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DIVERSITY IN *ACAENA* (ROSACEAE) IN SOUTH AUSTRALIA

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Abstract

Numerous population samples of *Acaena* in South Australia have been examined. In South Australia three species, *A. echinata* Nees, *A. ovina* A. Cunn, and *A. novae-zelandiae* Kirk, and the hybrid *A.* x *anserovina* Orchard have been recognised. The diversity of morphological characters within these samples indicates that the maintenance of varietal names is not supported. *Acaena ovina* and *A. echinata* are both variable species and a multivariate analysis indicated that these taxa tend to differ in a number of characters but still show some degree of overlap.

Introduction

Acaena is a genus is of perennial herbs either tufted or stoloniferous, slightly woody at the base, the leaves are imparipinnate, the leaflets mostly lobed or toothed, the flowers are small, more or less sessile, clustered in heads or interrupted spikes, petals are absent and the solitary carpels produce an achene enclosed in a spiny hypanthium. The plants are protogynous, Dawson (1960), wind pollinated and likely to be strongly outcrossing.

The genus belongs to the family Rosaceae s.l. and to the subfamily Rosoideae or to the Rosaceae s.str. if the several segregate families are removed.

Acaena occurs in all Australian states except the Northern Territory. It is widespread in New Zealand and South America with one or two species in Africa and is thus mainly Southern Hemisphere in distribution. One species has become established in Europe.

The plants occur in grassland, light woodland, coastal dunes and only in areas with moderate to good rainfall. They do not occur in our arid or tropical regions.

The barbed fruits (Plates 1–3) which are readily detached are ideal for transport by man or beast Ridley (1930), Kok (1975), Culwick (1982), Monillo and Brener (1993), Dean et al. (1994), and it is probable that their distribution in Australia is a dynamic one. While *A. novae-zelandiae* was collected from the southern Lofties by F. Mueller and from Kangaroo Island by R. Brown, it was not collected from Eyre Peninsula until 1967 or from York Peninsula until 1969. The genus is represented in Western Australia by *A. echinata* only. This taxon was collected in 1839 soon after white settlement. Certainly the environment of the south west of Western Australia is suitable for other species. One Australian species is now naturalised in New Zealand, *A. agnipila* sensu Orchard (1973), and *A. echinata* is only known there from one ephemeral collection in 1942. The Australian species *A. agnipila* has become a serious weed in New Zealand, Macmillan (1995) pers. com. In Britain *A. novae-zelandiae* has become established, Gynn and Richards (1985).

A Northern Hemisphere parallel of *Acaena* would seem to be *Sanguisorba*, 1–2 species of which are naturalised in Australia (see below).

In keys and floras the genus *Acaena* is usually first divided into species with globose heads and those that are spicate or with fruits below a globose head. The name *Acaena novae-zelandiae* is widely used for the most common of the globose-headed species in Australia, with possibly three other globose-headed *Acaena* species: *A. montana* in


A
B
C
del: dasHorst '98

Tasmania, *A. pallida* in Tasmania and New South Wales and *A.* sp. *A* Harden & Rodd in alpine New South Wales. The spicate flowered species however are not readily defined.

Hybrids between the globose and spicate-headed species have been recognised as *A.* × *anserovina* Orchard (1969). This has been characterised, in part, as having a globular head of flowers with some flowers on the scape below. Many collections of *A. echinata* have been misidentified as hybrids as this species frequently has its spike terminated by a distinct ball of flowers. Dawson (1960) in New Zealand indicated a degree of fertility in the hybrids while Orchard (1969) states that his in South Australia were all sterile. The hybrids occur frequently when the appropriate species are present and can be recognised by the well developed apical spines on the fruits with a few weaker spines below them (Plate 1), the few flowers below the globular head, the generally branched spreading stems and at times by their hybrid vigour.

The number of spicate-headed species is debatable. Orchard (1969) in the most recent Australia wide revision discussed three species, *A. agnipila* Gand. with four varieties, *A. echinata* Nees with five varieties and *A. ovina* A. Cunn. with two varieties.

Experience with the genus elsewhere from South Australia and major papers are indicated below.

Bitter (1911) monographed the genus *Acaena.* He named many new species and subspecific taxa. Bitter was a meticulous worker but had an inconsistent species concept, manifest also in his later work on the Solanaceae. Yeo (1973) says of this monograph that "there seems to be marked inequality in the variation allowed within species, some of them being very wide and embracing numerous subspecies, others being narrow and having the appearance of only minor variants."

Cockayne & Allan (1934) recorded 12 hybrids in the flora of New Zealand and stated *inter alia* "sowing seeds of suspected hybrids has always in our experience produced diverse offspring quite resembling forms occurring in nature," "the [hybrid] swarms are widespread and of great diversity," "large hybrid swarms," and "every transition in the hybrids occur". Dawson (1960) analysed and recorded hybrids in the vicinity of Wellington, New Zealand and stated such hybrids occurred in various other localities.

Allan (1961) in his Flora of New Zealand followed Bitter (1911) closely. He maintained 14 species and many varieties. All the native New Zealand species have capitate inflorescences and he finishes his treatment with a half page account of hybridism. He tells of frequent hybrids and complex hybrid swarms.

Grondona (1964) revised the species in Argentina. He maintained 20 species and reduced many earlier specific and subspecific names to synonymy.

Orchard (1969) published a revision of the *A. ovina* complex in Australia and maintained 11 varieties in 3 species. He stated "*Acaena* is well known for hybridisation at all taxonomic levels" ... "In fact *A. ovina* s.str. and *A. echinata* var. *subglabricalyx* are probably hybrid in origin, resulting from recent contact between *A. echinata* and *A. agnipila.* Other varieties within these latter two species also grade into each other to some extent" and later "During this period of expansion and diversification the original colonising species seems to have disappeared".

Walton & Greene (1971) in a study of *Acaena* on South Georgia island accepted two species, *A. decumbens* and *A. tenera,* with hybrids between them common. Both pollen fertility and seed germination of the presumed hybrids were measurably less than for either

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Plate 1. Fruit (×10). **A**, ***Acaena novae-zelandiae*** (*Symon 15220*, plant 5); **B**, ***A* ×*anserovina*** (Symon 15220, plant 9); **C**, ***A. echinata*** (Symon 15220, plant 10).

parent. Of general interest was the note that pilosity of leaves varied greatly even within one species, and that dioecious heads were found in *A. decumbens.* They noted that hermaphrodite heads might be replaced by female heads as the season advanced, and that stigma characters could be useful in determining species.

Yeo (1973) in discussing the species of *Acaena* with globose heads grown in Britain speaks of the "striking diversity in the colour and texture of the leaflets in *Acaena*" and under *A. magellanica* states "While the taxonomic problem is undoubtedly difficult, the morphological range these binomials represent is so enormous that one feels it ought to be possible to do something better than just lump the lot ...".

