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TAXONOMY OF THE SOUTH AUSTRALIAN SPECIES ALLIED TO *HAKEA ULICINA* R. BR. (PROTEACEAE)

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Abstract

Taking into account the recent publication of the new species *H. repullulans* H.M. Lee from western Victoria and South Australia, it is shown that the name *H. ulicina*, widely used in the past, does not apply to South Australian *Hakea*. The name *H. carinata* F. Muell. ex Meissner is re-instated for a species endemic to the Flinders and Mt Lofty Ranges and the South Eastern region. *H. muelleriana* J. Black is confirmed as a distinct species, occurring in drier regions from Eyre Peninsula to the South Eastern region and extending to Kangaroo Island and Victoria. The occurrence of exceptionally broad-leaved forms of this species on Kangaroo Island warrants further biological and taxonomic investigation. *H. aenigma* W.R. Barker & Haegi, a Kangaroo Island endemic apparently most closely related to *H. repullulans*, is described. This new species is unusual in its sterility, apparent genetic uniformity and complete dependence on suckering as a means of reproduction.

Introduction

In the absence of any comprehensive treatment of *Hakea* since that of Bentham (1870) taxonomic concepts within the genus have developed largely in regional floras. Included among the species of *Hakea* treated in the most recent flora account for South Australia (Black 1948) were *H. muelleriana* J. Black and *H. ulicina* R. Br., including its variety var. *latifolia* J. Black. In a supplement to Black's Flora, Eichler (1965) expressed doubt about the rank of *H. muelleriana*, suggesting it might better be treated at the infraspecific level, as "*H. ulicina* var. *flexilis* FvM. ex Black." Several years later Willis (1973) retained *H. muelleriana* without comment in his handbook on the Victorian flora but stated that recognition of var. *latifolia* within *H. ulicina* hardly seemed warranted. In an account of the native shrubs and trees of south-eastern Australia, however, Costermans (1981) applied Black's (1948) treatment, though without reference to the statements of either Eichler (1965) or Willis (1973).

Material of a Kangaroo Island *Hakea* first collected in 1924 by J. B. Cleland was initially regarded as close to *H. multilineata* (Cleland & Black 1927) and included in that species by Black (1948). Eichler (1965) found that all South Australian material previously assigned to *H. multilineata* was to be known as *H. francisiana*, and in an account of this group of species, Maconochie (1973) indicated that the Kangaroo Island *Hakea* known only from a small number of mostly sterile specimens, had close affinities with the latter. More recently, one of us (W.R.B.) recognised the affinity of this material with *H. ulicina*. The same conclusion was evidently drawn independently by Cleland (1967) who included "*H. ulicina* and var. nov." on a cyclostyled list of Kangaroo Island plants.

Against the background presented above a *Hakea ulicina* complex can be recognised. The existence of such a complex, requiring taxonomic clarification, has been evident from the uncertainty in application of names in the collections of the State Herbarium of South Australia. In particular, the apparently continuous gradation from very narrow, terete or triquetrous leaves c. 1 mm broad to linear-obovate leaves over a centimetre broad seems to have provided a significant impediment to distinguishing the described taxa.

On the basis of the study of these specimens and the collections of the National Herbarium of Victoria, combined with anatomical studies and fieldwork on mainland South Australia and Kangaroo Island, a revised classification is proposed. Names are applied

following examination of relevant type material from the above and other herbaria. In South Australia, the endemic species *H. carinata* F. Muell. ex Meissner is re-instated for plants from the Flinders and Mt Lofty Ranges, and the South-Eastern region. *H. muelleriana* J. Black is confirmed as a distinct species, occurring in drier regions including Eyre Peninsula, Yorke Peninsula, Murray and South-Eastern regions, Kangaroo Island and extending to western Victoria. *H. aenigma* W.R. Barker & Haegi, endemic to Kangaroo Island, is newly described.

