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A morphological assessment of *Adiantum hispidulum* Swartz and *A. pubescens* Schkuhr (Adiantaceae: Filicales) in New Zealand

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Abstract Two polymorphic members of the *Adiantum hispidulum* Swartz complex, *A. hispidulum* sensu stricto and *A. pubescens* Schkuhr, have been critically studied on a morphological basis, utilising frond and hair forms, pinnule shape and size, soral features, number of sporangia per sorus, sporangial size, annulus position and number of indurated cells, spore shape and size, rhizome and stipe paleae. Separation of the two taxa is traditionally based on frond form (*A. hispidulum* being described as pinnate and *A. pubescens* as pedate), and indumentum characteristics (*A. hispidulum* having medium to short stiff hairs, *A. pubescens* having long lax hairs). This study shows that only those characters associated with the pinnule hairs can be used to consistently separate the two taxa (*A. hispidulum* has short (63–815 μm), stiff, often pigmented hairs with enlarged basal cells, while *A. pubescens* has long (251–1003 μm), soft, pale hairs with narrow basal cells). However, even these characters showed a high degree of variability. *Adiantum pubescens* is given varietal status as *A. hispidulum* var *pubescens*.

Keywords ferns; Adiantaceae; *Adiantum hispidulum*; *Adiantum pubescens*; morphology; frond; hairs; spores; New Zealand

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INTRODUCTION

Adiantum was first described by Linnaeus (1753). The genus is characterised by sporangia borne on the inner face of a reflexed marginal extension of the pinnule. Approximately 200 species are distributed worldwide, about seven of which are found within New Zealand. Of these, *A. aethopicum* L., *A. diaphanum* Blume, *A. formosum* R. Br., *A. hispidulum* Swartz, and possibly *A. cunninghamii* Hook. (see Andrews 1990) are represented in Australia and the Pacific, whereas *A. viridescens* Col. (Parris & Croxall 1974) and *A. fulvum* Raoul are endemic.

One of the most polymorphic of these species is *A. hispidulum* and, as Parris (1980) suggests, its revision is long overdue. This work deals with the two New Zealand members of the complex (*A. hispidulum* sensu stricto and *A. pubescens* Schkuhr). Morphologically these two taxa are similar, having been distinguished at various times by frond form (*A. hispidulum* being described as pinnate and *A. pubescens* as pedate; Richard 1832; Christensen 1937) and indumentum characteristics (*A. hispidulum* having medium to short stiff hairs and *A. pubescens* having long lax hairs; Parris 1980). In general the two taxa are merged in New Zealand, with only *A. hispidulum* being recognised (e.g., Allan 1961; Crookes & Dobbie 1963). At most *A. pubescens* may be mentioned as a form of *A. hispidulum* (e.g., Brownsey & Smith-Dodsworth 1989, p. 48, who reference Parris 1980). The object of this paper is to examine in detail the variability of morphological characters used to identify and separate the taxa and thus indicate a basis for further direction.

MATERIALS

Living material of both *Adiantum hispidulum* and *A. pubescens* was collected in the wild. Fronds were removed at the time of collection and dried for comparative work. The rhizome stock was grown

on under standardised glasshouse conditions at the University of Auckland. A list of voucher specimens (held at the University of Auckland, AKU) for the living plants used in this study follows. In the remainder of this work individual plants are referred to by their collection code (*A. hispidulum* = c.c. numbers, and *A. pubescens* = c.c. letters).

A. hispidulum. NORTHLAND: Paihia, 1983, *M. F. Large* (AKU 15099, collection code 1); Opito Bay, 1982, *W. Booth* (AKU 15100, c.c. 2); Kerikeri, 1982, *W. Booth* (AKU 15101, c.c. 3); Wairau River, 1982, *E. A. Brown* (AKU 15103, c.c. 5); Kikipaka, 1982, *P. Mathews* (AKU 15105, c.c. 7); Whangarei, 1983, *J. E. Braggins* (AKU 15104, c.c. 6). AUCKLAND: Waitakere, 1982, *E. K. Cameron* (AKU 15106, c.c. 8); Auckland City, 1983, *M. F. Large* (AKU 15107, c.c. 9); Auckland City, 1983, *M. F. Large* (AKU 15109, c.c.11); Hobson Bay, 1982, *E. K. Cameron* (AKU 15108, c.c.10); Hobson Bay, 1983, *M. F. Large* (AKU 15110, c.c.12); Hobson Bay, 1983, *M. F. Large* (AKU 15111, c.c. 13); Mission Bay, 1983, *M. F. Large* (AKU 15112, c.c. 14); Mission Bay, 1983, *M. F. Large* (AKU 15113, c.c.15); St Heliers, 1983, *M. F. Large* (AKU 15114, c.c.16); St Heliers, 1983, *M. F. Large* (AKU 15115, c.c.17). COROMANDEL: Port Jackson, 1982, *M. F. Large* (AKU 15116, c.c. 18); Port Jackson, 1982, *M. F. Large* (AKU 15117, c.c. 19); Pauanui, 1982, *M. F. Large* (AKU 15118, c.c. 20), Pauanui, 1982, *M. F. Large* (AKU 15119, c.c. 21). OFFSHORE ISLANDS: Rimariki I., 1982, *E. K. Cameron* (AKU 15120, c.c. 22); Rimariki I., 1982, *E. K. Cameron* (AKU 15121, c.c. 23); Waiheke I., 1982, *K. Johns* (AKU 15122, c.c. 24); Lady Alice I., *E. K. Cameron* (AKU 15124, c.c. 26); Little Barrier I., 1982, *E. K. Cameron* (AKU 15125, c.c. 29). *A. pubescens.* CULTIVATED: University of Auckland, 1983 (AKU 15133, c.c. F*); University of Auckland, 1983 (AKU 15134, c.c. G*). NORTHLAND: Russel, 1983, *M. F. Large* (AKU 15128, c.c. A*); Russel, 1983, *M. F. Large* (AKU 15129, c.c. B*); Whangarei, 1982, *C. J. West* (AKU 15130, c.c. C*); Whangarei, 1982, *K. Johns* (AKU 15131, c.c. D*); Whangarei, 1982, *C. J. West* (AKU 15132, c.c. E*).

METHODS

Analysis of morphological variation

Frond form

The use of frond form as a character was investigated by assessing the shape of five fertile fronds from each plant in the glasshouse grown collection of New Zealand plants of both taxa.

Frond size

Frond lamina length was recorded for glasshouse plants (five fronds per plant) and from field collected material (all fronds available).

Pinnule characteristics

Pinnule shape, position, size, and venation patterns were recorded for each plant studied.

Pinnule size

Pinnule length and width were recorded from the glasshouse plants for 10 pinnules on each frond studied (five fronds per plant).

Size of reflexed margin

The length and width of the reflexed margin were recorded for 30 sori per plant. The size of this sample was restricted by the maximum number of intact sori available at any one time, and by the problem of variable maturity between and within fronds.

Numbers of sporangia per sorus

To obtain the number of sporangia present in each sorus, sporangia were counted for each marginal flap measured as above.

Sporangial size

Fifty fresh mature sporangia taken from each plant were mounted in water and their capsule width (from stomium to rear of annulus) and length (from tip of annulus to stalk) were recorded.