Orchard (1973) revised the *A. ovina* complex in New Zealand. He considered them all introduced from Australia. He recognised a single collection of *A. echinata* amongst "abnormal forms of *A. agnipila* v. *aequispina.* It is possible some introgression may have taken place, though none of the plants can be referred with certainty to *A. ovina* s.str." As well he found *A. agnipila* with 3 varieties largely overlapping in distribution. He also recognised *A.* × *anserovina.* His concept of this hybrid was that it included crosses with three globular headed species, *A. anserinifolia, A. novae-zelandiae* and *A. microphylla*, with both *A. agnipila* and *A. echinata.*

Walton (1975) further reduced many South American species names to synonymy. He says of Yeo (1973) "that he (Walton) saw a much wider range of specimens ... [these] ... show a complete intergradation between the characters he uses to delimit his species".

Macmillan (1983, 1985, 1991a, 1991b) raised one of Bitter's subspecies to species rank and described 5 more species from New Zealand.

Gynn & Richards (1985) wrote a biological account of *A. novae-zelandiae* now naturalised in Britain.

In the more recent *Flora of New Zealand*, Macmillan in Webb et al. (1988) listed 15 species with few varieties, including naturalised *A. agnipila* with 3 varieties and the rare occurrence of *A. echinata,* both as aliens from Australia.

Recent floras of the Australian states (or larger parts of them) have treated the genus differently, Curtis (1956), Willis (1972), Curtis & Morris (1975), Stanley & Ross (1983), Jessop in Jessop & Toelken (1986), Bennett in Marchant *et al.* (1987), Harden & Rodd in Harden (1990), Jeanes & Jobson in Walsh & Entwisle (1996). Several authors mention varieties but only Jessop describes them and only Stanley & Ross provide a key to them.

These accounts imply, perhaps, a caution in accepting many taxa of subspecific rank.

In the collection at AD a number of specimens with a globular head of fruits with several fruits on the stem below have been called *A.* ×*anserovina.* This character alone is not sufficient to indicate hybridity. An examination of three populations on Kangaroo Island (*Symon 15152; 15153; 15154*) showed plants uniform for this character though neither of the presumed parents *A. novae-zelandiae* and *A. ovina* s.l. were found locally. Most of these plants formed close rosettes with no evidence of stolons nor of the shiny green leaves characteristic of *A. novae-zelandiae* common elsewhere on the island. Using Orchard's (1969) key these all appear to be forms of *A. echinata* var. *retrorsumpilosa.* Many other collections of this taxon in AD, some identified by Orchard, bear a globular terminal head with scattered flowers below it.

This summary shows that almost wherever *Acaena* occurs it is hugely variable. These variants have been given species or subspecific names depending on the author's philosophy.

There is no suggestion in the literature of apomixis or of the peculiar breeding systems of *Rosa* and *Rubus*, the latter providing an infinite number of microspecies. Chromosome

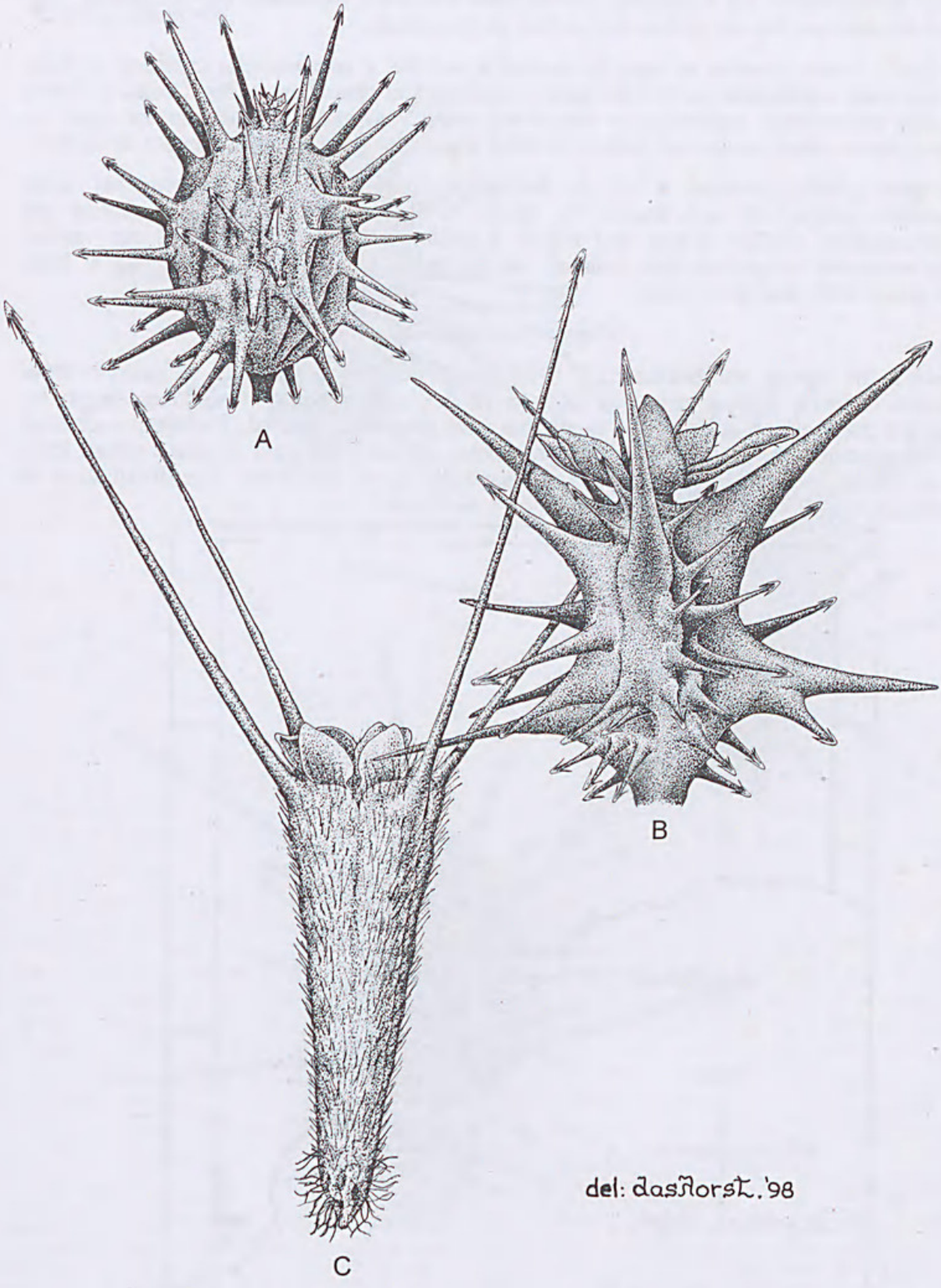

Plate 2. Fruit (×10). **A,** ***Acaena ovina*** (Symon 15223, plant 5); **B,** ***A. echinata*** (Bates 35616, plant 4); **C,** ***A. novae-zelandiae*** (Symon 15307).

counts reported for New Zealand species are 2n = 42, 84 and 126, Beuzenberg (1983), and polyploids are known from South America and the Falkland Islands, Moore & Walton (1970). The numbers for Australian species need checking, especially the occasional very robust populations that are at least suggestive of polyploidy.

In the *A. ovina* complex at least in Australia and the *A. anserinifolia* complex in New Zealand many combinations of individual morphological characters occur. Orchard (1969) uses leaf pubescence, inflorescence branching, fruits glabrous or pilose, spines equal or unequal, spines thickened at the base or slender, stipule length and stamen length in his key.