This study began in the form of an Honours Degree research project and the resulting thesis is referred to where aspects have been considered in more detail than can be reported here. During the extended course of the study another detailed investigation of *H. ulicina*, centred on Victorian populations, has led to the segregation of the new, very closely related species *H. repullulans* (Lee 1984). This species, which is taxonomically equivalent to *H. ulicina* var. *latifolia,* completes the representation of the *H. ulicina* complex in South Australia. Its main occurrence is in the western half of Victoria. *H. ulicina* s.str. does not occur in South Australia, but is found in central and eastern Victoria and New South Wales and on the islands of Bass Strait. *H. repullulans* is distinguished from *H. ulicina* s.str. principally in being lignotuberous. Except where they differ in this character, the other species of the complex are distinguished from *H. ulicina* s.str. essentially in the same features as those by which they differ from *H. repullulans.*

References to the works of earlier authors are arranged within the treatment of each species in such a way that the history of taxonomic concepts including the misapplication of names is made clear.

Morphology

Several diagnostic features brought to light in this study were obscured in the past by confusing variation. These, together with important distinguishing characters, some of a subtle nature requiring explanation, are discussed here.

Habit

The presence in *H. repullulans* (Lee 1984) and *H. aenigma* of a lignotuber and horizontal root system producing adventitious aerial shoots distinguishes these species from *H. carinata* and, so far as is known, *H. muelleriana.* Plants of the first two species resprout after fire while plants of the last two are killed by fire, regenerating only from seed (*H. carinata*: *Haegi 2703*). Some forms on Kangaroo Island assigned for the time being to *H. muelleriana* need to be investigated further with respect to this characteristic. The horizontal root-system is especially well developed in the sterile *H. aenigma*, in which new plants are established entirely from adventitious shoots arising from these roots. Leafy aerial shoots up to 50 cm tall arising at intervals of about 1 m along a horizontal root 2 cm in diameter and 4 to 5 cm under the soil surface were observed in one population (*Haegi 2287*). The stems of these shoots, 0.5 cm in diameter, were thickened to 2 cm in diameter below the soil surface and the root was swollen to c. 3 cm at the point of attachment but no finer roots were present at this point (figs 9B, C).

Branching habit is variable in all species but some distinct trends are apparent. Plants of *H. aenigma*, *H. carinata* and *H. repullulans* are usually single-stemmed and sparingly branched or bear short lateral branches. This trend is best developed in *H. carinata* which is usually a narrowly erect, divaricately branched shrub of somewhat irregular proportions. Plants of *H. muelleriana* generally have a rounded shape, resulting from free development of lateral branches from the very base upwards. Single-stemmed, arborescent forms of *H. muelleriana* are found in dry forest associations at some sites on Kangaroo Island.

Indumentum

As in most species of *Hakea* (Bentham 1870), the new shoots of the species considered here are beset with a dense indumentum of closely appressed horizontal hairs attached by a short central stalk. These T-shaped hairs are generally rust-brown in colour and have been largely lost from the leaves by the end of the first season of growth. This applies to all species of the *H. ulicina* complex, which have essentially glabrous leaves in the mature state, though in *H. repullulans* and, to an even greater degree in *H. aenigma*, the indumentum tends to persist sparsely beyond the first season. The type and persistence of the hair covering of the branchlets is more useful diagnostically.

The branchlets of *H. muelleriana* are soon glabrescent, being glabrous (and deep reddish-brown) by the time of flowering. In the other species a more or less persistent indumentum occurs and the underlying surface of the branchlet is deep grey-brown. In *H. aenigma* this indumentum consists of rust-brown appressed T-shaped hairs with a few colourless ones, most of the coloured ones eventually losing their colour with age. This hair-covering always persists until and down to the point where flowering begins on the branchlet and may persist a further season or two until it is eventually replaced by grey, smooth bark. *H. carinata* is similar but its indumentum has a finer texture and is deciduous a little sooner.

In *H. repullulans* the branchlet indumentum is more variable but almost always persists well beyond flowering. Early glabrescence has been seen only on vigorous new adventitious shoots. Usually, the indumentum is quite distinctive and consists of densely arranged, porrect, colourless or stramineous hairs. These hairs are usually forked with one long erect arm and the other very short or absent. In some specimens however, the hairs may be mixed and of up to three types: appressed horizontal (few, probably remnants of initial indumentum on new shoot); forked with equal oblique arms; forked with one main erect arm. The first two types are apparently always rust-brown at first, losing their colour with age. Frequently the tomentose axes are black because of the presence of a black fungus. In all cases, *H. repullulans* is distinct from the other species because a substantial component of the indumentum consists of non-appressed hairs.