The annulus

The annulus of both taxa is vertical, or nearly so, and is interrupted towards the capsule base. Copeland (1947) quotes 18 indurated annulus cells for the genus. To investigate the number present in *A. hispidulum* and *A. pubescens*, counts of indurated cells per plant were made for 20 of those sporangia used to measure capsule length and width.

Spores

At the beginning of this study there were no published descriptions of the spores of *A. pubescens* and very few of *A. hispidulum.* The most "extensive" works were the studies of Brown & Brown (1931), who recorded dimensions of spores from the Pacific material of *A. hispidulum*, and Harris (1955), who described spores of most *Adiantum* taxa in New Zealand, including *A. hispidulum.* To assess any

variation in spore form, a comparison of the physical characteristics of the spores of *A. hispidulum* with those of *A. pubescens* was made using light and scanning electron microscopy. Polar and equatorial sizes were also recorded from samples of 50 spores from each taxon. The results of this study are discussed by Large (1984) and summarised by Large & Braggins (1991), who suggest that spores of both taxa are morphologically identical. A detailed description applicable to spores of both taxa is given by Large & Braggins (1991, p. 36, fig. 127–129).

Polar equatorial ratio (P:E)

P:E ratios were calculated from the spore polar and equatorial dimensions. To compare the ratios obtained with those of Harris (1955) (who gives a ratio of 4.4:8 for *A. hispidulum*), all ratios were converted to base 8.

Indumentum

The original descriptions of *A. hispidulum* by Swartz (1801) and *A. pubescens* by Schkuhr (1809) differentiate the two taxa on frond shape and on hair type; *A. hispidulum* is described as having "hispid" hairs and *A. pubescens* as being "pubescent". Later descriptions have largely ignored hair status as a character and differentiated the taxa primarily on frond form (e.g., Richard 1832; Christensen 1937). Parris (1980) revived hair type as the primary character for taxa differentiation. She described *A. hispidulum* as having short, stout hairs (100–400 (700) μm in length) and *A. pubescens* as having long, thin, subrigid hairs (300–600 (900) μm in length).

To determine whether hair size is influenced primarily by genetic or environmental factors, measurements of 50 hairs were taken from pressed fronds collected in the field. These were later compared (see Table 6) with hair measurements taken from fronds (also pressed prior to study) of the same plants, after they had been grown in constant conditions for 3 months. Although this study was limited by the number of plants available with comparable field collected material, it did include plants from widely separated locations within the range of the two taxa (e.g., Bay of Islands, Coromandel).

To determine hair length variation between the taxa, samples of 50 hair measurements were taken from mature pressed fronds of *A. hispidulum* and *A. pubescens* plants. Measurements from the type specimens were also included in this investigation.

Hair density

Density was assessed by counting the number of hairs in 50 quadrats per plant, on the lower surface of the pinnule lamina. Hairs on the upper pinnule surface are often absent or are of extreme variability in occurrence.

A. Ecological variation: To determine whether variation in hair density is under predominantly genetic or environmental influence, samples were measured collected from the field, and later from the same plants when grown in glasshouse conditions.

B. Intertaxon variation: To determine to what extent (if any) variation in the density of hairs between the two taxa occurred on a genetic basis, data from glasshouse grown plants (50 quadrats per plant) were investigated.

Distribution of hairs was determined using the relative sizes of the mean and variance of the quadrat samples (Sokal & Rohlf 1973): for example, if mean = variance then distribution is random; if mean > variance, distribution is regular; if mean < variance, distribution is clumped.

Statistical analysis

Pilot studies (Large 1984) were carried out to investigate patterns of variation within the population. These were necessary to achieve samples that would accurately represent the population and be appropriate for analysis. Data and statistical processing was performed using the SAS package (see Ray 1982) on an IBM computer (model 4341).

Microscopy and photography

SEM preparation: An SEM model Philips 505 was used to examine both spore and pinnule material. Spores were fixed in glutaraldehyde, buffered with a phosphate buffer at pH 7.3, and dehydrated in graded ethanol series. The samples were then air dried in a desiccator containing silica gel (for a full description of the preparation methods see Large & Braggins 1991). Pinnule material was fixed in Crafs I solution (Beryln & Miksche 1976) then dehydrated and dried in the same way as the spores. All specimens were gold coated.

Light microscopy: The studies on spores, stomata, and sporangia were carried out on an Olympus BHC microscope. Photographs were taken on a Zeiss photomicroscope III with Ilford pan F(ASA 5O)

film, and on a Wild Macroscope 400 with Ilford HPS (ASA 400) film.

RESULTS AND DISCUSSION

Analysis of morphological variation

Frond form

The two taxa (*A. hispidulum* and *A. pubescens*) have at times been differentiated on the basis of frond morphology. For example, both Richard (1832) and Christensen (1937) differentiated plants with pinnate fronds as *A. hispidulum*, and plants with pedate fronds as *A. pubescens*. Parris (1980) reported *A. pubescens* to be always pedate and *A. hispidulum* as ranging in form from pinnate to pedate.

In this study, frond form observed from both the field and glasshouse material was divided into three general categories: pinnate (Fig. 1.1) pinnate-pedate (Fig. 1.2), and pedate (Fig. 1.3).

A. hispidulum exhibits fronds of all three categories although it is most commonly found with the first two forms. Occasionally, more than one form is produced on the same plant. *A. pubescens* displays the pinnate-pedate forms with very occasional fronds approaching the pinnate form. As with *A. hispidulum*, more than one form may occur on the same plant. The frond form exhibited by any particular plant is not affected by edaphic conditions. This is evident from the lack of change found when fronds collected from the field are compared with those later grown on the same plants when brought into glasshouse conditions.

The range of frond morphology present in both taxa, and the sporadic occurrence of more than one form on a single individual, indicates that frond form, as used by Christensen (1937) and Richard (1832) for differentiation of the two taxa, is inappropriate. A wider range in form than that suggested by Parris (1980) is noted in *A. pubescens*.

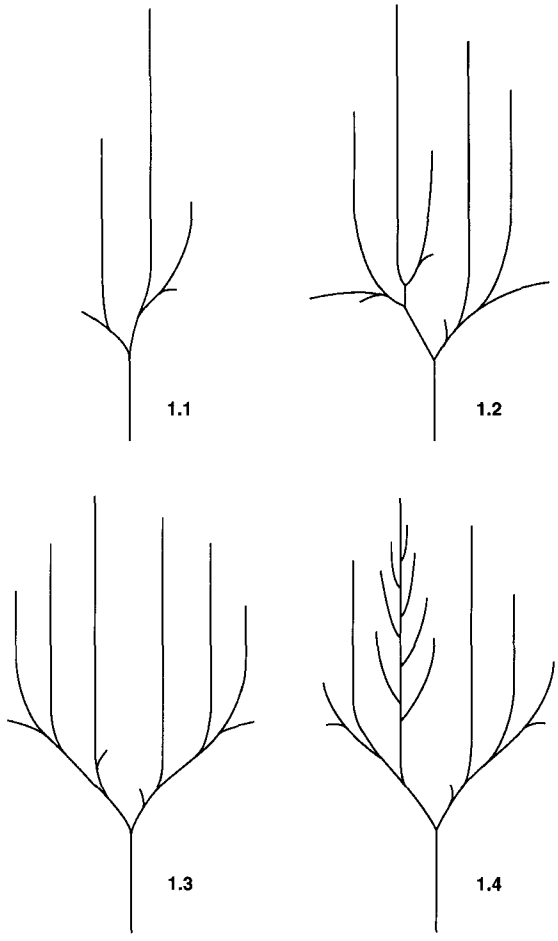


Fig. 1 **1.1**, Pinnate frond form as shown commonly by *A. hispidulum* and occasionally by *A. pubescens*. **1.2**, Pinnate-pedate frond form as shown by both *A. hispidulum* and *A. pubescens*. **1.3**, Pedate frond form shown commonly by *A. pubescens* and occasionally by *A. hispidulum*. **1.4**, Abnormal frond form with secondary pinnae forming along the axis of the longest pinnae. This form occurs in both taxa to varying degrees.