Orchard (1969) provided a key to the spicate-headed species. His principal leads (somewhat simplified) are shown in Table 1. *Acaena ovina* and *A. agnipila* are characterised by slender spines, and within *A. echinata*, Orchard recognised one variety (*A. echinata* var *subglabricalyx*) with all slender spines, and four varieties with at least some spines with thickened bases.

Population Samples

During the spring and summer of 1994 many population samples of *Acaena* were collected. A single fruiting stem was taken as the unit and specimens were taken simply by walking a transect and collecting a stem from each plant encountered. These have all been pressed, mounted and numbered and are deposited in AD. The plant numbers varied from five to fifty-four, the larger samples were obviously more significant. The distribution of population samples in South Australia is shown in Figure 1.

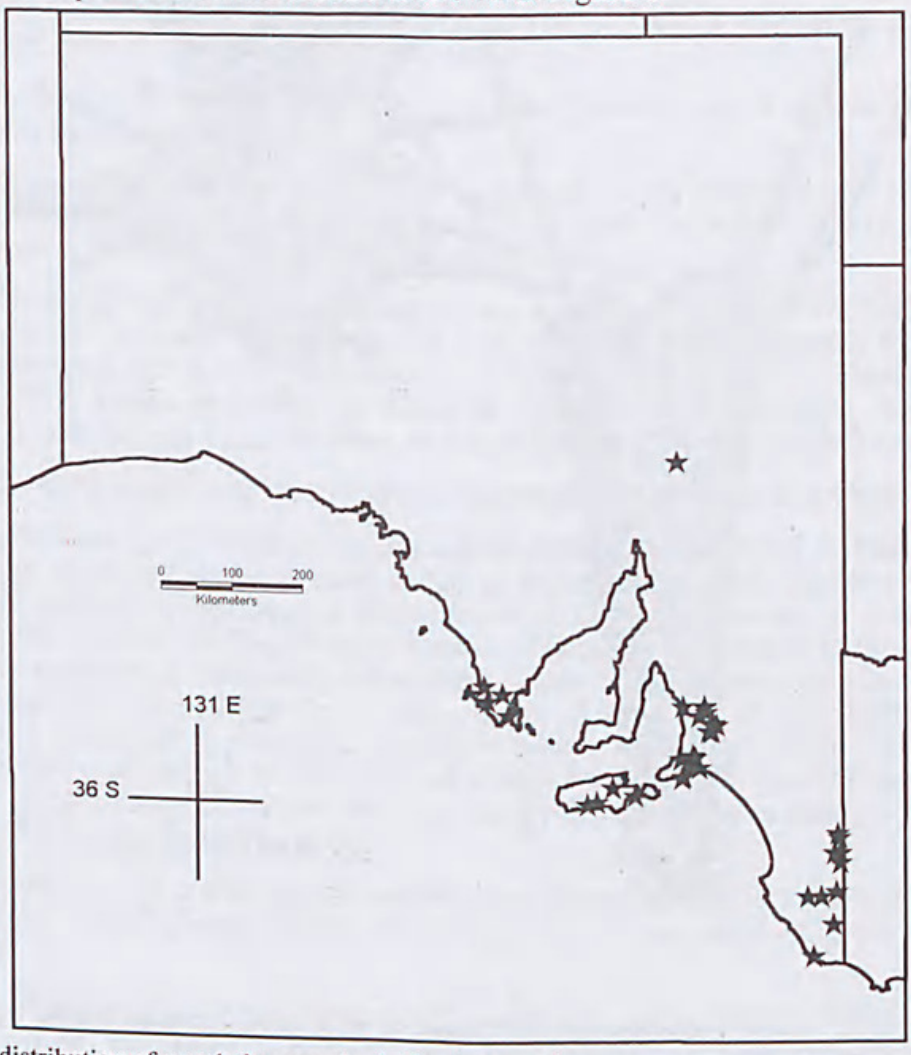

Fig. 1. The distribution of population samples in South Australia.

The collections were then scored for most of the characters previously used in keys to the species in Australia, i.e. pubescence of the leaves, nature of the inflorescence and characters of the fruit. They were not scored for stipules nor stamens, the latter usually absent from fruiting specimens.

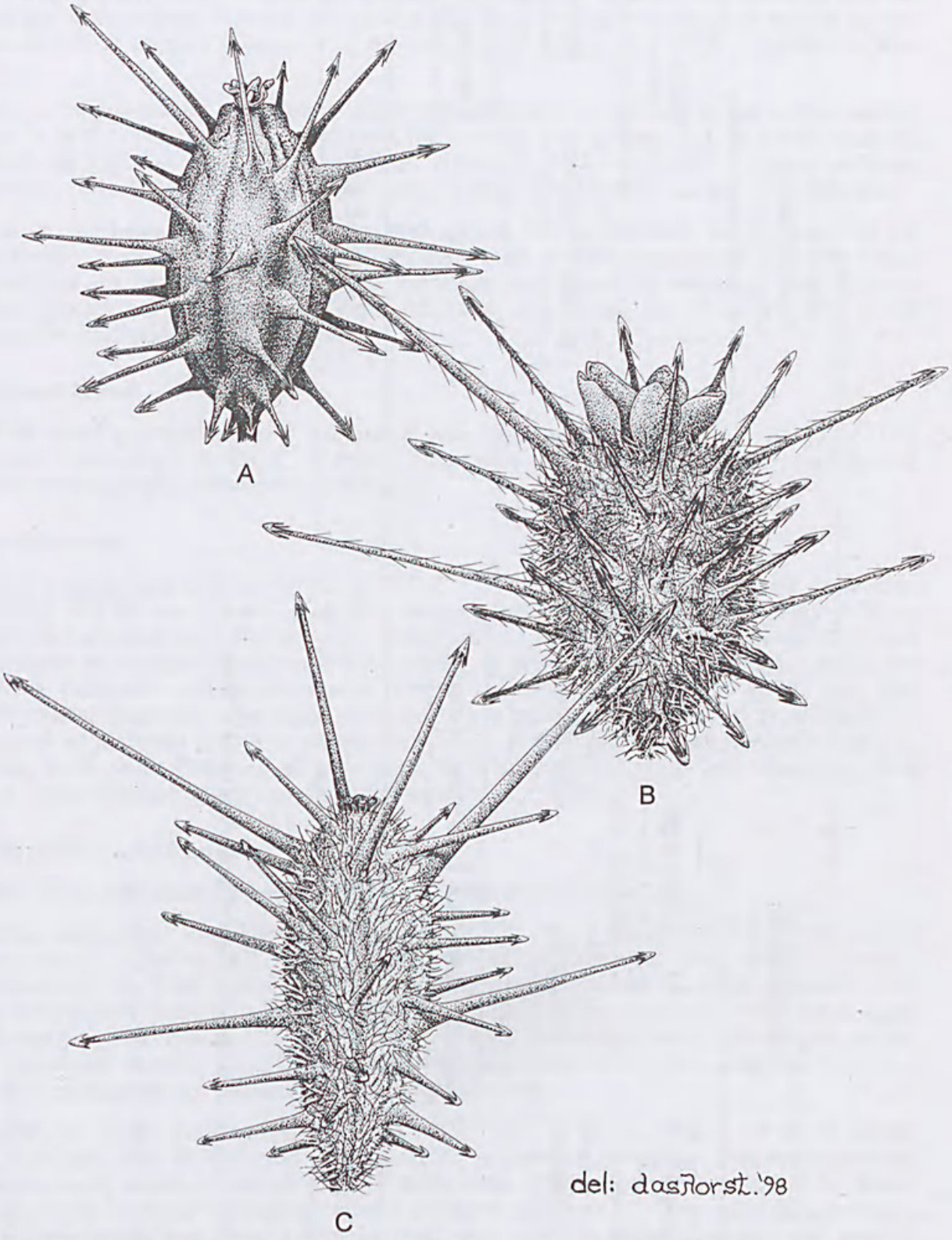

Plate 3. Fruit (×10). **A**, ***Acaena ovina*** (*Symon 15308*); **B**, ***A. ×anserovina*** (*Bates 35503*); **C**, ***A. ×anserovina*** (*Symon 15311*).

