THE SOUTH GEORGIAN SPECIES OF *Acaena* AND THEIR PROBABLE HYBRID

By D. W. H. WALTON *and* S. W. GREENE

ABSTRACT. The taxonomy and variability of the species of *Acaena* occurring on South Georgia have been investigated. The taxon belonging to the *A. magellanica* group has been referred to *Acaena decumbens* (Gaertn.) D. W. H. Walton **comb. nov.** and its relationship to other members of the group in South America and various sub-Antarctic islands has been considered. The validity of treating the second South Georgian taxon, *Acaena tenera* Alboff, as a distinct species has been verified and its relationship to *A. antarctica* Hook. f. and *A. masafuerana* Bitter has been considered. However, *A. microcephala* Schlect. has been shown to be a synonym of *A. antarctica* Hook. f. The characters of the two South Georgian species and of the populations intermediate between them have been defined and the probable hybrid origin of the intermediate plants, referred to *A. decumbens* × *tenera*, is discussed.

Acaena is a characteristically Southern Hemisphere genus with two main centres of variability: New Zealand where there are 13 species (Allan, 1961) and South America where some 28 species have been recognized (Grondona, 1964), although the number of species in South America in particular is likely to be reduced by further revision of taxa described by Reiche (1898) and MacBride (1937). In the New Zealand region a number of species also occur in Tasmania and Australia with one farther north in New Guinea. From South America some species extend into Central America and Mexico while one species is endemic to Hawaii and another to California. A single species is known from South Africa but the genus is represented on most of the sub-Antarctic, southern cool temperate and southern sub-tropical islands by a varying number of taxa, some of which are considered endemic.

Two species have been reported from South Georgia and these were assigned to *Acaena adscendens* Vahl ssp. *georgiae-australis* Bitter and *Acaena tenera* Alboff by Greene (1964), who pointed to the need for nomenclatural revision. Grondona (1964) referred these two taxa to *A. magellanica* (Lam.) Vahl and *A. microcephala* Schlect., respectively. Greene (1964) also reported the occurrence on South Georgia of populations intermediate between the two species.

The present paper reports an investigation into the variability and status of the South Georgian populations of *Acaena* based on field observations carried out during 1967–68 followed by a study of herbarium specimens and material in cultivation. Some material from other areas has also been examined.

TAXONOMY

Acaena decumbens

The first specimen of *Acaena* known to have been collected on South Georgia was obtained during the visit of J. R. and G. Forster on 17 January 1775 when they landed with Captain J. Cook in Possession Bay (Forster and Forster, 1776). This specimen, now in the herbarium of the British Museum (Nat. Hist.), is labelled as follows: "*Ancistrum decumbens*, Insula Georgiae Australis, Oceani Atlantici, J. R. and G. Forster", in what is presumably the handwriting of one of the Forsters. This name was first used in September 1787 by G. Forster in a paper he presented to the Royal Scientific Society of Göttingen but it was not published by him until 2 years later (Forster, 1789). As no description was included, the name must be treated as a *nomen nudum*. The first validly published description bearing this name was provided by Gaertner (1788) and was based on an account of a fruiting head, which was stated to have come from the herbarium of Sir Joseph Banks. Unfortunately no details of the collector or the locality of origin were given but, as it is known that many of the Forsters' specimens became part of the Banks collections, it is possible that the material used by Gaertner came from South Georgia and that the specimen in the British Museum is an isotype. There can be no certainty about this, however, as the holotype, originally at Tübingen, has unfortunately been lost (personal communication from K. U. Leistikow).

The existence of this authentic Forster specimen, together with the validation of Forster's

name by Gaertner, leaves no doubt that the earliest name for this South Georgian species is *Ancistrum decumbens* Gaertn. When transferred to the genus *Acaena* the following new combination is required:

Acaena decumbens (Gaertn.) D. W. H. Walton **comb. nov.**
Basionym: *Ancistrum decumbens* Gaertn. 1788, *De fructibus et seminibus plantarum*, **1**, p. 163, t. 32 (fig. 5).

The genus *Ancistrum* was established by Forster and Forster (1776) based on *Ancistrum anserinifolium*. Lamarck (1791) accepted *Ancistrum* but Vahl (1805) reduced it to a synonym of *Acaena*, a genus originally described by Linnaeus to accommodate the Mexican *Acaena elongata*.

Lamarck (1791) described a species and a variety almost identical to *Ancistrum decumbens* from material collected in Provincia de Magallanes, southern Chile, under the names of *Ancistrum magellanicum* and *Ancistrum magellanicum* var. β, which Vahl (1805) transferred to *Acaena*, *Ancistrum magellanicum* to *Acaena magellanica* and *Ancistrum magellanicum* var. β to his new species *Acaena adscendens*. Vahl also cited an *Ancistrum decumbens* Thunberg as a synonym of *Acaena latebrosa* Aiton, this epithet having been used illegally by Thunberg for a species from South Africa. A little later, Aiton (1810) described material brought back by Thouin, and cultivated at Kew, as *Acaena laevigata* and gave *Ancistrum magellanicum* var. β as a synonym. Hooker (1847) recognized all three species, *A. magellanica*, *A. adscendens* and *A. laevigata*, as well as describing *A. affinis*, *A. macrostemon* and *A. cadilla* which he regarded as closely related. Similar species were described by Gay (1846), Philippi (1860), Alboff (1896) and several other authors, so that by the time Bitter (1911) published his monograph the number of species in the *A. magellanica* group was considerable.

Bitter (1911) referred South Georgian material of *A. adscendens* to an endemic sub-species, ssp. *georgiae-australis* Bitter, which he subdivided into var. *minuscula* Bitter and var. *majuscula* Bitter. Philcox (1962) misunderstood these varieties and misidentified South Georgian material of *A. tenera* as *A. adscendens* ssp. *georgiae-australis* var. *minuscula*. Greene (1964) retained the sub-species but rejected the two varieties, while Moore (1968) considered *A. adscendens* as a synonym of *A. magellanica* and placed the South Georgian plants under that taxon.

Acaena tenera

The occurrence of a second species on South Georgia was not reported until after Skottsberg's visit in 1902, during the Swedish South Polar Expedition of 1901–03 (Skottsberg, 1905). This species, *Acaena tenera* Alboff, had been described by Alboff (1896) for material he collected on Monte Pyramidis, Tierra del Fuego, at around 600 m. (Alboff 233 and 234) and was distinguished by the following characters:

> "Low growing, glabrous and bright green; stem resembling a scape as it is completely unbranched. All leaves radical . . . leaflets ovate-orbicular with membranaceous toothed edge. Fruit with bases of sepals densely covered with sessile glands (manna)."

Skottsberg (1905) provided good accurate illustrations of the South Georgian plants, showing clearly the sessile glands or manna which are unique to this species.

Other species

Although the identity of the South Georgian plants referred to *Acaena decumbens* has been established satisfactorily, it is not yet possible to say how many other taxa of the *A. magellanica* group should be included in this species. This situation exists because successive reviewers of the genus (Citerne, 1897; Reiche, 1898; Duse, 1905; Bitter, 1911; Grondona, 1964) have shown little agreement over synonymy, and it is essential therefore to re-examine critically all nomenclatural types of taxa falling within this group. Grondona (1964), for example, in his review of the genus in Argentina, listed nearly 50 synonyms for *A. magellanica*. Two of the specimens he cited are from South Georgia and there is no doubt that these and other Argentinian material referred to *A. magellanica* should be placed under *A. decumbens*. The same is also true of material from the Falkland Islands, referred by Moore (1968) to *A. magellanica*, and of many specimens from South America, and the sub-Antarctic islands, variously identified as

A. magellanica, *A. adscendens* or *A. laevigata*. A list of specimens from the Falkland Islands and the sub-Antarctic islands now referred to *Acaena decumbens* is given in the Appendix.

The relationship of *Acaena tenera* to several other taxa, variously treated as distinct species or as its synonyms, was investigated, as was Grondona's (1964) suggestion that *A. tenera* should be treated as a synonym of *A. microcephala* Schlect.