Abnormal frond shape

The occasional occurrence of abnormal fronds in both taxa was observed amongst herbarium material (e.g., AKU 08359, AKU 08359, AKU 015087, AKU 01046) and in the field. The abnormalities almost always took the form of an enlargement of the central pinna, with formation of secondary pinnae along its length (Fig. 1.4). While the occurrence of these abnormalities is rare (c. ≤5% of the fronds examined), it does suggest that the frond shapes found in both taxa are derived from a basic pinnatifid form, perhaps not unlike that seen in *A. cunninghamii*. Hook. or *A. fulvum* Raoul (e.g., cf. Crookes & Dobbie 1963, p. 217 or Brownsey & Smith-Dodsworth 1989, fig. 45, 47).

Frond coloration

The young fronds of both taxa are often bright pink. Although the intensity of this coloration appears to be associated with light quality (the brighter the light the more vivid the colour), observations on plants grown in controlled glasshouse conditions at the University of Auckland indicate that the shade of colour produced varies between individual plants.

This variation outweighs any differentiation between the two taxa.

Frond size

A summary of frond lamina length is provided in Table 1. Variation between the two taxa was non-significant at the 95% level. The coefficient of variation is virtually the same for both taxa and decreases from field to glasshouse, as could be expected for a character affected by environmental factors.

Pinnule characteristics

Basic pinnule form is the same for both taxa and the following description is applicable to either. Pinnules are alternate, oblong to rhomboid in shape, and are stalked (although occasionally towards the upper fourth of the primary and secondary pinnae they may become almost sessile). Tip pinnules are often lost, but where present, are stalked, reduced in size, and usually sterile. Pinnules on young plants may be toothed along the tip and upper distal margin, with two or three sori on the distal margin. Mature plants show no teeth and produce sori on the distal and tip margins.

Pinnule size

Maximum pinnule size occurs approximately one-third of the way up the pinnae and decreases towards the pinnae tips. Results for pinnule length and width measurements are summarised in Table 1. Variation in these sizes between the taxa was non-significant at 95%.

Vein patterns

Secondary veins, which may dichotomise three, four,

Table 1 Summary statistics for 25 plants of *Adiantum hispidulum* and five plants of *A. pubescens* giving frond size in millimetres (data from field collected material is compared to that taken from the same plants when later grown in cultivation). Pinnule length and width (in mm) and reflex (R.) margin size (length and width in μm) along with the number of sporangia per sorus, capsule length and width (in μm), the number of annulus cells, and spore dimensions in μm (P = polar, E = equator, P:E = polar to equator ratios in the form E = 8). $\bar{x}$, mean; R, range; SD, standard deviation; CV, coefficient of variation; *N*, sample size; and CI, confidence interval.

Taxon	Character	$\bar{x}$	R	SD	CV	*N*	CI
A. hispidulum	Frond size (cult.)	170.24	120–236	24.49	14.39	125	
	Frond size (field)	149.71	75–220	33.09	22.10	70	
	Pinnule (length)	9.53	4–16	2.36	24.76	1250	
	Pinnule (width)	4.65	2–8	1.09	23.44	1250	
	R. margin (length)	840	440–1600	210	25.00	570	
	R. margin (width)	698	440–1600	129	18.50	570	
	No. sporangia	32.24	11–61	10.86	33.68	570	
	Capsule size (length)	196	160–230	13	6.63	900	±19.60
	Capsule size (width)	150	112–194	10	6.67	900	±15.00
	Annulus cells (number)	16.73	14–22	1.61	9.62	360	±0.42
	Spore dimensions (P)	35	30–43	2.12	6.00	900	±1.75
	(E)	49	40–58	3.00	6.12	900	±2.45
	(P:E)	5.8:8	4.5:8–8:8	0.43	7.40	900	±0.29
A. pubescens.	Frond size (cult.)	171.00	124–225	25.30	14.80	25	
	Frond size (field)	166.62	86–250	46.88	28.14	40	
	Pinnule (length)	9.72	6–17	2.45	25.21	250	
	Pinnule (width)	4.72	3–8	1.07	22.67	250	
	R. margin (length)	848	500–1600	191	22.52	120	
	R. margin (width)	703	440–1000	142	20.20	120	
	No. sporangia	38.45	17–62	11.66	30.33	120	
	Capsule size (length)	206	180–240	11	5.53	200	±20.60
	Capsule size (width)	161	135–180	10	6.21	200	±16.10
	Annulus cells (number)	15.47	10–21	1.39	8.91	80	±0.39
	Spore dimensions (P)	37	31–41	2.12	6.49	150	±1.85
	(E)	50	43–59	3.00	5.00	150	±2.50
	(P:E)	5.9:8	4.8:8–7:8	0.43	5.85	150	±0.30

or occasionally five times, arise from a primary vein running along the lower proximal pinnule margin. This vein may or may not be pigmented (brown to pink). In mature plants the dichotomous branches of the secondary veins terminate in sori at the pinnule margin, each sorus usually being supplied by four veinlets.

Reflexed marginal flap of the sorus

According to Copeland (1947) the genus *Adiantum* is distinguished by pinnule veinlets extending into a reflexed margin (false indusium) where sporangia are borne. The range of forms of the marginal flap found in the New Zealand species are illustrated in Allan (1961, p. 96, fig. 3). In *A. hispidulum* and *A. pubescens* the false indusia are reniform in shape and have hairs (which may or may not be darkly pigmented) on the central upper surface. Hair pigmentation appears to vary between plants and with maturity of sori and fronds. In both taxa the marginal flap is usually supplied by four pinnule veinlets. They continue through the flap, are approximately parallel, and do not anastomose.

Size of reflexed margin

A summary of length and width data of the reflexed margin is provided in Table 1. Variation between taxa was found to be non-significant at 95%.

Sporangia

Sporangia for both taxa are borne alone (i.e., without paraphyses or other accessory structures), on or between the veins beneath the marginal flap. The capsules of the sporangia are supported by slender stalks usually comprising 2–3 cells in diameter, and 3–4 in length. These cells may or may not have light (brown-gold) pigmentation in their walls.

Numbers of sporangia per sorus

The number of sporangia present in each sorus is summarised in Table 1. Because of the random maturation of sporangia within the sori, the number of sporangia varies from sample to sample. For this reason, the data obtained can be used only as an indication of the numbers of sporangia present at any one time in the life of the sorus. Variation between taxa was non-significant at the 95% level.