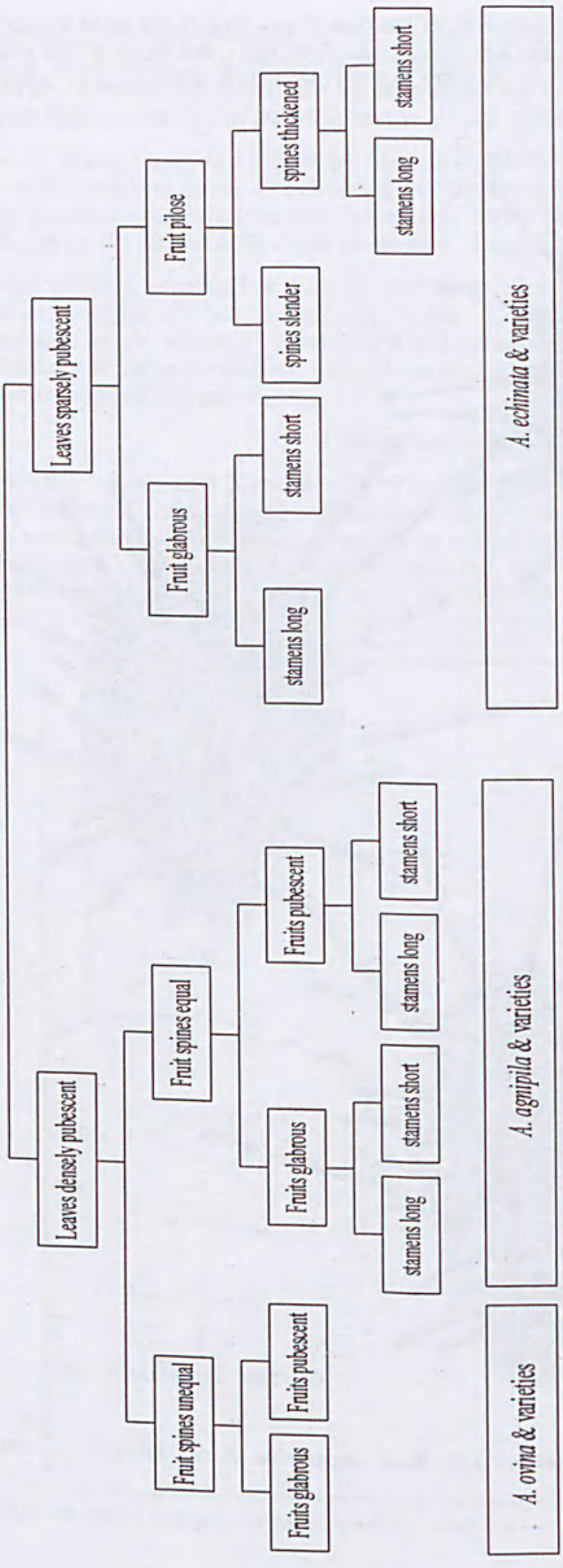

Table 1. Simplified synopsis of key to spicate-headed species from Orchard (1969).

In addition to the ball-headed *A. novae-zelandiae* the three species expected in South Australia are *A. agnipila*, *A. echinata* and *A. ovina*, Orchard (1969).

There is no doubt that where *A. novae-zelandiae* comes in contact with the other species hybrids frequently occur. These were given the name *A. ×anserovina* Orchard and the plants are intermediate between the parents and there is some evidence of hybrid vigour. Orchard (1973) applied this name to the progeny of intercrosses of five species in New Zealand.

Acaena novae-zelandiae is found along our temperate coasts and in the higher rainfall zones. It rarely occurs inland. Apart from the hybrids, it is uniform and in South Australia at least, variants have not been recognised. Although *A. novae-zelandiae* and *A. echinata* have been collected frequently from Kangaroo Island, hybrids have not yet been collected.

The spicate-headed species are more widespread, but nevertheless do not occur in the drier areas of South Australia. Almost all of these form variable populations and only where the samples are small has no significant variation been found. In this paper, two spicate-headed species are recognised in South Australia, *A. echinata* and *A. ovina* (with which *A. agnipila* is considered synonymous).

Kangaroo Island

Three small populations of 7–10 plants were collected, *Symon 15152, 15153, 15154.* These are considered to be *A. echinata.* They were all relatively slender, small-leaved, rosette forming plants with minimal variation.

Eyre Peninsula

Three populations, *Symon 15198, 15203 & 15211*, of 10, 37 and 54 plants have been examined. All are considered to be *A. echinata.* The small population was very uniform except for the occurrence of some very densely flowered late spikes. The second and third populations were more variable and both contained plants with leaves variously pubescent below, a branched inflorescence was present and spicate as well as spike plus ball inflorescences occurred. The fruits were uniformly pubescent in the third population and pubescent or glabrous (10%) in the second. Most of the prickles were markedly unequal and the larger ones flattened at their base. In addition some fruits had relatively short spines. These populations did not include elements of *A. ovina.*

Southern Mt Lofty Range

Many more populations have been sampled in the southern hills area.

Nairne area. Four samples, *Symon 15215, 15216, 15217, 15218* of 9–52 plants were predominantly *A. ovina.* All four recorded variable pubescence. Four single branched inflorescences occurred. Inflorescence form varied from spicate to spike plus ball. The fruits were mostly pubescent but glabrous fruits were also found. Spines varied from equal to unequal; e.g. in Symon 15218, 63% of *A. ovina* plants had more or less equal spines, 34% somewhat unequal and 3% markedly unequal, while 93% of *A. echinata* plants had markedly unequal spines and 7% had somewhat unequal.

Charleston Road. Four samples, *Symon 15220, 15221, 15222, 15223*, of 10–34 plants were collected. The first proved to be a mixed population including *A. novae-zelandiae, A. × anserovina* and primarily *A. echinata* with some *A. ovina* present (see Table 2). While the first two were readily recognised, the *A. echinata* consisted of plants variably pubescent, with inflorescences that were spike plus ball, with spines markedly unequal and usually flattened and with fruits pubescent (64%) or glabrous (36%).

An adjacent population but without *A. novae-zelandiae* had variable inflorescence form and 40% of the fruits were glabrous. A population in little disturbed natural scrub was more uniform though it differed in leaf pubescence. The last population varied in leaf pubescence, included a single branched inflorescence, and some glabrous fruits. This population contained a mixture of *A. echinata* and *A. ovina* (Table 2). All *A. echinata* plants had markedly unequal spines. Forty-five percent of *A. ovina* plants had more or less equal spines while 55% had somewhat unequal spines.