Leaves

Various characters of the leaves serve to distinguish the species of the complex though these have generally been poorly understood in the past. Lee (1984) has described the important features of the leaves of *H. ulicina* and *H. repullulans*. Probably the most distinctive and readily identifiable foliar character in the complex is the orientation of the lamina. In *H. repullulans* (and *H. ulicina*) the leaf is twisted through 90° at the base so that the lamina lies in a vertical plane. This readily distinguishes these species from the other South Australian species in which no twisting occurs and the lamina, though sometimes up- or down-curved, is horizontally oriented.

Leaf shape

Leaf shape and especially leaf width are extremely variable among the species of the complex. *H. aenigma* is perhaps most distinct, having considerably longer leaves than in the other species. Among the remaining species however, the high degree of variability in leaf shape has led to considerable confusion, especially in South Australia where the distributions of all three species overlap. In the past the narrowest-leaved plants were assigned to *H. muelleriana* (earlier as *H. ulicina* var. *flexilis*), the intermediate ones to *H. carinata* (as *H. ulicina* var. *carinata* or as *H. ulicina* and therefore not distinguished from Victorian *H. ulicina* s.str.) and the broadest ones to *H. ulicina* var. *latifolia* (now *H. repullulans*). Although this is in agreement with general trends, study of the patterns of variation in other characters

(including some of the leaf) indicate that leaf shape is unreliable as a diagnostic feature. In fact, it is variable within each species and highly so within *H. carinata* and *H. muelleriana*.

As a species, *H. carinata* is characterised by a high degree of within-population variation in leaf width. Some populations are less variable than others but among most of the 49 to which the specimens can be assigned, broad and narrow-leaved plants occur together and the leaves of the broader-leaved plants are usually at least twice or three times as broad as those of the narrower-leaved plants. In some populations they are up to five times as broad.

Superimposed on this within-population variability is a pattern of variation correlated with geographical occurrence. Broad-leaved plants are more common in the south-eastern part of the distribution and the broadest-leaved plants occur there. It is only in this area, from the south-eastern margin of the Mt Lofty Ranges to the southern limit of the species, in the upper South-Eastern Region, that plants with leaves over 8.5 mm (and up to 12.5 mm) broad occur. Throughout the remainder of the distribution, the usual range of leaf breadth is 1-6 mm and leaves up to 8.5 mm are uncommon. This pattern is illustrated in the distribution map of *H. carinata* (fig. 11) which distinguishes populations with plants having leaves more than 8.5 mm broad.

With few exceptions, very broad-leaved plants occur throughout the south-eastern populations, though at least some of them are also highly variable [e.g. at Padthaway: narrow-leaved 2 mm (*Canty AD 98146347*; broad-leaved 9 mm (*Fatchen et al. AD 97641206*)]. Plants with leaves over 8.5 mm broad are absent from the collections of only three populations. In one of these (6km E of Woods Well) only three plants were seen (*Haegi 532*) and the specimens have broad leaves mostly in the range 6-8.5 mm. The second population is represented by a single specimen (*J.R. s.n. AD 97107226*) collected from the 'Archibald and Makin Wild Life Reserve', a very general locality description. Further collections from this area could well bring to light broader-leaved plants.

Leaf length is also very variable in *H. carinata* but this variation is correlated neither with that of leaf breadth nor geographical occurrence.