Sporangial size

Results for sporangial capsule width and length are summarised on a species basis in Table 1. Variation in these capsule sizes was non-significant between taxa at the 95% level.

The annulus

The number of annulus cells in each taxon are summarised on a species basis in Table 1. The mean figures for both taxa (*A. pubescens* = 15.47, *A. hispidulum* = 16.73) are less than Copeland's (1947) 18 for the genus. Variation between taxa was non-significant at the 95% level.

Spore dimensions

Spore polar and equatorial sizes are summarised on a taxon basis in Table 1. The equatorial mean length and range obtained in this study are similar to those obtained by Harris (1955), who reported a spore diameter of mean = 47 μm; SD = 3; range 41–57 μm; Brown & Brown (1931), also recorded a mean spore diameter of 47 μm (standard deviation and sample size were not recorded). However, their reported range of 28–60 μm extends far lower than those obtained in either this study or that of Harris (1955). This may be a result of the accidental inclusion of immature spores by Brown & Brown (1931).

The two analyses of variance that were carried out, one on spore polar diameter (Table 2) and the other on equatorial diameter (Table 3), show (at the

Table 2 Analysis of variance with unequal sample size; for spore polar dimensions (in μm) measured from *Adiantum hispidulum* (18 plants, 50 spores from each) and *A. pubescens* (3 plants, 50 spores from each). *F* values for *F*α (V1 V2) are from Sokal & Rohlf (1973). Source = source of variation. d.f. = degrees of freedom.

Source	d.f.	Sums of squares	*F* value
Taxa	1	0.00041956	108.050
Plants	19	0.00102669	13.920
Error	1029	0.00399573	
Total	1049	0.00544198	

F 0.05 (1,∞) = 3.84, *F* 0.025 (1,∞) = 5.02, *F* 0.01 (1,∞) = 6.63.

Table 3 Analysis of variance with unequal sample size; for spore equatorial dimensions (in μm) measured from *Adiantum hispidulum* (18 plants, 50 spores from each) and *A. pubescens* (3 plants, 50 spores from each). *F* values for *F*α (V1 V2) are from Sokal & Rohlf (1973). Source = source of variation. d.f. = degrees of freedom.

Source	d.f.	Sums of squares	*F* value
Taxa	1	0.00024525	30.230
Plants	19	0.00082883	5.830
Error	1029	0.00834842	
Total	1049	0.00942249	

F 0.05 (1,∞) = 3.84, *F* 0.025 (1,∞) = 5.02, *F* 0.01 (1,∞) = 6.63.

95% level of significance) that both measurements vary significantly between the two taxa and between individual plants. A Duncan's multiple range analysis for polar diameter (Table 4) and equatorial diameter (Table 5) shows that individual plants of *A. pubescens* form intergrading groups with plants of *A. hispidulum* (i.e., plants C*, A* in both tables). Thus, while collective measurements on a species basis show a significant variation (at 95%) between the two taxa, data from individual plants cannot reliably distinguish two taxa.

Polar equatorial ratio (P:E)

P:E ratios are summarised on a species basis in Table 1. The P:E ratios obtained in this study are consistently higher than that given by Harris (1955). While a polar measurement is not recorded by Harris, one can be calculated as 26 μm (P:E 4.4:8 and assuming E = 47 μm). This is below the range found in this study for either *A. pubescens* (31–42 μm) or *A. hispidulum* (30–43 μm) and may have resulted from inclusion of partially collapsed spores obtained from herbarium samples.

Abnormal spores

The usual spore form for both taxa is trilete; however, very occasionally, smaller tetralete spores have also been found scattered among spores in both taxa. These are discussed in detail in Large & Braggins (1985).

Indumentum description

A. Mature plants: Parris (1980) is accurate in her description of the taxa. *A. hispidulum* has short to medium (63–815 μm) stiff hairs (Fig. 2, 3) comprising one, two, three, and occasionally four cells which are often pigmented. The basal cell of each hair is usually enlarged. Hairs on *A. pubescens* (Fig. 2, 4) are medium to long (251–1003 μm), soft, and comprise 2–4 cells, usually unpigmented. Basal cells are usually not enlarged.

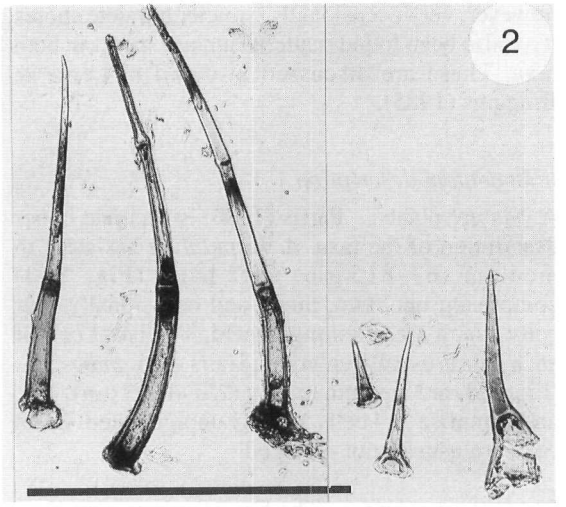
B. Immature plants: The first fronds produced by juvenile plants in both taxa have hairs similar to, but smaller than, those of *A. pubescens*. The hairs that occur on the stipe, rachis, and upper and lower surfaces of the pinnule lamina are soft and usually comprise 2–3 cells devoid of pigmentation. Basal cell enlargement is unusual. As the plant matures, successive fronds show a gradient in hair form towards that characteristic of the adult.

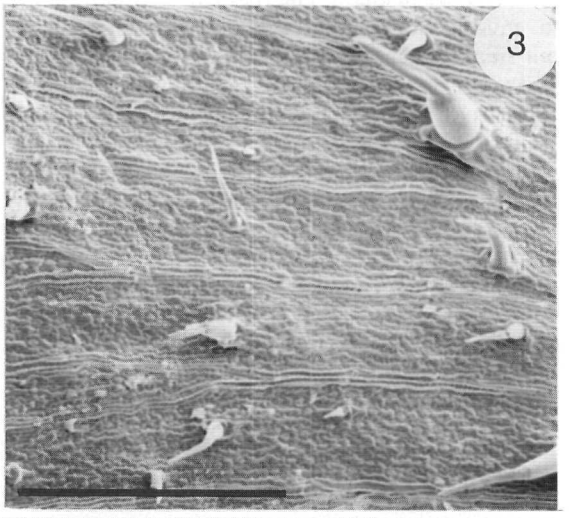
Table 4 Duncan's multiple range test for spore polar diameter (in μm) from *Adiantum hispidulum* (numbers) and *A. pubescens* (letters*). For means with the same letter (at 95%) variation is non-significant. Mean sizes are calculated from a standard sample size of 50 sporangia per plant.