Both *A. antarctica* Hook. f. and *A. microcephala* were accepted by Bitter (1911) as distinct species and he distinguished them from *A. tenera* on the basis of their having purplish articulated hairs between the cupules of the fruiting head as well as hairs on the leaflets. The main differences between *A. antarctica* and *A. microcephala* were said to lie in the colour of the leaves and the leaf hairs, *A. antarctica* having in addition aphyllous scapes while those of *A. microcephala* were leafy.

A. antarctica was described by Hooker (1847), who cited a specimen he had collected on Isla Hermite and a specimen from Isla de los Estados collected by Menzies, both of which he reported as sterile. When examining the Menzies specimen at Kew, the presence of a single fruit with purplish articulated hairs at its base was noted. *A. microcephala* was described by Schlectendal (1856) from two collections made by Lechler (2951 and 3029) in 1854 in the Cordillera del Ranco, Chile, isotypes being preserved at Kew. The results of an examination of the holotype of *A. antarctica* and the isotypes of *A. microcephala* are presented in Table I. The presence or absence of a scape bract was the main difference noted between the specimens but as this is known to be an extremely variable and unreliable character in the genus *Acaena* too much weight ought not to be attributed to it. Therefore, on the basis of these results, it is concluded that *A. microcephala* Schlect. should be treated as a synonym of *A. antarctica* Hook. f. and that the latter species is quite distinct from *A. tenera* Alboff. A list of the specimens now referred to *A. antarctica* is given in the Appendix.

TABLE I. COMPARISON OF *A. antarctica* AND *A. microcephala* FROM A STUDY OF TYPE MATERIAL

Character	*A. antarctica*	*A. microcephala*
Leaflets	Very hairy above with long yellow-white hairs, becoming barer with age. Pencillate, though hairs below mainly on veins Mean number 9	More or less hairy above depending on age. Hairs long, whitish. Markedly pencillate though hairs below mainly on veins Mean number 9
Scape	Pilose, bract absent	Pilose, bract usually present
Fruit	4 spines per fruit, each with glochids; fruit 2 mm. long, with purplish articulated hairs at its base Manna absent	4 spines per fruit, each with glochids; fruit 2–3 mm. long, with purplish articulated hairs at its base Manna absent

The relationship of *A. tenera* to *A. masafuerana* Bitter was also investigated. This species was originally described by Bitter (1911) from a sterile collection made by Skottsberg in the Juan Fernandez islands, but later collections allowed this description to be amplified by details of the flowers and fruits (Skottsberg, 1922). Bitter distinguished *A. masafuerana* from *A. antarctica* by the presence of one or two leaves on the scapes and from *A. microcephala* by the hairs on its leaves being more delicate and never yellow.

Leaf, scape and fruiting-head characters determined from type specimens of *A. antarctica* and specimens of *A. masafuerana* (C. & I. Skottsberg 395) preserved in Kew and the British Museum (Nat. Hist.) are compared in Table II with similar characters of South Georgian material of *A. tenera*. *A. masafuerana* possesses some of the characters of the other two species but the differences are considered to be sufficient for each to be retained with specific rank. In appearance, *A. masafuerana* resembles *A. tenera* more than *A. antarctica*.

Grondona (1964), when reducing *A. tenera* to a synonym of *A. microcephala*, quoted a second synonym, *A. pumila* Phil. (non Vahl), a name later changed by Philippi to *A. pearcei* Phil. Reference to the original description of *A. pumila* (Philippi, 1864) shows that it is probably more correctly assigned to *A. antarctica* than to *A. tenera* as it possesses hairy leaves and

TABLE II. COMPARISON OF *A. tenera* FROM SOUTH GEORGIAN MATERIAL WITH *A. antarctica* AND *A. masafuerana* FROM TYPE MATERIAL

Character	*A. tenera*	*A. antarctica*	*A. masafuerana*
Leaf	Bright green above, usually glabrous. Leaflets not pencillate	Dark green above, densely hairy with long yellowish hairs. Leaflets markedly pencillate	Apparently bright green above, sparsely hairy. Leaflets slightly pencillate
Scape	Glabrous with 1 or 2 leaf-like bracts	Densely pilose, often with leaf-like bracts	Almost glabrous with 1 or 2 leaf-like bracts
Fruiting head	Articulated hairs absent Golden-yellow subsessile glands (manna) present at base of cupules	Brown to purple articulated hairs present at base of cupules. Manna absent	Brown to purple articulated hairs present at base of cupules. Manna absent

brownish articulated hairs at the base of the cupule. As Philippi's type has not yet been examined, no final decision on its status is possible.

A. tenera is with certainty only known from South Georgia and Tierra del Fuego, and appears to be quite rare in the latter region (personal communication from D. M. Moore). The single specimen reported by Skottsberg (1916) from the Lago Nahuelhuapi region of Andean Patagonia has not been examined, but the identity of a specimen collected by Goodall (714) on Isla Grande, preserved in the herbarium of the University of Leicester, has been confirmed. The species is distinguished by its bright green glabrous leaves, glabrous scape and the presence of golden-yellow subsessile glands (manna) at the base of the fruits. *A. masafuerana* Bitter is, so far as is known, restricted to the Juan Fernandez islands and is distinguished by its bright green, slightly pencillate leaves, sparsely hairy scape and the presence of brown to purple articulated hairs at the base of the fruits. *A. antarctica* Hook. f. (including *A. microcephala* Schlect. and probably *A. pumila* Phil. non Vahl = *A. pearcei* Phil.) occurs in the Falkland Islands, Tierra del Fuego, Patagonia and Chile. It is distinguished by its dark green leaves which are usually covered with long yellowish hairs, a densely hairy scape and the presence of brown to purple articulated hairs at the base of the fruits.

MORPHOLOGICAL VARIATION

Characters investigated

A field study of *Acaena* on South Georgia during 1967–68 readily confirmed the report by Greene (1964) of the presence of populations with characteristics intermediate between those of *A. decumbens* and *A. tenera*. Following a preliminary examination, a number of characters were selected for detailed study to assess the variation shown by the two taxa and the intermediate plants designated *A. decumbens*×*tenera*. Most of the scoring was carried out on herbarium specimens, many collected specifically for the purpose, and was supplemented by observations on living material in cultivation at Birmingham; field data were used for some characters.

In all, 70 collections from South Georgia were fully analysed; a further 100 specimens, mainly of *A. decumbens*, from other sub-Antarctic islands, the Falkland Islands and southern South America were partially analysed. The characters of leaf, scape and capitulum were investigated as follows:

Leaf

a. Length of largest leaf from base of stipule to top of terminal leaflet.
b. Maximum width of largest leaf.
c. Length of terminal leaflet on largest leaf from base of petiolule to top of leaflet.
d. Pilosity, as very hairy, moderately hairy, sparsely hairy or not hairy.
e. Distribution of hairs on each surface of leaf.
f. Colour, using fresh material only.

TABLE III. COMPARISON OF CHARACTERS OF *A. decumbens*, *A. decumbens* × *tenera* AND *A. tenera*

Character	*A. decumbens*	*A. decumbens* × *tenera*	*A. tenera*
Leaf			
Normal number of leaflets	11–13	11–13	11–13
Position of widest point	$\frac{1}{3}$ length from apex	$\frac{1}{3}$ length from apex	$\frac{1}{4}$ length from apex
Length of largest leaf (cm.)	2·5–15·0	2·0–15·0	2·0–11·5(–13·5)
Mean length/breadth ratio of largest leaf	2·84 (σ = 0·51)	3·65 (σ = 0·81)	3·79 (σ = 0·77)
Mean length of terminal leaflet on largest leaf (cm.)	1·5	1·1	0·6
Colour	Glaucous	Intermediate between glaucous and bright glossy green	Bright glossy green
Pilosity	Very to sparsely hairy usually on lower surface	Sparsely hairy on tips of leaflets	Hairs absent
Scape			
Position	Terminal	Terminal	Axillary
Length (cm.)	4·0–18·5(–26·5)	4·2–12·0	1·2–12·5
Pilosity	Slightly hairy when young	Slightly hairy when young	Slightly hairy when young, glabrous when mature
Bract	Frequently present	Normally present	Normally present
Axillary flowers	Frequently 1, persisting on drying	Frequently 2 or more, persisting on drying, with or without secondary capitula	Normally 1, falling on drying
Capitulum			
Diameter (in fruit including spines) (cm.)	2·0–3·1	1·1–1·5	0·6–0·9
Length of fruit (including spines) (mm.)	8·0–15·0	3·0–5·5	2·0–3·5
Number of fruits per head	54–146 ($\bar{x}$ = 90)	33–57 ($\bar{x}$ = 43)	20–26 ($\bar{x}$ = 23)
Stigma type	X	Y	Z
Length of stigma (mm.)	5–[illegible]4)	1·2–2·8 ($\bar{x}$ = 1·97)	0·8–1·4 ($\bar{x}$ = 1·04)
Stigma length/breadth ratio	3·86 (σ = 0·79)	1·56 (σ = 0·21)	1·08 (σ = 0·11)
Anther length/breadth ratio	1·18 (σ = 0·48)	0·94 (σ = 0·14)	0·69 (σ = 0·07)
Sepal length (mm.)	1·9–4·6	1·5–3·1	1·1–1·8
Sepal width (mm.)	0·8–1·7	0·7–2·0	0·6–1·2
Sepal length/breadth ratio	2·63 (σ = 0·50)	1·97 (σ = 0·26)	1·86 (σ = 0·06)
Normal number of spines per fruit	4(3–6)	4 (variable)	4
Glochids	Present	Present	Present
Manna	Absent	Absent	Present