Southern Fleurieu Peninsula, Newland Head. Six samples, *Murfet & Taplin 2102, 2103, 2104, 2105, 2106, 2107* of 3–14 plants were collected. These varied from *A. novae-zelandiae,* and its hybrid *A. xanserovina* when present, with the two potential spicate parents to varied populations of *A. echinata* and *A. ovina.* There were no branched inflorescences except in the hybrid, all fruits were pubescent, one population (*2106*) had more or less equal spines that were acicular rather than flattened.

Hindmarsh Valley and *Hindmarsh Falls.* Six populations, *Bates 39664, 39659, Murfet 2096, 2109, 2111, 2113,* ranged from 4–15 plants each and thus were not large samples. Amongst them branched inflorescences occurred, there was some variation in pubescence and in one (*Murfet 2113*) there was considerable variation in fruit spines.

Mt Crawford, Anstey Hill, Kersbrook and *Cherry Gardens.* Eight samples, *Bates 35506, 35612, 35616, 39684, 40169, 40210, Taplin 643, 697* of 5–50 plants were seen. These collections contained a wide range of material – indeed all the species and hybrids recorded for South Australia. Variation in pubescence was noted, the glabrous fruits had more or less equal acicular spines, no fruits that were glabrous had notably unequal spines, and several branched inflorescences were noted. Only the smallest samples, *Taplin 643* (7 plants) and *Bates 35612* (5 plants) approached uniformity. Other populations were all of mixed characters. In one sample (*Bates 39684*) from Cherry Gardens some influence of *A. novae-zelandiae* seemed apparent though that species was not present in the sample.

Goolwa, Murfet 1908. This sample of 17 plants, nominally *A. echinata* was a robust lot with simple or branched inflorescences, and glabrous or pubescent fruits, but all with unequal spines.

Myponga, Bates 40208. These 8 plants nominally *A. echinata* were uniform.

Mt Compass, Bates 40224. These 11 plants nominally *A. ovina,* were varied and included branched inflorescences, a single pubescent fruit, and varied spines.

South East of South Australia

Ten collections ranging from six to 27 plants were available. *Murfet & Taplin 2300, 2301, 2311, 2319, 2323* and *Symon 15287, 15288, 15289, 15294* were all *A. echinata* though varying in pubescence and some fruit characters. *Symon 15298* included a single *A. ovina* amongst *A. echinata.* However population *Symon 15307 - 15311* (incl) was an example of the occurrence of the hybrid *A. × anserovina* in the presence of the parents *A. novae-zelandiae* and *A. ovina.*

Northern Mt Lofty Range

Penwortham and *Hilltown,* two samples *Bates 40320, 40322* of 8–10 plants were available. These two samples from north of Adelaide were both nominally *A. echinata* and were both uniform though the second was of a very robust form.

Flinders Ranges

Wilpena, Symon 15349. The occurrence of *Acaena* here is isolated and is a considerable distance from the nearest more southerly populations at Mt. Remarkable. Thirty-eight

samples were collected along about 1km of the creekline leading into the Pound. These were all *A. echinata*. The foliage was relatively uniform, gracile and sparsely pubescent on the main veins below. The fruits were relatively small, more globular and more sparsely spined than many more southern populations. Fruit pubescence was variable, with pubescent, puberulent and glabrous fruits being present.

These samples show that several characters used to base varieties upon commonly occur in one population. The *A. ovina* characteristics are confined to the higher rainfall areas and outlying populations tend to be more uniform and are nominally *A. echinata*.

New South Wales

All the collections referred to so far are from South Australia. Of interest therefore are three from New South Wales, *Lepschi 1715* from between Lake George and Yass, *Lepschi 1720* from near Mt Ainslie, plus *Lally & Lafay 512–513* from the Brindabella Range.

The first, primarily *A. ovina*, of 31 plants had varied leaf pubescence, several branched inflorescences. Of the *A. ovina* plants, 96% had spicate and 4% had spike plus ball inflorescences, 48% had pubescent fruits and 52% had glabrous fruits. *Acaena ovina* plants had equal or unequal spines, and acicular or flattened spines. The second, primarily *A. ovina*, was variable in leaf pubescence. It included some branched inflorescences, and pubescent and glabrous fruits, as well as equal and unequal spines. It is of interest that both are just as varied as several of the larger South Australian collections and again contained *A. echinata* and *A. ovina* (Table 2).

A collection from a higher altitude, 1400 m of the Brindabella Range was in part a hybrid swarm including *A. novae-zelandiae, A.* × *anserovina* and *A. ovina*. *Lally & Lafay 512–513* was of 53 plants and demonstrated minor variation in leaf pubescence, a few weakly branched inflorescence, and no glabrous fruit. The hybrid *A.* × *anserovina* was common and was readily recognised by the inflorescence. The collection included a higher percentage of plants than usual with leaves pubescent on the upper surface.

Western Australia

Two collections were examined, *Lepschi & Lally 3305* from ca. 13.5km NE of Kirup and *Lally & Lepschi 805* from 1.2km N of Mt Barker. Both collections are considered to be *A. echinata*.

Patterns of Morphological Variation

As noted above, several characters upon which varieties have been based vary within populations. For example, glabrous and pubescent fruits co-occur in some populations of *A. echinata*, e.g. *DES 15220, 15349*. Similarly, glabrous and pubescent fruits co-occur in some populations of *A. ovina*, e.g. *DES 15223, Lepschi 1715*. Hence these results throw considerable doubt on the utility of the many varietal names already published.

Leaf pubescence is variable and as the leaves are readily glabrescent care should be taken in assessing that character. In general terms pubescence on the main veins below is associated with pubescent fruits and unequal spines, and leaves densely pubescent below is associated with glabrous fruits though by no means exclusively. Glabrous or pubescent fruits occur with both equal and unequal spines.

Branched inflorescences are scattered through the collections usually at low frequencies and do not appear to be a significant character. In South Australia the inflorescence strictly in a ball is confined to *A. novae-zelandiae*. Spicate and spike plus ball inflorescences are not always easy to categorise but the latter is associated with unequal spines.

The fruit spine character (Plate 1) is very variable. The more or less equal spines tend to be acicular and the larger of the unequal ones tend to be flattened at their base and emphasise the ribbing of the fruit. The spines themselves as distinct from the body of the fruit may be pubescent or glabrous. The body of the fruit may be near-globular to ellipsoid. This character has not been used to date. Anthocyanin pigment varies and is often difficult to assess in old herbarium specimens. In fresh material there are striking differences, the fruits varying from light green to almost purple-black in extreme cases.

Delimitation of Taxa

Varieties based on fruit pubescence or on branched inflorescences scarcely seem tenable (see above). Nor do stipules or stamens appear to be reliable characters at least by observation.

In places *A. echinata* forms more or less uniform populations when assessed by reduced leaf pubescence, spike and ball inflorescence and markedly unequal spines. It also extends to the drier margins of the distribution of the genus.