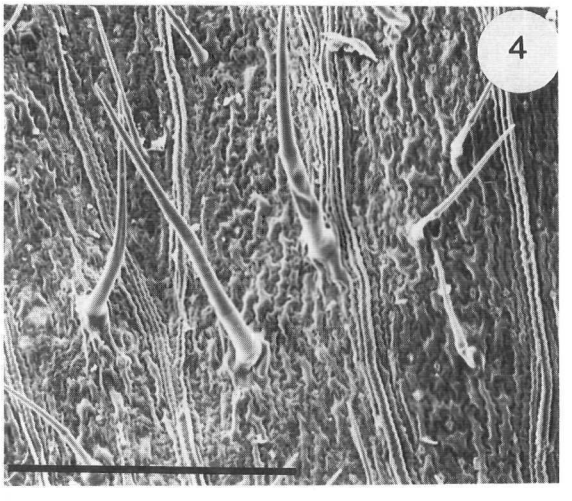
Duncan's grouping	Mean	Plant collection code
A	38.98	E*
B	37.77	3
C	36.48	A*
C D	36.28	4
C D E	36.10	23
C D E F	35.68	14
C D E F	35.66	25
D E F G	35.53	C*
D E F G	35.49	5
E F G H	35.38	19
F G H I J	35.00	6
F G H I J	35.00	24
F G H I J	34.91	15
F G H I J	34.89	16
G H I J K	34.67	18
H I J K	34.51	20
H I J K	34.47	22
I J K	34.28	10
J K	34.23	26

Table 5 Duncan's multiple range test for spore equatorial diameter (in μm) from *Adiantum hispidulum* (numbers) and *A. pubescens* (letters*). For means with the same letter (at 95%) variation is non-significant. Mean sizes are calculated from a standard sample size of 50 sporangia per plant.

Duncan's grouping	Mean	Plant collection code
A	50.95	E*
A B	50.12	19
A B C	49.83	A*
A B C	49.76	18
A B C	49.72	23
B C D	49.43	25
B C D E	49.30	3
B C D E	49.13	16
B C D E F	49.02	24
B C D E F G	48.86	C*
C D E F G H	48.75	20
D E F G H I	48.16	15
D E F G H I	48.14	5
E F G H I	48.05	6
F G H I	47.78	26
G H I	47.59	10
H I	47.43	4
I	47.34	14
I	47.17	22







Hair length

A. Variation with maturity: A pilot study (Large 1984) designed to obtain an ideal sample size for hair length measurement on an individual plant basis, showed that hair length varied between immature and mature fronds of adult plants, and within individual fronds from base to apex. Immature fronds and the tips of mature fronds generally have hairs smaller than those from the central regions of mature fronds. The variation observed in both cases is likely to be age related and can be eliminated by only measuring hairs from central positions on mature spore bearing fronds. The results from this pilot study provided the basis for assessment of the population used in the rest of the study.

B. Ecological variation: An analysis of variance (Table 7) performed on hair size taken from fronds collected in the field and compared (Table 6) with hair measurements taken from fronds of the same plants grown in constant conditions for 3 months, shows that (at the 95% level of significance) variation in hair length is significant between individual plants. However, variation is non-significant between material from the field and that grown in a controlled environment. It appears,

Fig. 2 Detail of hairs. Left-hand side, 2–3 celled hairs of *A. pubescens*. Right-hand side, 1–2 celled hairs of *A. hispidulum* with enlarged basal cell shown at the extreme right. Larger hairs occasionally found on this taxon are similar to but smaller than those shown for *A. pubescens*. Scale 500 μm.

Fig. 3 Pinnule of *Adiantum hispidulum* (SEM, lower surface) showing short to medium (63–815 μm) stiff hairs comprising one, two, three, and occasionally four cells which are often pigmented. The basal cell of each hair is usually enlarged. Scale 500 μm.

Fig. 4 Pinnule of *Adiantum pubescens* (SEM, lower surface) showing medium to long (251–1003 μm) soft hairs comprising 2–4 cells, usually unpigmented. Basal cells are not usually enlarged. Scale 500 μm.

therefore, that hair length is influenced primarily by genetic rather than environmental factors.

C. Intertaxon variation: A summary of the statistics on hair length is given on a species basis in Table 8. The coefficients of variation given in this table are large for both taxa. However, that for *A. pubescens* (28.9) is almost half that for *A. hispidulum* (48.9). An analysis of variance (Table 9) performed on the data showed that (at the 95% level of significance) there is significant variation between taxa and between individual plants. A Duncan's multiple range test for the same data (Table 10) suggests that the plants fall into three groups. Plants of *A. pubescens*, including the lectotype (TP*) and the lectosyntype (GF*), can be found in the first group, which is independent. Specimens of *A. hispidulum* form their own group of intergrading plants, which also includes holotype (TH). Two plants (4 and 28) with hairs of the *A. hispidulum* form (i.e., stiff, often pigmented hairs with enlarged basal cells) comprise the third group. This is independent of, and lies between, the *A. pubescens* and *A. hispidulum* groups.

Hair type can be used to distinguish the two taxa, as can hair length (after allowing for variation with maturity). For example, in the Duncan's multiple range test (Table 10), all plants of *A. pubescens* are separated from plants of *A. hispidulum*, a discontinuity that is maintained even when the confidence interval of ±10% is taken into account. An examination of herbarium material (e.g., AKU 15126, AKU 15127) produced plants with mean hair lengths between those of plants 4 and 10, supporting an association of plant 4 with the main *A. hispidulum* group of plants (10–20). No material was observed with hair sizes between plants E* and 4. While hair length can, in broad terms, be used to distinguish between the two taxa, the overall proportion of the mean represented by variation is high. Because of this variation, the use of hair length as a valid character needs to be based on large samples.

Table 6 Summary statistics for hair size (in μm) measured on the underside of pinnules taken from *Adiantum hispidulum* (plant collection code = numbers) and *A. pubescens* (plant collection code = letters*). Data from field collected material (in italics) is compared to that taken from the same plants when later grown in cultivation. $\bar{x}$, mean; CI, confidence interval; SD, standard deviation; R, range; CV, coefficient of variation. Sample size is 50 measurements from each location.

Collection code		Location	$\bar{x}$	CI	SD	R	CV
E*	*field*	*Whangarei*	*502*	*±50.2*	*155*	*251–815*	*30.9*
	cultivation	glasshouse	499	±49.9	143	251–752	28.6
2	*field*	*Northland*	*290*	*±29.0*	*125*	*125–564*	*43.1*
	cultivation	glasshouse	270	±27.1	110	125–564	40.6
13	*field*	*Auckland*	*288*	*±28.8*	*132*	*125–564*	*45.8*
	cultivation	glasshouse	305	±30.6	129	125–564	42.2
16	*field*	*Auckland*	*271*	*±27.1*	*127*	*125–564*	*46.9*
	cultivation	glasshouse	262	±25.6	115	125–502	44.9
14	*field*	*Auckland*	*268*	*±26.8*	*135*	*125–627*	*50.4*
	cultivation	glasshouse	297	±29.7	135	125–627	45.5
3	*field*	*Northland*	*261*	*±26.1*	*126*	*125–564*	*48.3*
	cultivation	glasshouse	270	±27.8	135	125–627	48.6
6	*field*	*Whangarei*	*258*	*±25.8*	*125*	*125–564*	*48.4*
	cultivation	glasshouse	273	±27.7	129	63–564	46.6
9	*field*	*Auckland*	*237*	*±23.7*	*110*	*125–564*	*46.4*
	cultivation	glasshouse	251	±25.2	117	125–627	46.4
17	*field*	*Auckland*	*231*	*±23.1*	*92*	*125–502*	*39.8*
	cultivation	glasshouse	222	±22.2	96	125–502	43.2
19	*field*	*Coromandel*	*207*	*±20.7*	*78*	*63–439*	*37.7*
	cultivation	glasshouse	211	±21.1	75	125–376	35.5
20	*field*	*Coromandel*	*144*	*±14.4*	*51*	*63–314*	*35.4*
	cultivation	glasshouse	179	±17.9	55	63–314	30.7

Hair density

A. Ecological variation: Hair density results for samples collected from the field and later from the same plants grown under glasshouse conditions are summarised in Table 11. An analysis of variance performed on the data (Table 12) showed that (at the 95% level of significance) there is significant variation between plants and between environments.