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Scape

a. Position, whether axillary or terminal.
b. Presence or absence of bract.
c. Presence or absence of flowers or secondary capitula in axil of bract.
d. Length of scape from point of attachment of second leaf to base of capitulum.
e. Pilosity, as presence or absence of hairs.

Capitulum

a. Position, whether axillary or terminal.
b. Diameter in fruit, including spines.
c. Length of fruit, including spines.
d. Number of fruits per head.
e. Stigma type, as X, Y, Z or XY (Fig. 1).
f. Stigma length.
g. Stigma breadth.
h. Dehisced anther length.
i. Dehisced anther breadth.
j. Sepal length.
k. Sepal breadth.
l. Normal number of spines per fruit.
m. Presence or absence of glochids.
n. Presence or absence of manna.

Floral characters were examined microscopically after soaking in 30 per cent ethanol for 30 min. followed by mounting in gum chloral and drying on a slide for at least 24 hr. The occurrence of three stigma types was noted in South Georgian material (Fig. 1), type "X"

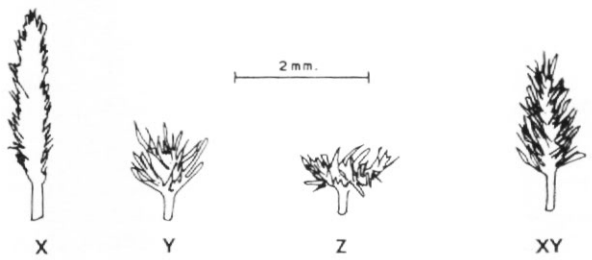

Fig. 1. Stigma type in the genus *Acaena*. For further explanation see text.

being longer than broad, type "Y" having length and breadth more or less equal, while in type "Z" the width was greater than the length. Type "X" stigmas were finely laciniate while types "Y" and "Z" were coarsely laciniate. In some material from Tierra del Fuego, a fourth stigma type, designated "XY" was found, resembling type "X" in length but type "Y" in laciniation.

In the leaf

The results of the various scorings carried out on the South Georgian material of *A. decumbens*, *A. tenera* and *A. decumbens* × *tenera* are summarized in Table III.

Much variation in leaf dimensions was noted and, although the number of leaflets per mature leaf was similar in each taxon, it can be seen from Table III that the length of the terminal leaflet on the largest leaf proved greatest in *A. decumbens* and least in *A. tenera*, *A. decumbens* × *tenera* being intermediate. A typical leaf outline for each taxon is given in Fig. 2.

Differences in leaf colour were quite striking and provide one of the best field characters for separating the taxa but unfortunately they cease to be visible in herbarium material. Both

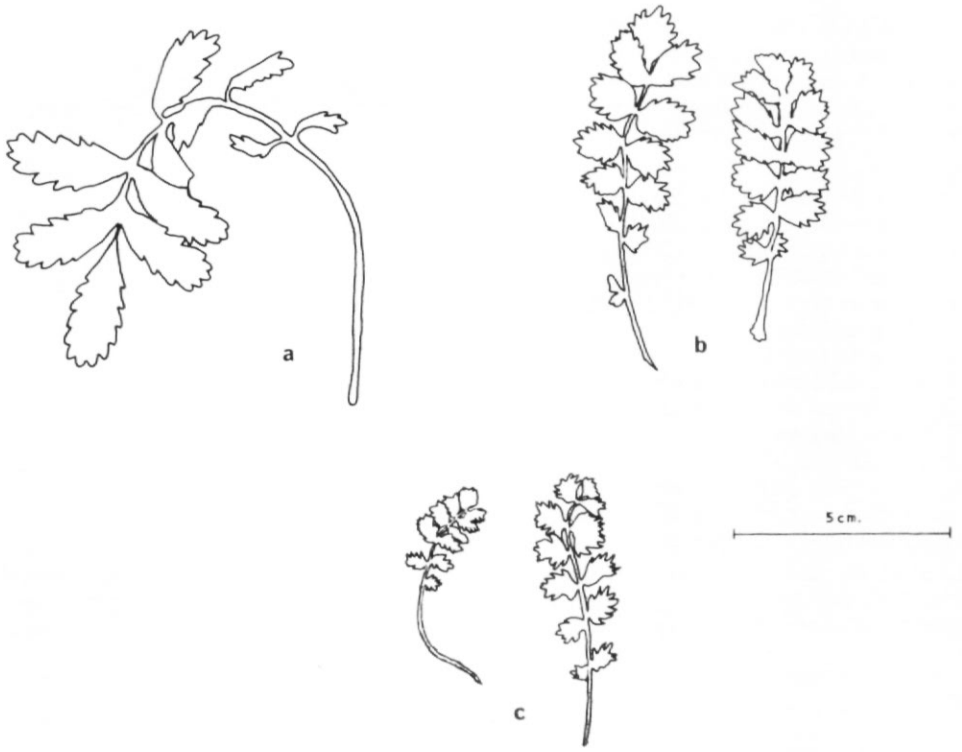

Fig. 2. Leaf outlines of (a) *A. decumbens*, (b) *A. decumbens* × *tenera* and (c) *A. tenera* from South Georgian material.

A. decumbens and *A. tenera* have red-tipped marginal dentations to the leaflets but a noticeable feature of *A. tenera* was that a few young leaves on many plants were completely red. Although intermediate in colour between the other two taxa, the leaves of *A. decumbens* × *tenera* are more like those of *A. decumbens*.

Considerable differences were also observed in the pilosity of leaves, even within a single plant. In *A. decumbens*, for example, young leaves tended to be much hairier than mature leaves, although in both young and old leaves a complete range from densely pilose to sparsely hairy was found; none was glabrous. Hairs were mostly restricted to the lower surface and were further confined to the veins in sparsely hairy leaves. When hairs occurred on the upper surface they were usually situated near the marginal dentations. In contrast to *A. decumbens*, the leaves of *A. tenera* were glabrous; only very exceptionally were a few hairs noted on the veins on the underside of the leaves. In the sparsely hairy leaves of *A. decumbens* × *tenera*, hairs were confined to the tips of the leaflets in the mature leaf.

In the scape

The scape in *A. decumbens* and *A. decumbens* × *tenera* was found to be terminal but axillary in *A. tenera*. In all three taxa, its length (Table III) was somewhat variable and appeared to be controlled by environmental conditions. Young scapes of all three taxa were found to be regularly slightly hairy but only in *A. tenera* were the mature scapes consistently glabrous. In *A. decumbens*, a single bract was frequently present, often with a single flower in its axil; only very rarely was more than one flower noted. Table IV gives the figures obtained from an analysis of 300 fruiting scapes. The rudimentary flowers usually developed normally at first, but shrivelled and died without maturing. During the field work, a single bract was noted in

TABLE IV. DISTRIBUTION OF BRACTS AND AXILLARY FLOWERS IN 300 SCAPES OF *Acaena decumbens*

Condition	*Percentage*
Scapes with bracts	78
Scapes with a rudimentary flower in axil of bract	51
Scapes with a fully developed flower in axil of bract	11

about 90 per cent of *A. tenera* scapes and the majority of these had a single flower in the axil, no bract being found with two or more axillary flowers. However, the axillary flower readily falls on drying and is, therefore, usually absent in herbarium material. Greater variability was shown by *A. decumbens* × *tenera*, one or two bracts being regularly present on the scape with two or more flowers normally present in each axil, although they were often replaced by a stalk bearing a secondary capitulum. One South Georgian specimen was found with ten single flowers, each in the axil of a separate bract, spirally arranged down the scape from the base of the capitulum.