Those plants with leaves densely pubescent below were previously divided into *A. ovina* and *A. agnipila* on the basis of spine differences Orchard (1969). Those with spines unequal in length but not greatly flattened were called *A. ovina* and those more or less equal and acicular were called *A. agnipila*. The two are not recognised as distinct taxa here because of the extensive overlap of characters (see Figure 4 below), as *A. ovina* is the older name *A. agnipila* becomes a synonym.

Numerical Analysis

Character Coding

Eight characters were scored and included in the analyses. Characters were scored for seven *Acaena* populations from South Australia, one from Western Australia and two from New South Wales (see Tables 2 and 3).

Population	Locality	Taxa			
		A. ovina	*A. echinata*	*A. × anserovina*	*A. novae-zelandiae*
DES 15218	SA E of Nairne (SL)	35	15		
DES 15220	SA Charleston Rd (SL)	6	22	3	3
DES 15223	SA Near Harrogate (SL)	11	15		
DES 15198	SA Eyre Peninsuala, Lincoln N.P. (EP)		10		
DES 15211	SA Kellidie Bay, Eyre Peninsula (EP)		35		
DES 15349	SA Wilpena Creek (FR)		36		
DES 15307-15311 (incl.)	SA "Oaklea" Stn, 4km from Blackfellows Cave on road to Bucks Bay (SE)	11		3	1
Lepschi 1715	NSW 12.5km W of Gundaroo	23	6		
Lepschi 1720	NSW Near Mt Ainslie CP	29	1		
Lepschi & Lally 3305	WA 13.5km NE of Kirup		16		

Table 2. Localities and numbers of plants sampled for numerical analysis

For leaf abaxial surface (character LEAF1), leaves were scored as pilose on main veins (0), or pilose below (1). For leaf adaxial surface (character LEAF2), leaves were scored as not pilose above (0), or pilose above (1). Four fruit characters were scored and included in the analyses. For fruit spine type (SPINE1), two categories were recognised - acicular spines (1), i.e. fruits with all acicular spines, and flattened spines (0), i.e. fruits with at least some spines flattened at their base. Relative size of fruit spines (SPINE2) was categorised into three states - equal (0), i.e. spines equal to subequal in length, somewhat unequal (1), i.e. spines unequal in length but not markedly unequal in thickness, and markedly unequal (2), i.e. spines unequal in length and markedly unequal in thickness. For fruit type (FRUIT1), fruits were scored as ribbed (0), or smooth (1). Three categories of fruit pubescence (FRUIT2) were recognised - glabrous (0), pubescent (1), and puberulent (2). Two inflorescence characters were also scored - INFLOR1, depending on whether inflorescences were ball only (0), spicate and ball (1) or spicate (2); and INFLOR2, depending on whether inflorescences were branched (0) or simple (1).

		TAXON							
		A. ovina		*A. echinata*		*A. × anserovina*		*A. novae-zelandiae*	
		Count	Col %	Count	Col %	Count	Col %	Count	Col %
SPINE1	flattened	51	44.3	150	96.2				
	acicular	64	55.7	6	3.8	6	100	4	100
SPINE2	equal	60	52.2	1	.6			4	100
	somewhat unequal	52	45.2	7	4.5	6	100		
	markedly unequal	3	2.6	148	94.9				
FRUIT1	ribbed	75	65.2	149	95.5	5	83.3	4	100
	smooth	40	34.8	7	4.5	1	16.7		
FRUIT2	glabrous	48	41.7	27	17.3				
	pubescent	67	58.3	112	71.8	6	100	4	100
	puberulent			17	10.9				
INFLOR1	only ball							4	100
	spic & ball	46	40.0	141	90.4	6	100		
	spicate	69	60.0	15	9.6				
INFLOR2	branched	7	6.1	1	.6	2	33.3		
	simple	108	93.9	155	99.4	4	66.7	4	100
LEAF1	pilose main veins	26	22.6	92	59.0				
	pilose below	89	77.4	64	41.0	6	100	4	100
LEAF2	not pilose above	51	44.3	137	87.8	6	100	4	100
	pilose above	64	55.7	19	12.2				

Table 3. Distribution of character states for plant specimens included in numerical analysis.

Statistical Analysis

Data on the eight morphological traits listed above were subjected to an ordination analysis to further examine relationships among characters and among characters and taxa. Five of the eight morphological characters used in the present analysis were two-state or binary variables and three (SPINE2, FRUIT2 and INFLOR1) had three character states. Accordingly, we used a nonlinear principal components analysis which is appropriate for

data measured on a nominal or ordinal scale. The PRINCALS routine in the SPSS (version 8) software package was utilised for the analysis. To simplify graphical interpretation, a two-dimensional solution was produced from the analysis. This analysis seeks to group together objects (plants) that share the same character states and it indicates the relative