Table 7 Two-way analysis of variance with equal sample size; for plants with field and cultivation measurements of hair length. Environment = field versus cultivation. Plants are those listed in Table 6. *F* values for $F\infty$ (V1 V2) are from Sokal & Rohlf (1973). Source = source of variation. d.f. = degrees of freedom.

Source	d.f.	Sums of squares	*F* value
Environment	1	0.440	0.125
Plants	10	1635.565	46.452
Interaction	10	19.900	0.567
Error	1078	3782.200	
Total	1099	5438.105	

F 0.05 (1,∞) = 3.84, F 0.025 (1,∞) = 5.02, F 0.01 (1,∞) = 6.63.

Table 8 Summary statistics for hair size (in μm) measured on the underside of pinnules taken from 26 plants of *Adiantum hispidulum* and six plants of *A. pubescens*. $\bar{x}$, mean; CI, confidence interval; SD, standard deviation; R, range; CV, coefficient of variation; and *N*, sample size.

Taxon	$\bar{x}$	CI	SD	R	CV	*N*
A. hispidulum	266	±26.6	130	63–815	48.9	1300
A. pubescens	547	±54.7	158	251–1003	28.9	300

Table 9 Analysis of variance with unequal sample size; for hair length (in μm) measured from *Adiantum hispidulum* (26 plants, 50 hairs from each) and *A. pubescens* (6 plants, 50 hairs from each). *F* values for $F\alpha$ (V1 V2) are from Sokal & Rohlf (1973). Source = source of variation. d.f. = degrees of freedom.

Source	d.f.	Sums of squares	*F* value
Taxa	1	19.158	1180.990
Plants	30	4.016	8.250
Error	1568	25.436	
Total	1599	48.610	

F 0.05 (1,∞) = 3.84, F 0.025 (1,∞) = 5.02, F 0.01 (1,∞) = 6.63.

Interpretation of the statistics (Table 11) on a plant-to-plant basis, indicates that there is a trend towards decreasing hair density in samples taken from the field grown plants to the glasshouse grown plants. This trend is accompanied by an increase in the amount of variability within plants (as is shown by the coefficients of variation in Table 11). The decrease in hair density (probably caused by the moderation of most climatic factors and increase in temperature that occurs in the glasshouse), is apparent to a greater extent on some pinnules than on others; however, no obvious pattern was observable.

Table 10 Duncan's multiple range test for hair length (in μm) from 26 plants of *Adiantum hispidulum* (numbers) and six plants of *A. pubescens* (letters*). For means with the same letter (at 95%) variation is non-significant. Mean sizes are calculated from a standard sample size of 50 hairs per plant.

Duncan's grouping	Mean	Plant collection code
A	577	F*
A	574	TP*
A	555	GF*
A	549	C*
A B	535	A*
B	499	E*
C	387	4
D E	312	10
D E F	305	13
D E F G	297	25
D E F G	297	14
D E F G	290	24
E F G H	273	29
E F G H	273	6
E F G H I	270	2
E F G H I	270	3
E F G H I	265	5
E F G H I J	265	12
E F G H I J	262	16
E F G H I J K	257	23
F G H I J K	251	9
G H I J K L	244	TH
G H I J K L	240	22
H I J K L	222	17
H I J K L	216	18
I J K L	211	19
J K L	203	26
K L	198	8
L	191	21
L	179	20

B. Intertaxon variation: Hair density is summarised on a taxon basis in Table 13. An analysis of variance for this (Table 14) showed that (at the 95% level of significance) variation is significant between both species and individual plants. However, a Duncan's analysis of variance for this data (Table 15) shows plants of *A. pubescens* (i.e., F* and E*, A* and C*) form intergrading groups with plants of *A. hispidulum.*

In contrast to hair length, where environment has no apparent effect, hair density appears to be influenced by both genetic and environmental factors. In field collected material, unknown environmental effects complicate the assessment of hair density as a character. Even in constant conditions, hair density (for the material studied at least) cannot be used to differentiate between the two taxa, as is shown by the very high variation within this character (see coefficients of variation, Table 13) and the way individual plants of *A. pubescens* are dispersed among plants of *A. hispidulum* (Table 15).

Distribution of hairs

In both taxa, hairs are distributed on the marginal flap of the sorus, on the stipe, rachis, and on the upper and lower surfaces of the pinnule lamina. Hairs on the lamina occur only between and never on the pinnule veins. In all the specimens studied, mean density of hairs (per mm^2) is greater than the variance (i.e., hair distribution is "regular") (Table 13).

Table 11 Summary statistics for hair density (per mm^2) measured on the underside of pinnules taken from *Adiantum hispidulum* (plant collection code = numbers) and *A. pubescens* (plant collection code = letters*). Data from field collected material (in italics) is compared to that taken from the same plants when later grown in cultivation. $\bar{x}$, mean; CI, confidence interval; SD, standard deviation; R, range; CV, coefficient of variation. Sample size is 50 measurements from each location.