In the capitulum

A single terminal capitulum is the normal arrangement in *A. decumbens* and *A. tenera*, only a few South Georgian plants of the former species having been found with secondary axillary capitula. In contrast, secondary capitula normally arise from the axils of the scape bracts and occasionally from the upper leaves in *A. decumbens* × *tenera* and are one of its most characteristic features.

A. decumbens was the largest of the three taxa in respect of size of capitula and fruit, and it had the greatest number of flowers (and consequently fruits) per capitulum, while *A. tenera* had the smallest capitula and fruits with the least number of flowers (and consequently fruits) per head (Table III). *A. decumbens* × *tenera* was intermediate in size although the secondary heads were normally smaller than the main head, frequently over-topping it when full grown, but inevitably a little behind in development.

The differences in the three types of stigma are well reflected in their length and breadth measurements (Table III). It may be noted that the shortest and longest stigmas in *A. decumbens* were invariably associated with dioecious heads, the shortest occurring in male and the longest in female flowers, the normal range in hermaphrodite heads being from 2·1 to 4·7 mm.

Dioecious heads were found fairly frequently in material of *A. decumbens* from South Georgia, and field observations suggest that there is a tendency for normal hermaphrodite heads to be replaced by predominantly female heads as the season advances. Predominantly male heads were never as common as female heads at any time in the season. The normal "X" type stigma was present in the female heads but it was usually longer than in hermaphrodite flowers. The anthers retained their normal proportions but were larger in hermaphrodite heads (Table V); a varying number had aborted.

TABLE V. MEAN STAMEN LENGTH IN FEMALE AND HERMAPHRODITE HEADS OF *Acaena decumbens*

Type of head	*Number of heads*	*Mean stamen length in each* (mm.)
Female	4	0·93, 0·43, 0·68, 0·65
Hermaphrodite	4	6·73, 7·40, 6·97, 5·57

In all three taxa, it was found that the normal number of spines per fruit was four, each bearing terminal glochids. However, the number of spines per fruit was rather variable in

A. decumbens × *tenera*, while in *A. decumbens* fruits with between three and six spines have been seen. The upper parts of the ripe fruits in *A. tenera* were normally glabrous, but long white hairs were often found between the base of the spines in *A. decumbens* and in *A. decumbens* × *tenera*.

A. tenera was the only taxon to have manna present on the sides of the fruit.

The relationships between some of the characters are illustrated graphically in Figs. 3–5. These figures further emphasize that *A. decumbens* × *tenera* is intermediate between the other two taxa, with characters sometimes approaching one taxon more than the other. They also show that *A. decumbens* is, in some respects, more variable than *A. tenera*.

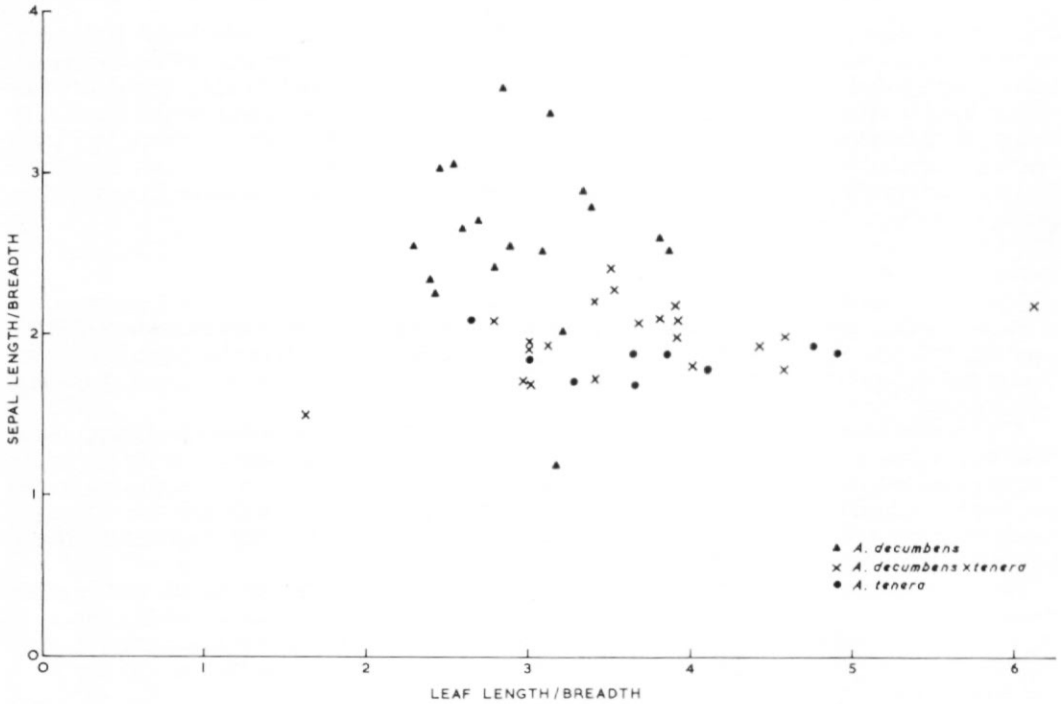

Fig. 3. Relationship between length/breadth of leaves and length/breadth of sepals in South Georgian populations of *Acaena*.

Pollen and Seed Viability

Pollen viability was studied in material in cultivation by staining anther squashes in cotton blue and lactophenol using anthers from three heads each for *A. decumbens*, *A. tenera* and *A. decumbens* × *tenera*. High values were obtained for *A. decumbens* and *A. tenera*, with means of 95 and 93 per cent, respectively, but for *A. decumbens* × *tenera* the mean was only 52 per cent.

A number of germination tests on seeds collected on South Georgia was carried out in Birmingham at 20° C in the light and gave values of 40–80 per cent for *A. decumbens*, 50–95 per cent for *A. tenera* but less than 5 per cent for *A. decumbens* × *tenera*.

Descriptions of South Georgian Taxa

Descriptions of *A. decumbens* (under the name of *A. adscendens* ssp. *georgiae-australis*) and of *A. tenera* as they occur on South Georgia were provided by Greene (1964). However, no description is yet available for the group of intermediate plants here referred to *A. decumbens* × *tenera* and it is primarily to facilitate their recognition that the following brief comparative notes are provided. A list of the specimens referred to each taxon is given in the Appendix.

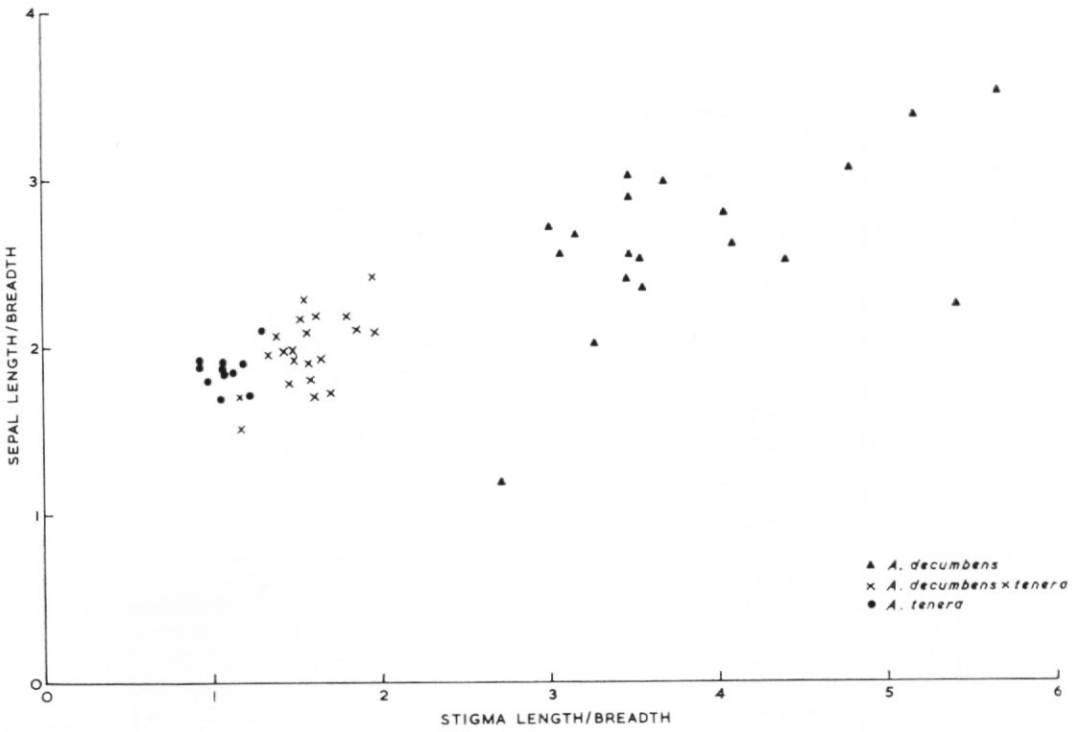

Fig. 4. Relationship between length/breadth of stigmas and length/breadth of sepals in South Georgian populations of *Acaena*.