Throughout most of its range, *H. muelleriana* exhibits much less variation in leaf shape than *H. carinata*. On the mainland, where the greater part of its distribution occurs, *H. muelleriana* has subterete or trigonous leaves. The leaves usually dry with a shallow groove

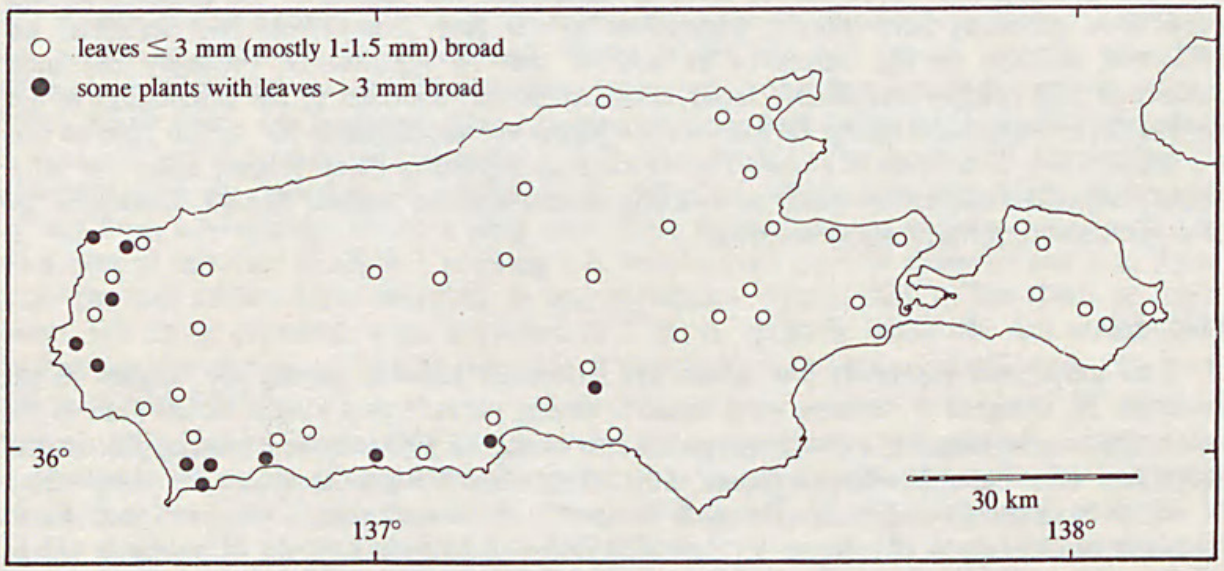

Fig. 1. Distribution of narrow-leaved and broad-leaved populations of *H. muelleriana* on Kangaroo Island, South Australia.

on the upper side (though this may not be conspicuous in the fresh state) and in transverse section are deeper than wide. This shape, an inverted isosceles triangle with two long sides, becomes more pronounced in more northern populations, especially those from northern Eyre Peninsula.

On Kangaroo Island *H. muelleriana* exhibits a much wider range of variability in leaf-shape, although subterete leaves are largely absent. Over much of the island plants with deeply trigonous leaves 1 to 1.5 mm broad and 1.5 to 2 mm deep, as sometimes seen on the mainland, occur in more or less uniform populations. However, near the southern coast in the western half and near the western coast, plants with broader more or less flat leaves mostly 3 to 6 mm broad are found (fig. 1). The broadest leaves found on mature plants, located in the far south-west near Remarkable Rocks, are up to 10 mm broad.

Populations in which broad-leaved plants occur are always variable in leaf width and in many cases individual plants are heteromorphic. This condition is characteristic of some species of *Hakea* (e.g. *H. trifurcata* (Smith)R.Br.). In *H. muelleriana* it arises because the first leaves on a new shoot are exceptionally broad while subsequent leaves exhibit a marked acrotonic decrease in breadth and are deeply trigonous in shape (fig. 2). In many cases, individual leaves are deeply trigonous at the base, passing rapidly into a broad, concave to flat form in the distal part.

Although the occurrence of broad leaves is restricted geographically in *H. muelleriana*, to date no evidence has been found of correlation with other characters. Despite the marked differences of the extreme forms, the observations on the pattern of variation do not support recognition of distinct taxonomic entities at any level. Investigations into biological aspects of the variation, particularly in relation to regeneration after fire, are continuing.