Collection code		Location	$\bar{x}$	CI	SD	R	CV
20	*field*	*Coromandel*	*7.90*	*±0.79*	*2.80*	*4.8–11.2*	*35.4*
	cultivation	glasshouse	4.70	±0.47	2.13	1.6–8.0	45.3
19	*field*	*Coromandel*	*6.88*	*±0.68*	*2.18*	*3.2–12.8*	*31.7*
	cultivation	glasshouse	5.44	±0.54	1.81	3.2–9.6	33.3
3	*field*	*Northland*	*6.11*	*±0.61*	*1.81*	*3.2–9.6*	*29.6*
	cultivation	glasshouse	3.36	±0.34	1.33	1.6–4.8	39.6
14	*field*	*Auckland*	*5.31*	*±0.53*	*1.52*	*3.2–9.6*	*28.6*
	cultivation	glasshouse	4.22	±0.42	1.31	1.6–6.4	31.0
E*	*field*	*Whangarei*	*5.15*	*±0.52*	*1.50*	*3.2–8.0*	*29.1*
	cultivation	glasshouse	5.41	±0.54	1.54	3.2–8.0	28.5
2	*field*	*Northland*	*4.96*	*±0.50*	*1.17*	*3.2–6.4*	*23.6*
	cultivation	glasshouse	3.42	±0.34	1.15	1.6–6.4	33.6
4	*field*	*Northland*	*4.54*	*±0.45*	*1.47*	*1.6–8.0*	*32.4*
	cultivation	glasshouse	3.62	±0.36	1.39	1.6–8.0	38.4
A*	*field*	*Northland*	*4.48*	*±0.45*	*1.31*	*1.6–6.4*	*29.2*
	cultivation	glasshouse	3.01	±0.30	1.18	1.6–4.8	39.2
6	*field*	*Whangarei*	*4.42*	*±0.44*	*1.79*	*1.6–9.6*	*40.5*
	cultivation	glasshouse	3.58	±0.36	1.38	<1–6.4	38.5
12	*field*	*Auckland*	*4.29*	*±0.43*	*2.45*	*1.6–6.4*	*57.1*
	cultivation	glasshouse	2.94	±0.29	1.38	1.6–6.4	46.9
7	*field*	*Northland*	*4.10*	*±0.41*	*1.50*	*1.6–6.4*	*36.6*
	cultivation	glasshouse	3.04	±0.30	1.12	1.6–4.8	36.8
13	*field*	*Auckland*	*3.87*	*±0.39*	*1.44*	*1.6–6.4*	*37.2*
	cultivation	glasshouse	2.85	±0.29	1.30	1.6–4.8	45.6
9	*field*	*Auckland*	*3.26*	*±0.33*	*1.47*	*<1–6.4*	*45.0*
	cultivation	glasshouse	2.37	±0.24	1.33	<1–4.8	56.1
17	*field*	*Auckland*	*2.26*	*±0.23*	*1.17*	*<1–4.8*	*51.8*
	cultivation	glasshouse	1.70	±0.17	1.04	<1–3.2	61.2
16	*field*	*Auckland*	*2.56*	*±0.26*	*1.20*	*<1–4.8*	*46.9*
	cultivation	glasshouse	1.66	±0.17	1.10	<1–3.2	66.3

Hair loss

Field (1890) and Cheeseman (1925) have previously reported that hairs normally present on the stipe and rachis are lost with increasing plant maturity. In glasshouse conditions, both taxa retained stipe hairs. However, evidence from plants in the field suggests some do suffer hair loss from the stipe and from the first pinnules of sporeling plants. There is no evidence to suggest hairs are lost from the lamina surfaces or marginal flaps of mature plants.

Paleae

Paleae cover the rhizome and the base of the stipe of young and some old fronds in both taxa. As relatively few specimens in herbaria are complete with these parts, the investigation into their form was based on an examination of live plants. The results show that the nature of the paleae is essentially the same in both taxa, and thus the following descriptions are applicable to either.

Rhizome paleae: The rhizome (which is short, stout, slow creeping, and may be subterranean) is densely covered with paleae 1200–2500 μm long and 270–550 μm wide. The paleae are long and tapering, the maximum width occurring at about one-eighth of the way from the basal end. They are darkly pigmented, one cell thick, have irregularly serrated margins (the serrations are the result of marginal cells projecting slightly beyond adjacent cells), and usually are terminated by one or two cells forming a hair-like tip. Cells of the main body of the paleae are elongate, becoming shorter and isodiametric towards the base. There is a marginal zone of slightly narrower cells.

Stipe paleae: The paleae, which may be lost with increasing age of the frond, are initially present on the lower one-third to two-thirds of the stipe. They are sometimes longer than rhizome paleae and are usually narrower (200–400 μm). Pigmentation also differs. The paleae closest to the lamina are lightly pigmented (yellow gold), whereas those near the base of the stipe are darker (brown) with a light base. The irregular serrated margin of stipe paleae is occasionally less distinct than that of the rhizome paleae. In all other features they are the same.

Table 12 Two-way analysis of variance with equal sample size; for plants with field and cultivation measurements of hair density (per mm^2). Environment = field versus cultivation. Plants are those listed in Table 11. *F* values for *F*α (V1 V2) are from Sokal & Rohlf (1973). Source = source of variation. d.f. = degrees of freedom.

Source	d.f.	Sums of squares	*F* value
Environment	1	41.307	42.210
Plants	14	669.477	48.866
Interaction	14	281.333	20.534
Error	1470		
Total	1499		

F 0.05 (1,∞) = 3.84, *F* 0.025 (1,∞) = 5.02, *F* 0.01 (1,∞) = 6.63.

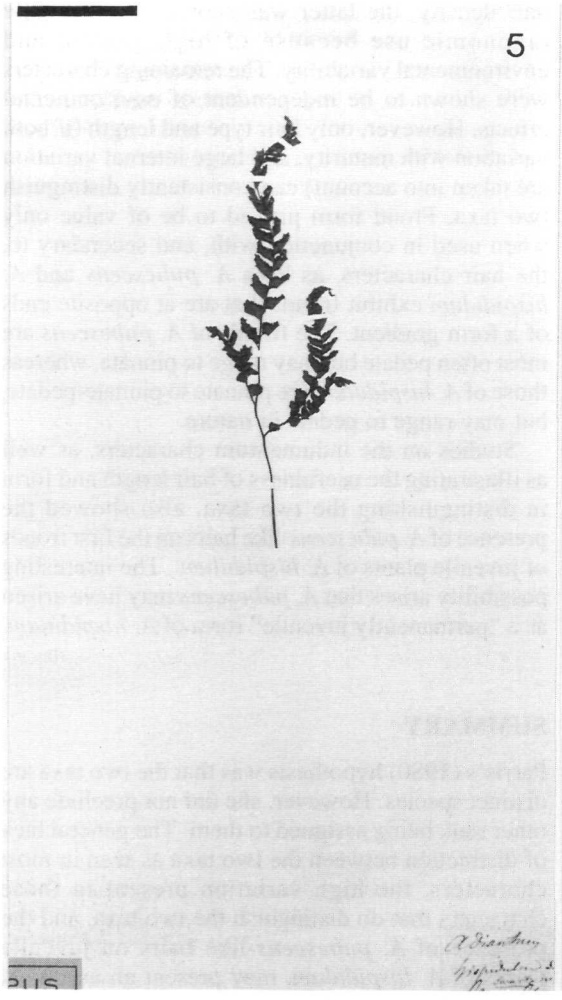
Table 14 Analysis of variance with unequal sample size; for hair density measurements from *Adiantum hispidulum* and *A. pubescens*. Plants are those listed in Table 13. *F* values for *F*α (V1 V2) are from Sokal & Rohlf (1973). Source = source of variation. d.f. = degrees of freedom.

Source	d.f.	Sums of squares	*F* value
Taxa	1	19.158	1180.990
Plants	30	4.020	8.250
Error	1519	3114.240	
Total	1549	5661.433	

F 0.05 (1,∞) = 3.84, *F* 0.025 (1,∞) = 5.02, *F* 0.01 (1,∞) = 6.63.

Table 13 Summary statistics for density (per mm^2) measured on the underside of pinnules taken from 25 plants of *Adiantum hispidulum* and four plants of *A. pubescens*. $\bar{x}$, mean; CI, confidence interval; SD, standard deviation; R, range; CV, coefficient of variation; and *N*, sample size.