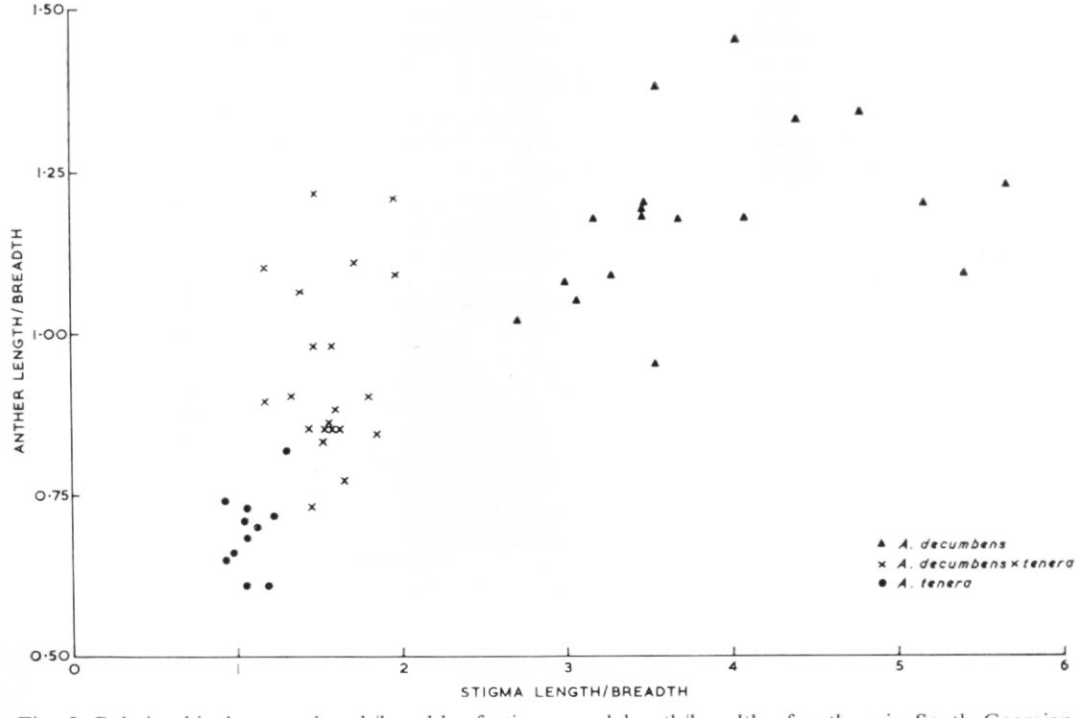

Fig. 5. Relationship between length/breadth of stigmas and length/breadth of anthers in South Georgian populations of *Acaena*.

Acaena decumbens (Gaertn.) D. W. H. Walton

Leaves glaucous, sparsely to very hairy mostly on lower surface, widest one-third of length from apex. Scape terminal, with terminal capitulum frequently bearing a bract with often 1, rarely more, axillary flowers, which persist on drying. Capitulum *c.* 2–3 cm. diameter (in fruit including spines), hermaphrodite or dioecious, stigma 1·5–5·1 mm. long, very much longer than broad, finely laciniate, with 54–146 fruits each lacking manna at the base.

Acaena decumbens × *tenera*

Leaves intermediate in colour between glaucous and bright glossy green, sparsely hairy on tips of leaflets, widest one-third of length from apex. Scape terminal, with larger terminal and normally at least 1 smaller lateral capitulum, normally bearing 1 or 2 bracts with, frequently, secondary capitula or 2 or more axillary flowers which persist on drying. Capitulum 1·1–1·5 cm. diameter (terminal, in fruit including spines), hermaphrodite, stigma 1·2–2·8 mm. long, ± isodiametric, coarsely laciniate, with 33–57 fruits each lacking manna at the base.

Acaena tenera Alboff

Leaves bright glossy green, glabrous, widest one-quarter of length from apex. Scape axillary, with terminal capitulum, normally bearing a bract with usually 1 axillary flower which falls on drying. Capitulum < 1 cm. diameter (in fruit including spines), hermaphrodite, stigma 0·8–1·4 mm., broader than long, coarsely laciniate, with 20–26 fruits each bearing manna at the base.

Distribution on South Georgia

Fig. 6 provides the detailed distribution, based on presence or absence in each 5 km. square of the South Georgian grid, of both *A. decumbens* and *A. tenera* as known at present on South Georgia. The new records given by Greene (1969) are included. It can be seen that *A. decumbens* occurs in 63 squares and *A. tenera* occurs in 53 squares, i.e. respectively almost 27 and 23 per cent of the 234 squares with land.

There are 12 squares containing *A. decumbens* which are not known to contain *A. tenera*, although only three contain the latter but not the former. Field experience suggests that *A. decumbens* is likely to be found in most of the squares with snow- and ice-free coastal land below 200 m. and that the final distribution of *A. tenera* could be as extensive.

Fig. 6 also shows the known distribution of *Acaena decumbens* × *tenera*. Although the latter has only so far been recorded from 15 squares, i.e. 6 per cent of the total possible, it is seriously under-recorded as mapping was only begun during 1967–68.

Variation in Extra-South Georgian Material

No comparisons were possible of the relative variability of *A. tenera* between South America and South Georgia, owing to the shortage of specimens from the former region. However, some information and figures are available for *A. decumbens*, resulting from the examination of specimens considered by the authors to be close to or identical with *A. decumbens* as it occurs on South Georgia.

Figures for leaf length/breadth ratios are presented in Table VI and it can be seen that there is no significant difference in the mean values between the geographical areas, although the range is slightly greater in Argentina than elsewhere. Material from Macquarie Island, Archipel de Kerguelen and Tierra del Fuego showed a similar degree of leaf and scape pilosity to that noted in South Georgian plants, but some collections from Chile and Argentina were often densely pilose on leaf and scape. A few Falkland Islands plants were seen with rather small leaves and it is thought likely that these may prove to be distinct ecotypes (personal communication from D. M. Moore).

Some variation was noted in the shape and composition of capitula. For example, some plants from the Falkland Islands had cylindrical rather than spherical capitula. Female heads were occasionally noted in material from Chile, Argentina, Tierra del Fuego, the Falkland Islands, Archipel de Kerguelen and Marion Island, but no evidence of dioecy was seen in specimens from Heard or Macquarie Islands.