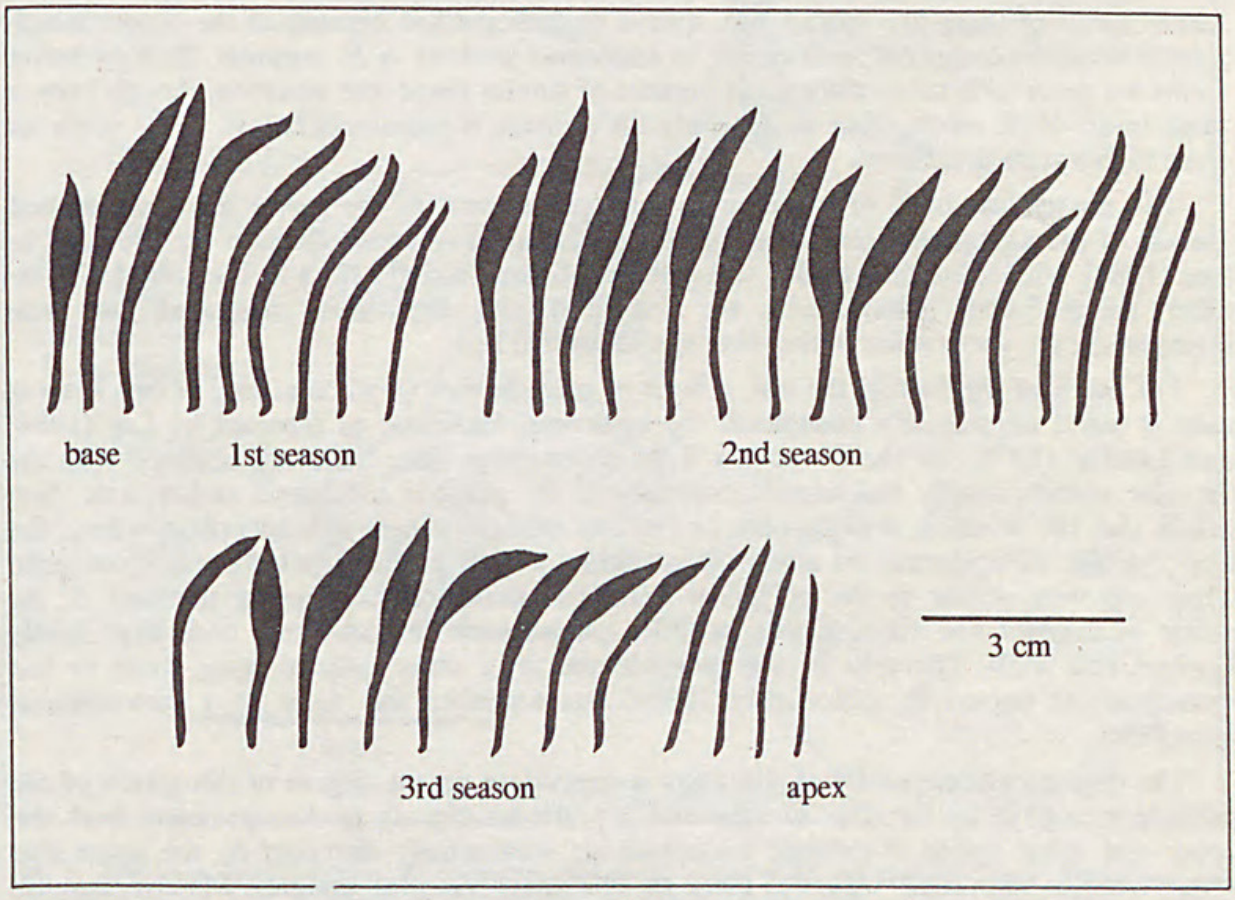

Fig. 2. Heteromorphic foliage in *H. muelleriana*: silhouettes of leaves from a single axis showing acrotonic decrease in leaf-width within each of three successive seasons' growth (*Haegi 341*).

Vein Prominence and its Anatomical Basis

The absence of conspicuous venation on the upper surface of the leaf was a distinguishing feature noted by Meissner (1856) in the original description of *H. carinata*; *H. ulicina* had been described as having one to three longitudinal veins prominent on both sides. In general, these observations still apply to the more broadly circumscribed *H. carinata* and to *H. repullulans*, a close relative of *H. ulicina*.

Usually only the veins along each margin and the midvein on the underside are prominent in *H. carinata*. The upper surface of the leaf is smooth. In some broad-leaved forms, two or rarely more additional longitudinal veins may be prominent on the underside. The veins of the lamina are only rarely visible on the upper surface in fresh material, but usually become faintly visible in dried material of broad-leaved plants.

