had written to WAGNER to arrange my visit and his reply had not revealed any intended changes in our cooperation, I found, despite unsuccessfully requesting access from him, that the Hawai'ian fern cupboards in this public herbarium, of which he is not the curator, were especially locked in preparation for my visit, at his request. This was not, as he told me at the time, the normal way they were kept and was ostensibly said to be due to their active research on Hawai'i - but presumably then on other genera which I was not studying if his *Dryopteris* work had been shelved. I was also unable to see the long-term loans of Hawai'ian *Dryopteris* from A, GH, UC etc., which herbaria I had come to America to visit. For this reason there may always be a few errors in the identification of specimens that I was unable to re-confirm, or some gaps in distribution due to the withholding of these collections; for these I can only apologise. It is to be hoped that before too long a true spirit of international cooperation, if it still survives in the face of nationalistic competition, may be restored in this well-known University's botany department to be a credit to their nation and an example for others to follow.

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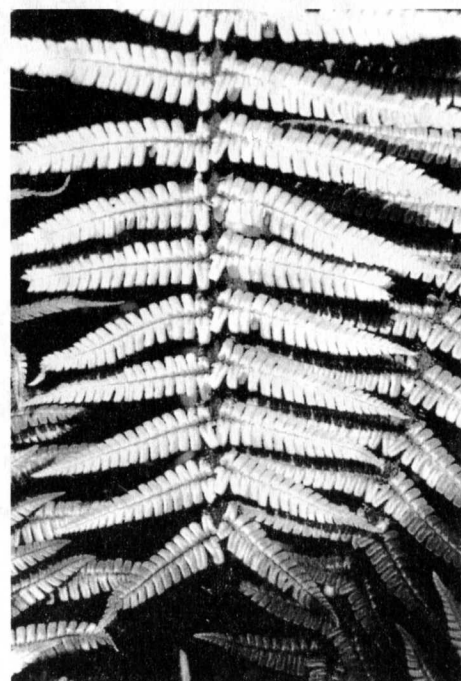
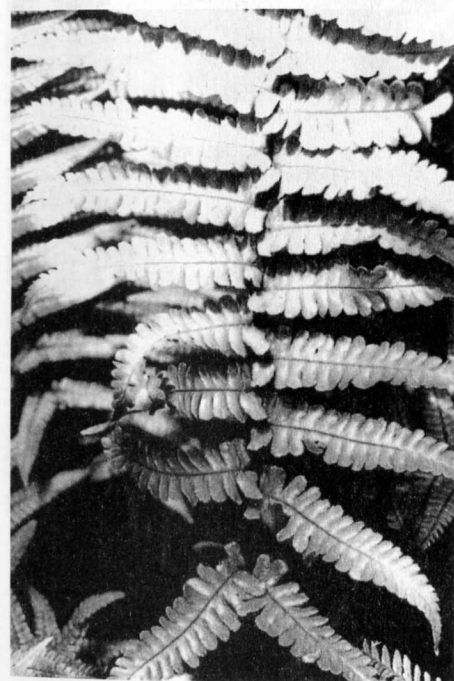
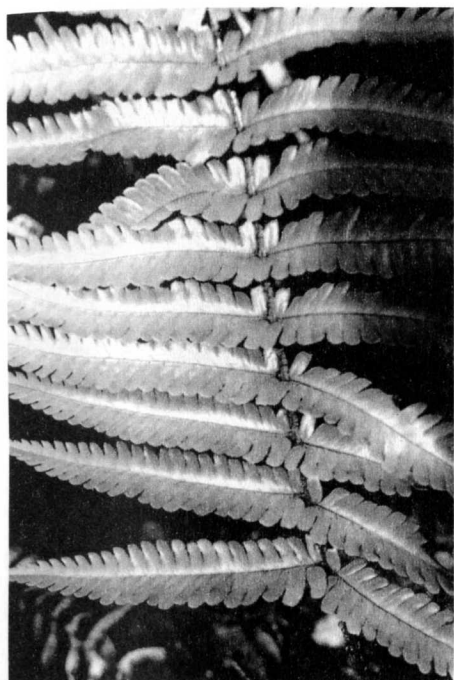
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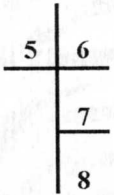
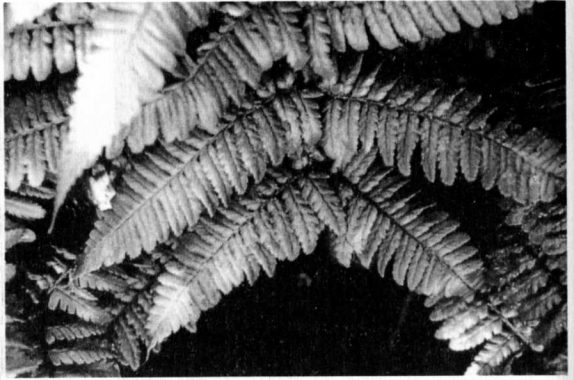
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Figures

1. *Dryopteris fusco-atra* var. *fusco-atra*. Makawao Forest, Maui, CRFJ 14900 (Field no. 88/136).
2. *Dryopteris fusco-atra* var. *lamoureuxii*. Makawao Forest, Maui, CRFJ 14914 (Field no. 88/150).
3. *Dryopteris fusco-atra* ? form towards *D. wallichiana*. Makawao Forest, Maui, CRFJ 14899 (Field no. 88/135).
4. *Dryopteris wallichiana*. Waipoli Road, Maui, CRFJ 14778 (Field no. 88/16).
5. *Dryopteris palikuensis*. Makawao Forest, Maui, CRFJ 14922 (Field no. 88/158).
6. *Dryopteris palikuensis*. Makawao Forest, Maui, CRFJ 14922 (Field no. 88/158).
7. *Dryopteris mauiensis*. 4000', Hana'aula, Maui, CRFJ 14865 (Field no. 88/101).
8. *Dryopteris sandwicensis*. Waipoli Road, Maui, CRFJ 15036 (Field no. 88/272).
9. *Dryopteris unidentata* var. *paleacea*. 4000', Hana'aula, Maui, CRFJ 14871 (Field no. 88/107).
10. *Dryopteris unidentata* var. *unidentata*. Waipoli Road, Maui, CRFJ 15038 (Field no. 88/274).
11. *Dryopteris unidentata* var. *unidentata*. Waipoli Road, Maui, CRFJ 15038 (Field no. 88/274).

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