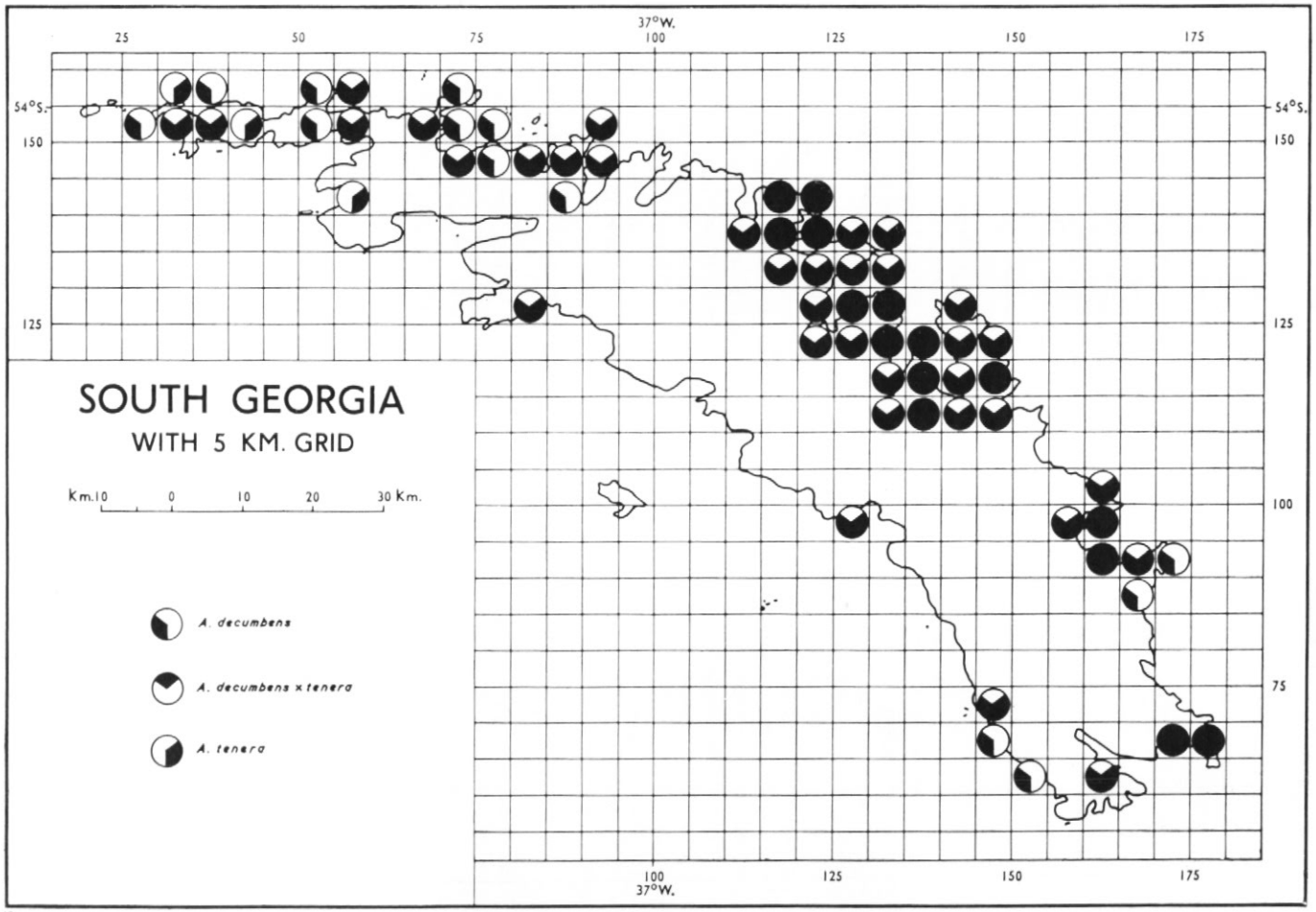

Fig. 6. The known distribution on South Georgia, by 5 km. squares, of *A. decumbens*, *A. decumbens* × *tenera* and *A. tenera*.

TABLE VI. LEAF LENGTH/BREADTH RATIO OF LARGEST LEAVES IN *Acaena decumbens* FROM DIFFERENT GEOGRAPHICAL AREAS

	Number of collections	*Range*	*Mean*
South Georgia	22	1·72–3·86	2·84 ($\sigma = 0·51$)
Other sub-Antarctic islands	13	2·14–3·86	2·98 ($\sigma = 0·77$)
Tierra del Fuego	17	2·46–4·00	3·04 ($\sigma = 0·95$)
Chile	10	1·96–3·93	2·91 ($\sigma = 0·62$)
Argentina	14	1·78–4·50	3·12 ($\sigma = 0·65$)

Type "X" stigmas were the commonest in specimens from Argentina and Chile but some material from Tierra del Fuego had, in addition, stigmas of type "XY". Moreover, these shorter "XY" type stigmas appeared to be associated with smaller anthers, a sample of 72 anthers from eight collections giving a mean anther length/breadth ratio of 0·89 ($\sigma = 0·20$) with a range in length of 0·75–1·18 mm. compared with the normal South Georgian length range of 0·90–1·45 mm. and ratio mean of 1·18 ($\sigma = 0·48$).

In general, it can be said that the material of *A. decumbens* from other sub-Antarctic islands and the Falkland Islands showed a closer similarity to South Georgian specimens than did many of the collections from Tierra del Fuego and South America. Specimens from Macquarie Island, in particular, were found not to differ in any important respect from South Georgian material in spite of the doubts expressed by Skottsberg (1915). Furthermore, as plants from Macquarie Island have been shown to have the same chromosome number as those from South Georgia (Moore, 1960; Moore and Walton, 1970), all the Macquarie Island specimens have been referred to *A. decumbens*. But in view of the variability of plants from parts of South America, it is impossible to determine whether they belong to one or more taxa until a thorough cytotaxonomic investigation has been undertaken.

DISCUSSION

From the evidence presented on the South Georgian plants provisionally named *A. decumbens* × *tenera*, it is clear that they have morphological characteristics intermediate between *A. decumbens* and *A. tenera*, although in some characters approaching one species more closely than the other. This is entirely consistent with their presumed hybrid origin and, since the range of variation is at times high, it is reasonable to suggest that more than F_1 hybrids are represented. The production of viable pollen and the capacity of a small amount of seed to germinate, admittedly under culture conditions, suggest that breeding populations may be maintained at a low level. The capacity for vegetative survival is, of course, high in plants with an extensive rhizome system. The cytological evidence provided by Moore and Walton (1970) is also consistent with a hybrid origin, all counts on South Georgian material being $2n = 42$. However, some doubt must remain about the status of this intermediate group until the results are known of attempts to cross *A. decumbens* with *A. tenera* and to back cross *A. decumbens* × *tenera* with its putative parents.

The occurrence of hybrids between the two species in other parts of their range is unknown and indeed natural hybridization elsewhere in the genus has only been reported between some species in New Zealand (Allan, 1961). Grondona (1964) in fact makes reference to the non-occurrence of hybridization between *A. magellanica* and *A. ovalifolia* in South America, a fact which has been confirmed by D. M. Moore (personal communication). Hybridization has not been reported either between *A. decumbens* or *A. minor* where they occur together on Macquarie Island. From present knowledge of the distribution of *A. tenera* in South America, hybrids between it and *A. decumbens* could be expected in Tierra del Fuego in the mountains to the east of Ushuaia, but even here hybridization may not be possible since only *A. decumbens* with $2n = 84$ is as yet known from southern South America (Moore, 1960; Moore and Walton,

1970). The results of a cytotaxonomic investigation of *Acaena* in this part of Tierra del Fuego would, therefore, be of particular interest as it might help to throw light on the origins of the South Georgian species.

Although the identity of the two species of *Acaena* on South Georgia now appears to have been established satisfactorily, and a sound basis laid for a study of their distribution within the island, further work on their relationship to other taxa is necessary before their world distribution can be stated with certainty. Indeed, in the case of *A. decumbens* it is clear that a thorough re-examination of all the nomenclatural types of the *A. magellanica* group, as well as a thorough cytotaxonomic study of living plants, particularly from South America, is necessary before the taxonomy of this group can be put on a sound basis.

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REFERENCES

AITON, W. T. 1810. *Hortus Kewensis, or a catalogue of the plants cultivated in the Royal Botanic Gardens at Kew by the late William Aiton. Vol. 1.* 2nd edition. London, Longman, Hurst, Rees, Orme and Brown.

ALBOFF, N. 1896. Contributions à la flore de la Terre de Feu. II. Enumération des plantes du Canal de Beagle et de quelques autres endroits de la Terre de Feu. *Revta Mus. La Plata*, **7**, Pt. 2, 355–92.

ALLAN, H. H. 1961. *Flora of New Zealand. Vol. 1.* Wellington, Government Printer.

BITTER, G. 1911. Die Gattung *Acaena*. Vorstudien zu einer Monographie. *Bibliothca bot.*, **17**, Ht. 74, 1–336.