The conspicuous, prominent longitudinal venation on both sides of the leaf in *H. aenigma* and *H. repullulans* usually distinguishes these species readily from broad-leaved forms of both *H. carinata* and *H. muelleriana*. In *H. aenigma* a greater number of veins (six to nine) is conspicuous on the underside of the leaf and these are usually more prominent than the one to four veins seen on the upper surface. The usually greater number of prominent veins and their closer spacing distinguishes *H. aenigma* from *H. repullulans*. In *H. repullulans*, five (or rarely three or seven) veins in addition to the marginal veins are usually equally conspicuous on both sides of the leaf.

The trigonous-leaved forms of *H. carinata* and *H. muelleriana* are similar in venation, with two marginal veins prominent together with the midvein on the underside. This venation is largely masked in subterete-leaved forms of *H. muelleriana* though it is somewhat more apparent in dried specimens, the leaves of which are often grooved above. The narrow-leaved forms of these two species can always be distinguished because of the proportionally greater breadth (compared with depth, in transverse section) in *H. carinata*. Broader-leaved forms are more difficult to distinguish because of similar shape and venation, though even in these forms of *H. muelleriana* usually only the midvein is prominent below. Only rarely are three to five veins prominent.

The anatomical basis of variation in vein prominence in the leaves has been studied. Details of the anatomy of the leaves of *H. repullulans* in transverse section are provided by Lee (1984) who refers also to the observations of Hamilton (1927) and Lamont (1976) on other species. Lee's observations are confirmed and the tissues described and their arrangement are very similar in the other species treated here.

For much of the bulk of the leaf, a layer of palisade mesophyll consisting of two rows of cells is found immediately underneath the epidermis. However, as reported by Lee (1984) and Lamont (1976) for the *H. sulcata* R.Br. group, large fibre bundles associated with the vascular strands disrupt the lateral continuity of the palisade mesophyll and it is at these points that the venation is prominent on the leaf surface. Where this disruption occurs, the fibre bundle and epidermis are always separated by a layer of thick-walled parenchyma cells. These are very similar to the polygonal starch-containing cells occupying the bulk of the centre of the leaf and staining with acidified phloroglucin indicates that both have lightly lignified cell walls. The cells of the subepidermal layer differ only in being more or less rectangular in transverse section. Lee (1984) has described this tissue as a *discontinuous hypodermis*.

The degree of prominence of the veins is dependent on the degree of disruption of the palisade mesophyll by the fibre bundles and hypodermis (fig. 3). In *H. repullulans* both the upper and lower bands of palisade mesophyll are substantially disrupted by the upper and lower bundles associated with the three or five main vascular bundles. Massive bundles associated with large vascular strands also disrupt the palisade mesophyll at the margins. This occurs also in *H. carinata*, but only the band of mesophyll along the underside of the leaf is