Taxon	$\bar{x}$	CI	SD	R	CV	*N*
A. hispidulum	3.364	±0.336	1.874	<1–12.8	55.70	1350
A. pubescens	4.312	±0.431	1.966	1.6–9.6	45.59	200



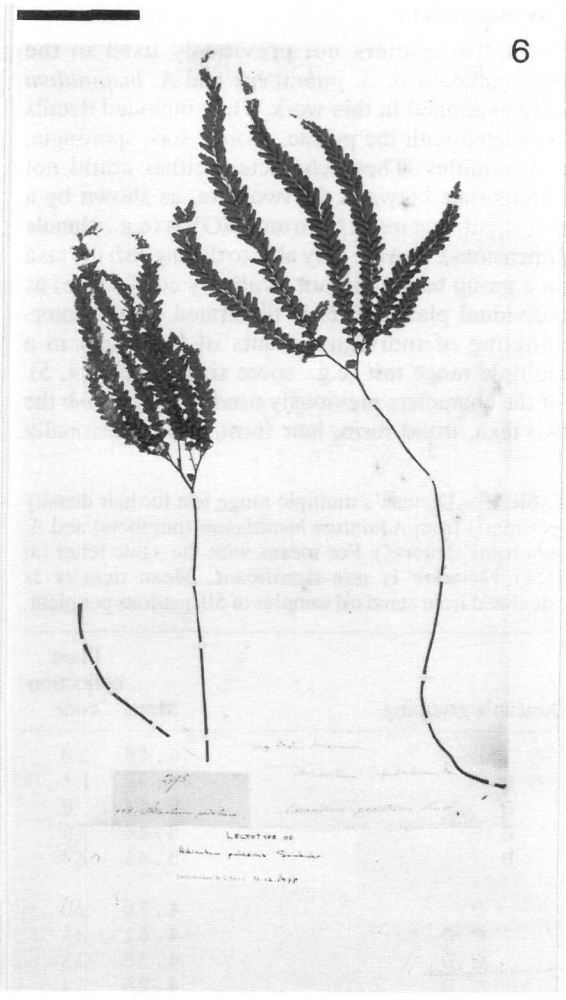


Fig. 5 Holotype specimen of *Adiantum hispidulum* held at the Riksmuseum Stockholm. The label reads "*Adiantum hispidulum* Swartz, Swartz scripsit, N. Holland, herb Swartzii". Scale 10 cm.
Fig. 6 Lectotype specimen of *Adiantum pubescens* selected from George Forsters herbarium at the British Museum by Parris (1980). The label reads "295.458 *Adiantum pedatum*" and is also annotated "*Adiantum hispidulum* Sw. and *Adiantum pedatum* Linn." The larger sheet on which they are mounted is annotated "*Adiantum pubescens* Schkuhr". Scale 10 cm.

GENERAL DISCUSSION

Nomenclature and typification

Adiantum hispidulum Swartz (in Schrader, Journal für die Botanik, 1800 (2): 82 (1801) and Synopsis Filicum 124, 1806) was described from Australian material. It is not known whether a type specimen was designated by Swartz; however, only one specimen (Fig. 5) from Swartz's herbarium, with the title "*Adiantum hispidulum* Swartz", and the locality "N. Holland" is held at Stockholm. In the absence of any other material this specimen has been assumed by Parris (1980) to be the holotype. *A. pubescens* Schkuhr, Kryptogamishe Gewächse 1: 108, tab. 116, 1809, was published as a *nomen novum* for *A. pedatum* Forster f., Prodromus 83, 1786 non Linnaeus (1753). There is no designated type material for *A. pubescens*, but as Schkuhr apparently saw Forster's material of *A. pedatum* and based his description on it, Parris (1980) designated a lectotype (Fig. 6) and syntypes for this material.

The characters

Several characters not previously used in the differentiation of *A. pubescens* and *A. hispidulum* were examined in this work. They included details associated with the paleae, spores, sori, sporangia, and pinnules. These characters either could not differentiate between the two taxa, as shown by a non-significant result from an ANOVA (e.g., pinnule dimensions), or were only able to distinguish the taxa on a group basis, and not (with any confidence) as individual plants. This is illustrated by the intermingling of individual plants of both taxa in a multiple range test (e.g., spore sizes, Tables 4, 5). Of the characters previously used to distinguish the two taxa, frond form, hair form, and occasionally hair density, the latter was shown to be of little taxonomic use because of high genetic and environmental variability. The remaining characters were shown to be independent of environmental effects. However, only hair type and length (if both variation with maturity, and large internal variation are taken into account) can consistently distinguish two taxa. Frond form proved to be of value only when used in conjunction with, and secondary to, the hair characters, as both *A. pubescens* and *A. hispidulum* exhibit fronds that are at opposite ends of a form gradient. The fronds of *A. pubescens* are most often pedate but may range to pinnate, whereas those of *A. hispidulum* are pinnate to pinnate-pedate, but may range to pedate in nature.

Studies on the indumentum characters, as well as illustrating the usefulness of hair length and form in distinguishing the two taxa, also showed the presence of *A. pubescens*-like hairs on the first fronds of juvenile plants of *A. hispidulum* . The interesting possibility arises that *A. pubescens* may have arisen as a "permanently juvenile" form of *A. hispidulum.*

Table 15 Duncan's multiple range test for hair density (per mm^2) from *Adiantum hispidulum* (numbers) and *A. pubescens* (letters*). For means with the same letter (at 95%) variation is non-significant. Mean density is calculated from standard samples of 50 quadrats per plant.

Duncan's grouping	Mean	Plant collection code
A	6.46	18
A B	5.92	F*
B	5.44	8
B	5.44	19
B	5.41	E*
C	4.70	20
C D	4.61	21
C D	4.35	23
C D	4.26	14
C D	4.22	4
D E	4.00	10
E F	3.58	6
E F G	3.42	2
F G	3.36	3
F G H	3.04	A*
F G H	3.04	15
F G H	3.04	7
F G H	3.04	5
F G H I	2.94	12
G H I J	2.88	13
G H I J	2.88	C*
H I J	2.59	22
H I J	2.53	25
H I J	2.50	24
H I J	2.37	9
I J	2.34	29
K L	1.70	17
L	1.66	16
L	1.50	26

SUMMARY

Parris's (1980) hypothesis was that the two taxa are distinct species. However, she did not preclude any other rank being assigned to them. The general lack of distinction between the two taxa as seen in most characters, the high variation present in those characters that do distinguish the two taxa, and the presence of *A. pubescens*-like hairs on juvenile plants of *A. hispidulum*, may present an argument against division at the species level. The possible occurrence of apomixis in the taxa (e.g., Manton & Sledge 1954; Abraham et al. 1962) and the absence of information on living foreign material further complicate the decision as to what level any division should be made. However, the consistent differences in hair morphology that do not overlap between the taxa, and the slight difference in frond form, support some recognition of separate taxa. As there is no geographical or ecological separation of the two taxa in New Zealand that could justify recognition at subspecific level, it is here proposed to recognise Schkuhr's *A. pubescens* as a variety of *A. hispidulum.*

Adiantum hispidulum Swartz var. ***pubescens*** stat. nov.

Synonymous taxa

A. pubescens Schkuhr, Kryptogamishe Gewächse 1: 108, tab. 116, 1809.

A. pedatum Forster f., Prodromus 83, 1786 non Linnaeus (1753).
Lectotype: George Forster's herbarium, BM (Parris 1980).

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