CITERNE, P. 1897. Du genre *Acaena*. *Rev. Sci. nat. Ouest*, **7**, No. 1, 21–24; No. 2, 33–44.

DUSE, E. 1905. Revisione delle *Acaena* degli erbari di Firenze, Roma e Monaco. *Nuovo G. bot. ital.*, Ser. 2, **12**, No. 3, 349–62.

FORSTER, G. 1789. Fasciculus plantarum magellanicarum. *Comment. Gotting.*, **9**, 13–45.

FORSTER, J. R. *and* G. FORSTER. 1776. *Characters generum plantarum quas in itinere ad insulas maris australis, collegerunt, descripserunt, annis 1772–1775.* London, B. White, T. Cadell and P. Elmsley.

GAERTNER, J. 1788. *De fructibus et seminibus plantarum, accedunt seminum centuriae quinque priores. Vol. 1.* Stuttgart, Academiae Carolinae.

GAY, C. 1846. Flora chilena. (*In* GAY, C. *Historia fisica y politica de Chile: Botanica. Vol. 2.* Paris, en casa del autor; Chile, Museo de Historia Natural de Santiago.)

GREENE, S. W. 1964. The vascular flora of South Georgia. *British Antarctic Survey Scientific Reports*, No. 45, 58 pp.

————. 1969. New records for South Georgian vascular plants. *British Antarctic Survey Bulletin*, No. 22, 49–59.

GRONDONA, E. 1964. Les especies argentinas del género "Acaena" ("Rosaceae"). *Darwiniana*, **13**, Nos. 2–4, 208–342.

HOOKER, J. D. 1847. *The botany of the Antarctic voyage. Vol. I. Flora Antarctica. Pt. 2. Botany of Fuegia, The Falklands, Kerguelen's Land, etc.* London, Reeve Brothers, 209–574.

LAMARCK, J. B. 1791. *Tableau encyclopédique et méthodique des trois règnes de la nature: botanique, première livraison. Vol. 1.* Paris, Chez Panckouche.

LANJOUW, J. *and* F. A. STAFLEU. 1964. Index herbariorum. Pt. 1. The herbaria of the world. 5th edition. *Regnum veg.*, **31**, 1–251.

MACBRIDE, J. F. 1937. Flora of Peru. Part II, No. 2. *Publs Field Mus. nat. Hist.*, Botanical series, Ser. 5, **13**, Pt. 2, 257–661.

MOORE, D. M. 1960. Chromosome numbers of flowering plants from Macquarie Island. *Bot. Notiser*, **113**, No. 2, 185–91.

———. 1968. The vascular flora of the Falkland Islands. *British Antarctic Survey Scientific Reports*, No. 60, 202 pp.
———. *and* D. W. H. WALTON. 1970. Chromosome numbers of *Acaena* from South Georgia. *British Antarctic Survey Bulletin*, No. 23, 101–02.
PHILCOX, D. 1962. Recent records for the flora of South Georgia. *Kew Bull.*, **16**, No. 2, 243–45.
PHILIPPI, R. A. 1860. *Reise durch die Wueste Atacama auf Befehl der chilenischen Regierung im Sommer 1853–54 unternommen und beschrieben*. Hall, Eduard Anton.
———. 1864. Plantarum novarum chilensium. *Linnaea*, **33**, Ht. 1, 1–128.
REICHE, C. 1898. *Flora de Chile. Vol. 2*. Santiago de Chile, Cervantes.
SCHLECTENDAL, D. F. L. 1856. Plantae lechlerianae. *Linnaea*, **28**, Ht. 3–4, 463–546.
SKOTTSBERG, C. J. F. 1905. Die Gefässpflanzen Südgeorgiens. *Wiss. Ergebn. schwed. Südpolarexped.*, Bd. 4, Lief. 3, 1–12.
———. 1915. Notes on the relations between the floras of subAntarctic America and New Zealand. *Pl. Wld*, **18**, No. 5, 129–42.
———. 1916. Die Vegetationsverhältnisse längs der Cordillera de los Andes S. von 41°S. *K. svenska VetenskAkad. Handl.*, **56**, Ht. 5, 1–366.
———. 1922. The phanerogams of the Juan Fernandez islands. (*In* SKOTTSBERG, C., *ed. The natural history of Juan Fernandez and Easter Island. Vol. 2*. Botany, Pt. 2. Uppsala, Almquist and Wiksells, 95–240.)
VAHL, M. H. 1805. *Enumeratio plantarum vel ab aliis, vel ab ipso observatarum, cum earum differentiis specificis, synonymis selectis et descriptionibus succinctis. Vol. 1*. Köbenhavn, J. H. Schubothe.

APPENDIX

DETAILS OF THE SPECIMENS DETERMINED AS *Acaena antarctica*, *A. decumbens*, *A. decumbens* × *tenera* AND *A. tenera* TOGETHER WITH THE HERBARIA† WHERE THEY ARE HOUSED

Acaena antarctica Hook. f.
(Including specimens formerly determined as *A. laevigata* or *A. microcephala*.)

Chile *Ñuble:* Aguas Calientes, Baños de Chillan, iii.1927, Werdermann 1303 (BM, K). *Valdivia:* Cordillera del Ranco, xii.1854, Lechler 2951 (K), xii.1854, Lechler 2929 (K), xii.1854, Lechler 3029 (K). *Llanquihue:* Volcan Yates, iii.1925, Werdermann 660 (K).

Tierra del Fuego *Isla Grande:* Campo Loma Larga Norte, Estancia Harberton, 17.i.1967, Goodall 553 (LTR); mountain at head of Río Chico, Estancia Moat, 26.i.1968, Moore 1667 (LTR); Río Lashifashaj valley, 1.iii.1968, Moore 2086 (LTR); Río Azopardo, Seno Alimrantazgo, 20.iii.1968, Moore 2301 (LTR). *Isla de los Estados:* i.1787, Menzies s.n. (BM, K). *Islas Wollaston:* Hermite Island [Isla Hermite], Cape Horn [Cabo de Hornas], 1839–43, Hooker s.n. (BM, E, K).

Falkland Islands *West Falkland:* TC88 near summit of Mount Adams, 1909–11, Vallentin s.n. (K). *East Falkland:* UC77 north side of summit of Mount Usborne, 18.i.1964, Moore 600 (LTR). *Unlocalized:* 1839–43, Hooker s.n. (E).

Acaena decumbens (Gaertn.) D.W.H. Walton
(Including specimens formerly determined as *A. adscendens*, *A. adscendens* ssp. *georgiae-australis*, *A. affinis* or *A. magellanica*.)

Falkland Islands *West Falkland:* TC68 Roy Cove, iii.1909, Vallentin s.n. (K), 1909–11, Vallentin s.n. (K); TC88 Hill Cove, 1909–11, Vallentin s.n. (K, 2 specimens), 17.xii.1949, Sladen Fa 94/49 (BM). *East Falkland:* VC18 western limit of Berkeley Sound, 4.xii.1949, Sladen Fa 36/49 (BM); VC28 Port Louis, Vallentin s.n. (BM); Long Island, 1.v.1949, Sladen JB 111/3 (BM); VC37 Port Stanley, Walton 641 (BM).

South Georgia

075 145 Salisbury Plain, 10.iii.1962, Holdgate 604 (BIRM*).
115 135 north valley, Husvik, 27.i.1961, Greene 1489 (BIRM*, K).
120 130 west side of Olsen Valley, 17.iii.1961, Greene 3055 (K).
125 095 north-east of Ducloz Head, 10.iii.1961, Greene 2583 (BIRM*, K).
125 125 valley running north-west from Echo Pass, 1.ii.1961, Green 1629 (BIRM*); valley west of north Bore Valley, 11.iii.1961, Greene 2886 (K).
130 120 King Edward Cove, 30.xii.1913, Stammwitz s.n. (BM); between King Edward Point and Penguin River, 11.iii.1949, Sladen JB 10/2 (BM); King Edward Point, 31.xii.1956, Bonner 14 (BM), 31.xii.1956, Bonner 15 (BM), 27.i.1957, J. Smith M1001 (BIRM*, K), J. Smith M1001A (BIRM*), 28.xi.1957, J. Smith M1073 (BIRM*, K), 26.i.1958, J. Smith M1082 (BIRM*, K), 3.i.1968, Walton 454 (BIRM*, BM, E), 26.ii.1968, Walton 559 (BM, E), 27.iii.1968, Walton 580 (BM), 28.iii.1968, Walton 585 (BM, E); west end of King Edward Point, 26.i.1968, Walton 491 (BIRM*, BM); lower slopes of Mount Duse, 3.i.1968, Walton 455 (BIRM*, BM, E), 3.i.1968, Walton 456 (BM, E), 27.ii.1968, Walton 560 (BM, E),

† Herbarium abbreviations follow those recommended by Lanjouw and Stafleu (1964), except that BIRM* has been used for the British Antarctic Survey herbarium at present housed in the Department of Botany, University of Birmingham. The South Georgian specimens are arranged according to the 5 km. squares of the South Georgian grid.