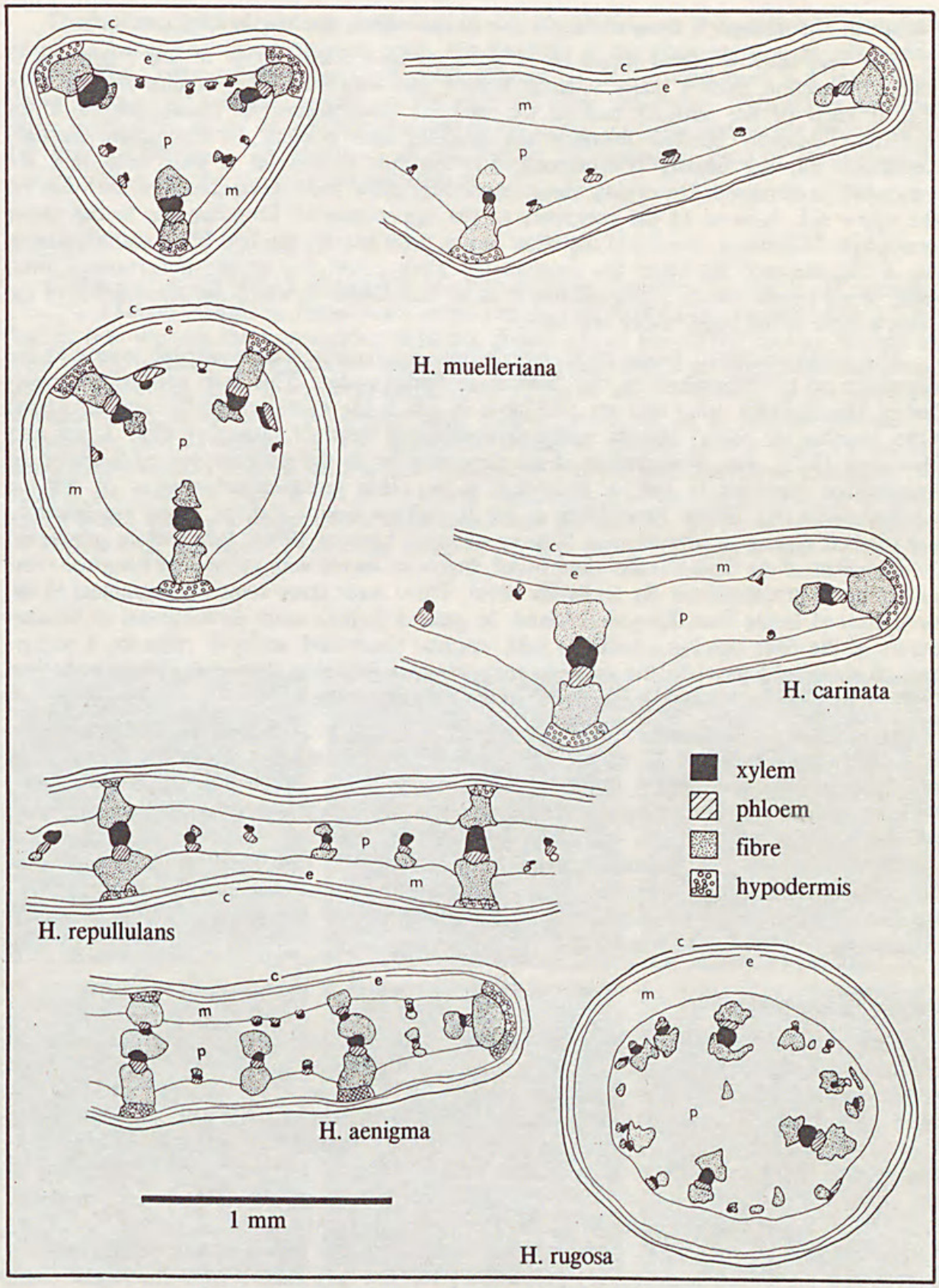

Fig. 3. Anatomical zone diagrams of transverse sections of leaves of *H. muelleriana* (*Haegi 341*, 3 sections), *H. carinata* (*Haegi 261*), *H. repullulans* (*Haegi 535*), *H. aenigma* (*Haegi 2288* and *Barker*) and, for comparison, *H. rugosa (Haegi 271*, 20.ii.1973, 5½ km S of Ashbourne on Goolwa road, AD), a terete-leaved species from Section *Hakea* lacking hypodermis; c, cuticle; e, epidermis; m, mesophyll; p, parenchyma.

disrupted. The mesophyll along the upper side is continuous, resulting in a smooth surface.

The very narrow-leaved forms of *H. carinata* have leaves more or less triangular in transverse section, with a major vascular bundle and associated fibre bundles at each apex (i.e. at each of the margins and at the midvein underneath). In broader-leaved forms additional vascular bundles between the midvein and margins become more strongly developed but are usually conspicuous only beneath because it is only here that the mesophyll is disrupted. On drying, these leaves may show some prominence of the veins on the upper side because of the proximity of the upper massive fibre bundles to the upper mesophyll. In contrast to most of the other tissues these heavily lignified fibres scarcely shrink on drying. Because the veins are considerably more prominent on the undersurface, even these broad leaves remain distinguishable from *H. repullulans* in which the prominence of the veins is more or less equal above and below.