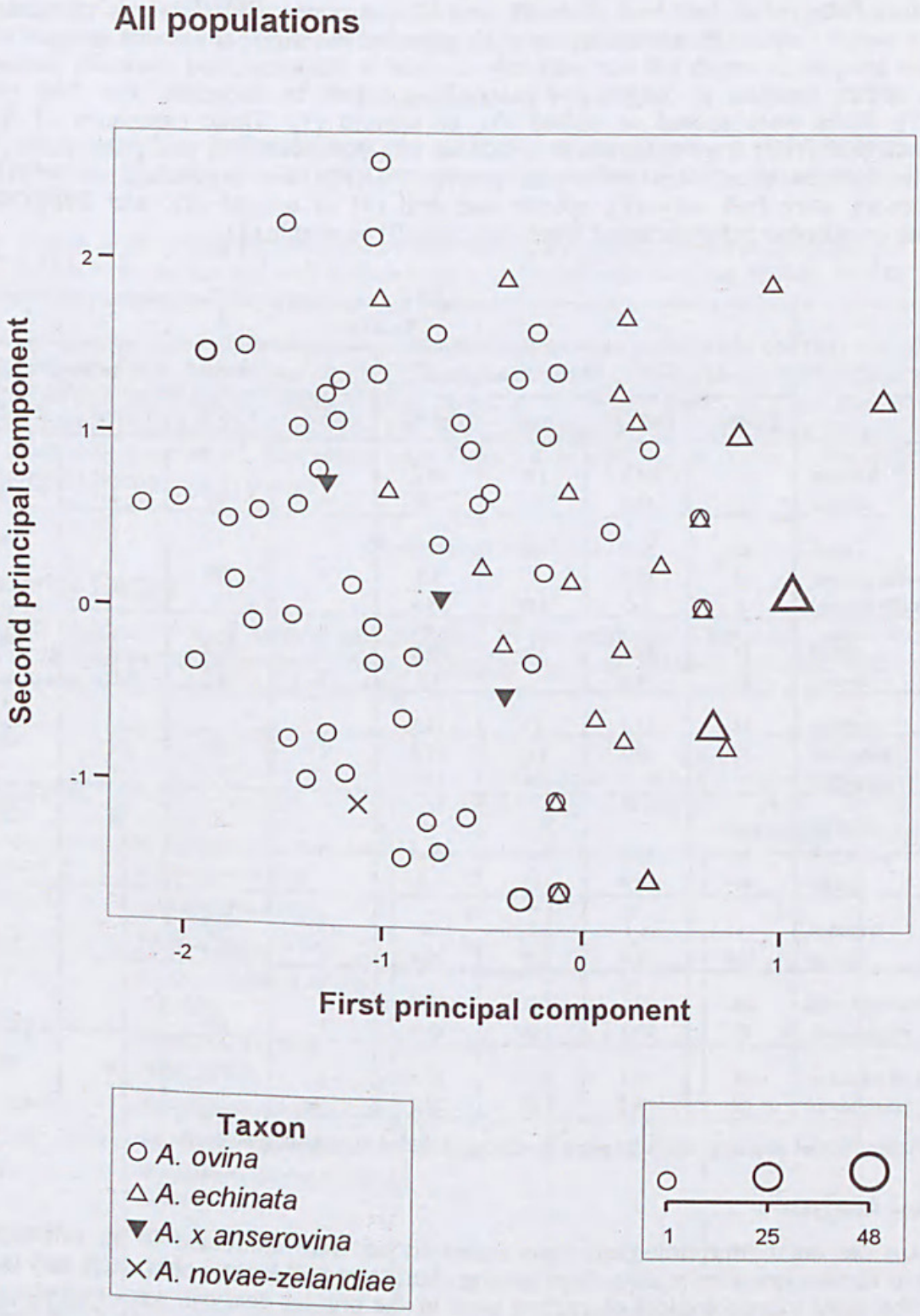

Fig. 2. Plot of the distribution of taxa against the first two principal component axes from the PRINCALS analysis. Symbol sizes are proportional to the number of individuals at that position (see adjacent key).

importance of different categorical variables in contributing to the separation or clustering of different objects. Two analyses were conducted, one on all populations listed above, and one on populations from South Australia.

Results

In the first analysis, the first two principal component axes together accounted for 36% and 20%, respectively, of the overall variation in the data. Inspection of the loadings of the original variables upon these axes showed that variation in the spine characters SPINE1 and SPINE2 was responsible for much of the variation along the first axis, while differences in the pubescence characters, FRUIT2 and LEAF2, accounted for much of the variation along the second axis. Figure 2 shows the distribution of all plants from the sampled populations when plotted against these axes. A weak separation of the taxa was obtained, with a tendency for plants of *A. echinata* to have greater scores than those of *A. ovina* along the first axis. Differences between these two taxa along the second axis were less marked. Plants of *A. novae-zelandiae.* can be distinguished by their having four spines, in contrast to plants of *A. ovina* and *A. echinata* which have more than four, but this trait was not included in the numerical analysis.Hybrid individuals had roughly intermediate values.

When the principal components analysis was repeated on plants from South Australian collections similar results were obtained, with the first two principal component axes accounting for 39% and 21%, respectively, of the overall variation in the data. However, the separation of *A. ovina* and *A. echinata* was considerably more pronounced, with little overlap in the distribution of the taxa (Figure 3). Again, there was less differentiation of these two taxa along the second axis than along the first, confirming the importance of the spine characters in distinguishing them.

In summary, *A. ovina* and *A. echinata* differed in the following characters:- most *A. echinata* plants (95%) had markedly unequal spines; in contrast most *A. ovina* plants had equal spines or somewhat unequal spines and only 3% had markedly unequal spines (Table 3). Orchard distinguished *A. ovina* with unequal spines and *A. agnipila* with equal spines. These are not recognised as two distinct taxa here, *A. agnipila* being considered as synonymous with *A. ovina.* Figure 4 shows that within *A. ovina* as delimited here, there is no clear separation in the principal components analysis between individuals with equal and unequal spines. Flattened spines were more common in *A. echinata* plants (96%) than in plants of *A. ovina* (44%). Glabrous and smooth fruits were more common in *A. ovina* plants than in *A. echinata* plants (Table 3). Spicate plus ball inflorescences predominated in *A. echinata* plants (90%) but were only seen in 40% of *A. ovina* plants. Branched inflorescences were only occasionally observed (Table 3). Regarding leaf pubescence characters, 56% of *A. ovina* plants were pilose above and 77% were pilose below, while only 12% of *A. echinata* plants were pilose above and 41% were pilose below.

Conclusion

In South Australia one uniform species *A. novae-zelandiae,* two variable and weakly differentiated entities *A. echinata* and *A. ovina* and one hybrid *A.* × *anserovina* may be recognised.

A. echinata Nees

Leaves generally pubescent on the main veins below. Inflorescence an irregular spike terminated by a ball of flowers. Spines markedly unequal, the larger ones with flattened bases resulting in a more conspicuously ribbed fruit which may be pubescent or glabrous.

Distribution in all areas of the genus in South Australia.

A. ovina A. Cunn.

Leaves generally densely hirsute-villous below often sparsely pubescent above.