14.iii.1968, Walton 570 (BIRM*); south shore of King Edward Cove, 30.i.1968, Walton 496 (BIRM*), 2.ii.1968, Walton 516 (BM, E), 5.iii.1968, Walton 564 (BIRM*); Grytviken whaling station, 25.ii.1968, Walton 547 (BIRM*); below Gull Lake, 9.i.1968, Walton 465 (BM, E).
130 125 Burnet Cove, 26.ii.1968, Walton 555 (BIRM*, BM).
140 115 3 miles [4·6 km.] south of Sandebugten, 30.i.1955, Bonner 9 (BM).
145 110 Lönnberg Valley, 2.ii.1964, Longton 371 (BIRM*).
155 095 Moltke Harbour, 19.ii.1961, Greene 2311 (BIRM*, K).
160 090 near Will Point, 31.iii.1968, Walton 593 (BIRM*).
Inadequately localized: Possession Bay, 17.i.1775, J. R. and G. Forster, s.n. (BM, as *Ancistrum decumbens*); South Georgia, 5.iv.1906, H.M.S. *Sappho* (K, 2 specimens), i.1922, Shackleton-Rowett Expedition 28 (BM); Leith Harbour, 16.iii.1949, Sladen JB 15/3 (BM).

Prince Edward Islands *Marion Island:* south of Juniors Kop, 18.iii.1963, van Zinderen Bakker 1186 (K).
Unlocalized: xii.1873, Moseley s.n. (E, K), 1874, Crosbie s.n. (E).

Iles Crozet *Possession Island:* i.1960, Proctor 21 (BM).

Archipel de Kerguelen Christmas Harbour, v. 1840, Hooker 764 (K), 1874, Thomson s.n. (E); Observation Bay, i.1902, Herb. Corn. Osten 8668 (MVM, 2 specimens).
Unlocalized: 1839–43, Hooker s.n. (E), i.1874, Crosbie s.n. (E), 1874, Crosbie s.n. (E), i.1874, Moseley s.n. (E), 1908–09, Bossière s.n. (E), i.1960, Proctor 15 (BM), Rallier du Baty s.n. (K).

McDonald Islands *Heard Island:* Spit Bay, Kenny 371 (BIRM*).

Macquarie Island Below Half Way Hill, 7.ix.1948, Laird 50–53 (K); near Half Way Hill, 18.xii.1949, Haysom M1/49/Y8 (BIRM*); Gadget Gully, 18.xi.1950, Taylor s.n. (BIRM*), 3.ii.1951. Taylor s.n. (K); Wireless Hill, 15.i.1964, Filson 5713 (BIRM*).
Unlocalized: Fraser s.n. (K), 28.xii.1950, Taylor s.n. (K).

Acaena decumbens × *tenera*

South Georgia
115 135 near Husvik, 15.xii.1967, Walton 435 (BIRM*).
120 135 Grass Island, 15.xii.1967, Walton 436 (BIRM*).
125 120 Echo Pass, 27.ii.1968, Walton 562 (BIRM*).
125 125 Sphagnum Valley, 20.i.1968, Walton 486 (BM).
130 120 King Edward Point, 26.i.1968, Walton 492 (BM), 1.ii.1968, Walton 509 (BIRM*, BM, E); west end of King Edward Point, 5.ii.1968, Walton 528 (BIRM)*; side of Mount Duse, 5.ii.1968, Walton 526 (BIRM*, BM, E); Hope Point, 1.ii.1968, Walton 508 (BIRM*, BM); between Grytviken and King Edward Point, 27.iii.1968, Walton 581 (BIRM*, BM); south shore of King Edward Cove, 27.xii.1967, Walton 448 (BIRM*, BM, E), 13.i.1968, Walton 469 (BIRM*, BM, E), 2.ii.1968, Walton 517 (BIRM*, BM); Gull Lake, 29.i.1961, Greene 1503 (BIRM*, K); cirque behind Mount Hodges, 12.ii.1968, Walton 535 (BIRM*).
130 125 northern part of Bore Valley, 15.ii.1964, Longton 434 (BIRM*), 15.ii.1964, Longton 436 (BIRM*); Bore Valley, 26.ii.1968, Walton 558 (BM, E).
135 110 foothills of Mount Paget, 13.iii.1968, Walton 138 (BM).
135 120 Dartmouth Point, 27.i.1968, Walton 495 (BIRM*, BM, E).
145 115 pass between Ocean Harbour and Cumberland Bay, 5.iii.1957, Bonner 75 (BM).
155 095 Pirner Point, 25.ii.1961, Greene 2414 (K).
160 090 near Will Point, 31.iii.1968, Walton 592 (BIRM*, BM, E).
170 065 near Hamilton Bay, 1.iv.1968, Walton 597 (BIRM*, BM, E).
175 065 Cooper Island, 1.iv.1968, Walton 604 (BM, E).

Acaena tenera Alboff

Tierra del Fuego *Isla Grande:* Cerro No Top, Estancia Harberton, 4.iii.1967, Goodall 714 (LTR).

South Georgia
070 145 near Markham Point, 22.i.1961, Greene 1173 (BIRM*, K), 22.i.1961, Greene 1178 (K).
080 125 Holmestrand, 1.x.1957, J. Smith M1051 (K).
090 145 north shore of North Bay, Prince Olav Harbour, 2.ii.1961, Greene 1761 (K).
120 130 west side of Olsen Valley, 17.iii.1961, Greene 3059 (BIRM*).
120 140 Leith Harbour, 14.i.1914, Stammwitz s.n. (BM), 16.iii.1949, Sladen JB15/2 (BM), 17.i.1957, Bonner 38 (BM).
125 095 north-east of Ducloz Head, 10.iii.1961, Greene 2582 (BIRM*).
130 120 west end of King Edward Point, 27.xii.1967, Walton 446 (BM), 26.i.1968, Walton 493 (BIRM*, BM, E), 14.iii.1968, Walton 569 (BM); King Edward Cove, 11.iii.1949, Sladen JB 10/1 (BM); behind Grytviken, 8.i.1968, Walton 460 (BIRM, BM, F); Brown Mountain, 7.i.1957, Bonner 32 (BM); Hestesletten, 30.i.1957, Bonner 54 (BM).
130 125 Bore Valley, 21.i.1957, Bonner 42 (BM), 26.xii.1967, Walton 444 (BM); northern part of Bore Valley, 15.ii.1964, Longton 435 (BIRM*); slopes of Spencer Peak, 15.ii.1961, Greene 2039 (BIRM*, K); plateau below Mount Duse, 5.ii.1968, Walton 527 (BIRM*, BM, E).
140 115 valley north of Sörling Valley, 16.i.1964, Longton 220 (BIRM*).
140 120 corrie with three lakes, north of Sandebugten, 15.i.1961, Greene 1066 (BIRM*, K), 15.i.1961, Greene 1067 (K).

145 115 pass between Ocean Harbour and Cumberland Bay, 5.iii.1957, Bonner 71 (BM), 5.iii.1957, Bonner 78 (BM).

160 090 near Will Point, 31.iii.1968, Walton 591 (BM).

Inadequately localized: Royal Bay, 23.i.1883, Will s.n. (K); South Georgia, i.1922, Shackleton Rowett Expedition 7 (BM), i.1922, Shackleton-Rowett Expedition 35 (BM); Grytviken, 1.ii.1957, J. Smith M1003 (BIRM*, K); Bird Island, 2.i.1958, J. Smith M1078 (K).