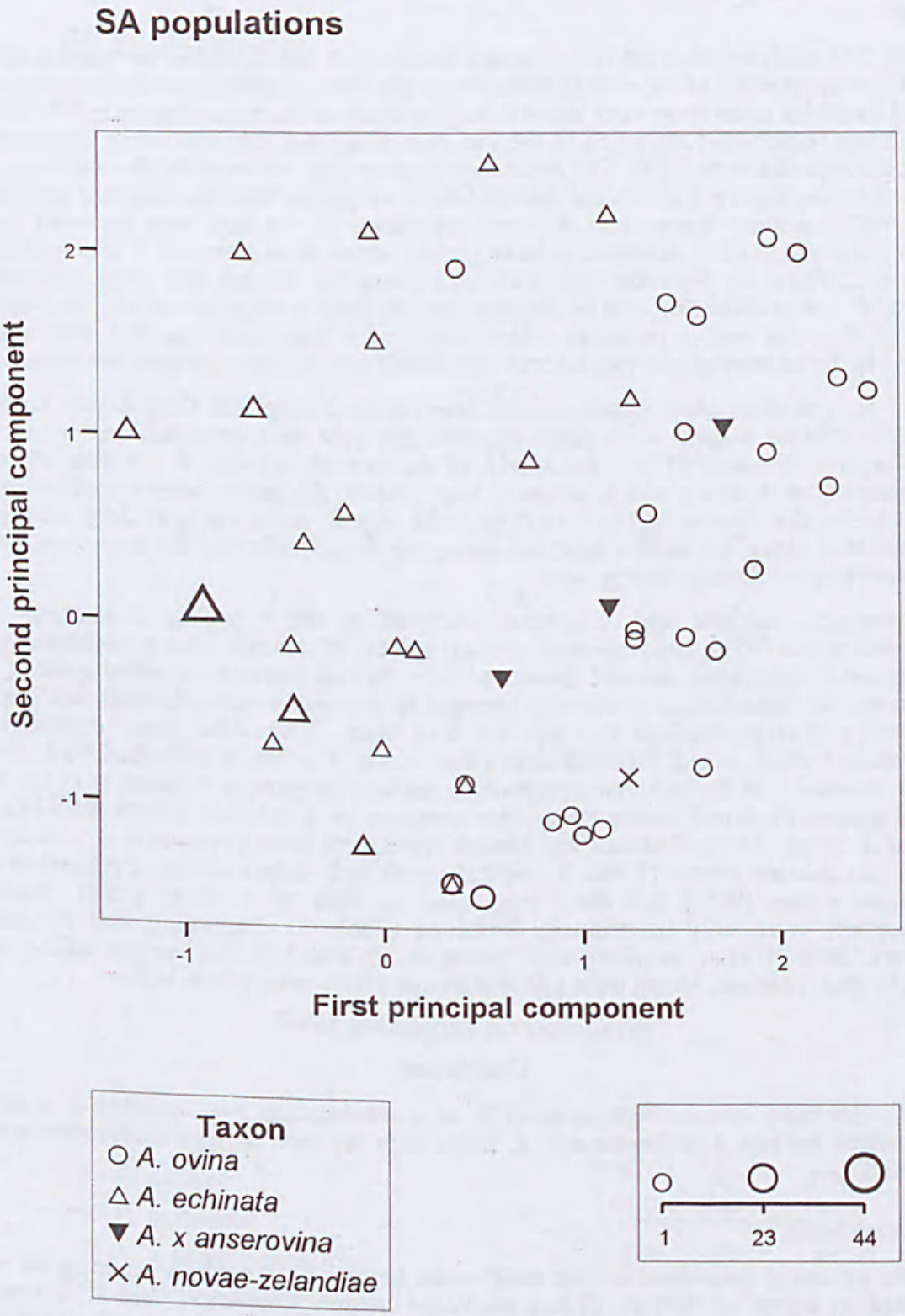

Fig. 3. Plot of the distribution of South Australian taxa against the first two prinipal component axes from the PRINCALS analysis. Symbol sizes are proportional to the number of individuals at that position (see adjacent key).

Inflorescence more uniformly spicate with some apical aggregation but commonly no terminal ball of flowers. Spines equal or unequal (almost always a few larger than the rest) their bases not markedly flattened, fruit less clearly ribbed, glabrous or pubescent.

Distribution in higher rainfall areas of the generic distribution in South Australia.

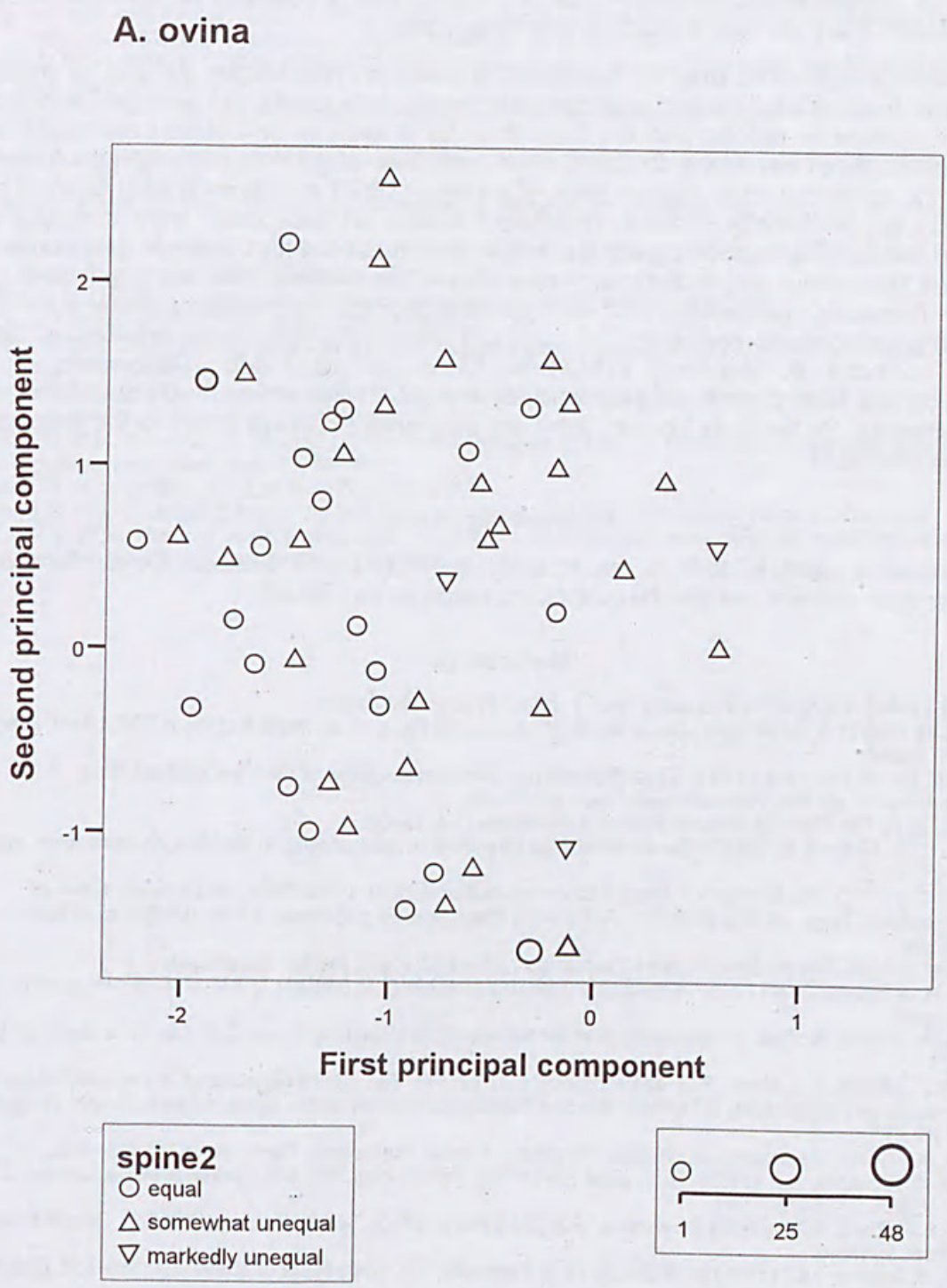

Fig. 4. Plot of the distribution of specimens of *A. ovina* against the first two principal component axes from the PRINCALS analysis, showing the distribution of the SPINE2 character. Symbol sizes are proportional to the number of individuals at that position (see adjacent key).

A. novae-zelandiae Kirk.

Sprawling, weakly woody shrubs, producing long stolons, the infloresence always in a ball. This taxon is frequently subcoastal in dune swales , less commonly inland.

A. × ***anserovina*** Orchard.

Where *A. novae-zelandiae* occurs in close proximity to *A. echinata* or *A. ovina*, hybrids may be found. They are intermediate in most characters.

The genus *Sanguisorba* may be considered a Northern Hemisphere parallel of *Acaena*. The species have similar incised imparipinnate leaves, lack petals, are wind pollinated, the heads are globose or oblong and the fruits may be smooth or reticulate, commonly have wings and the faces have long or short, stout, papillose outgrowths. The species *S. minor* parallels the problems with *Acaena* here. Nordborg (1967) maintains 6 subspecies which are weakly geographically distinct. Overlaps between all subspecies were common and Nordborg states "The morphological studies in combination with cytologic data could not resolve the taxonomic and evolutionary problems of the section. Nor was it possible with the help of anatomy, palynology and ecology. However all investigations made, pointed to a relatively pronounced continuity." "... all crosses within ssp. *minor* resulted in fertile progeny." Proctor & Nordborg (1968) in *Flora Europaea* add "Differences in the hypanthium are often clearly marked, but they are not always satisfactorily correlated with other characters. So far as is known, there are no sterility barriers between the subspecies which are described."

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