The subterete-leaved forms of *H. muelleriana* are usually slightly angled, owing to the disruption of the mesophyll by the three main fibre bundles. This is in contrast to terete-leaved species from other sections of *Hakea* in which the vascular bundles and associated fibre bundles are found entirely within a continuous band of mesophyll (fig. 3; see also Hamilton 1927). The development of the fibre bundles in the subterete-leaved forms of *H. muelleriana* however is not as extensive as in other terete-leaved species of Section *Conogynoides* (e.g. Series *Teretifoliae* or the *H. sulcata* group) and the leaves are therefore not markedly striate or ribbed as in those species (see Lamont 1976). When more substantial development of the fibre-bundles does occur, trigonous leaves with prominent marginal veins and midvein prominent on the underside occur. These same three veins are prominent in the broad-leaved forms from Kangaroo Island. In general there is more development in broader leaves of the fibre bundles associated with vascular tissue and, as in *H. carinata*, a pair or two of veins additional to the midvein may, on rare occasions become prominent below. Some venation may become visible above in dried broad leaves.

H. aenigma has a distinctive leaf anatomy. It is similar to *H. repullulans* in having some veins prominent on both sides of the leaf. However, whereas the prominence of the veins on the upper and lower surfaces results from the development of the upper and lower fibre bundles associated with a single vascular strand in *H. repullulans*, it is attributable in *H. aenigma* to fibre bundles from two different vascular strands, one positioned above the other and separated by a fibre bundle. Among the species studied here, such paired strands have been observed only in *H. aenigma*. A similar arrangement was observed by Lamont (1976) for the two main vascular bundles in *H. gilbertii* Kipp. ex Meissner, a species of the *H. sulcata* group with ribbed terete leaves.

Pollen Morphology

Differences in gross morphology of the pollen grains provide useful diagnostic characters. Pollen from mature dehiscing anthers from one or two specimens of each species was studied using a scanning electron microscope. The resulting observations were confirmed by study of pollen stained with methyl green/phloxine or 0.1% cotton blue in lactophenol from several specimens of each species using a compound light microscope. Pollen grains of the different species differ in overall shape, sculpturing of the surface and degree of distinctness of the pore membrane (fig. 4). The pollen of *H. repullulans* is indistinguishable in external appearance from that of *H. ulicina* s.str., as observed also by Lee (1984). In this type, the sides of the triporate, triangular grain are convex and the almost smooth, very prominent pores are very distinct from the rugose exine of the body of the grain. The undersized, sterile and apparently empty pollen grain formed in *H. aenigma* (see Breeding System) are similar to the *H. ulicina* type but the texture of the sculpturing on the body is finer. A closer relationship of *H. aenigma* with *H. repullulans* and *H. ulicina* than with the other species is suggested by pollen morphology.

The pollen of *H. carinata* is similar to that of *H. ulicina* and *H. repullulans* in overall shape, including the very prominent pores, but the sides of the grain are straight rather than convex. The surface characteristics are quite different. In *H. carinata* there is a moderately dense covering of tubercles which extends onto the pore membrane. The grains therefore differ from those of the *H. ulicina* type also in the pores not being noticeably distinct from the body of the grain. The grains of *H. muelleriana* are similar to those of *H. carinata* in surface texture but the tubercles are more sparse.

Follicle

Characters of the follicle distinguish *H. carinata* from the other species of the complex (fig. 5). The distinguishing features are most readily observed in the median view of the follicle (i.e. viewing the suture rather than the dorsal side of one of the valves). In median view, the follicles of *H. carinata* are elliptic to ovate-elliptic with a gradually attenuated base and an acuminate apex tapering gradually into a slender beak. The beak is the persistent thickened base of the style and being fragile readily breaks off. In *H. muelleriana* and *H. repullulans* (and *H. ulicina*: cf. Lee 1984), the follicle in median view is ovate in outline, being proportionally broader and narrowed much less at the base than in *H. carinata*. The apex is not gradually tapered but has a lateral protuberance of varying prominence on each valve, which may be a vestige of the horn found near the apex on the valves of other species of *Hakea* (e.g. see Black 1948). The beak (1-2.5 mm in *H. repullulans* and 1-3.5 rarely

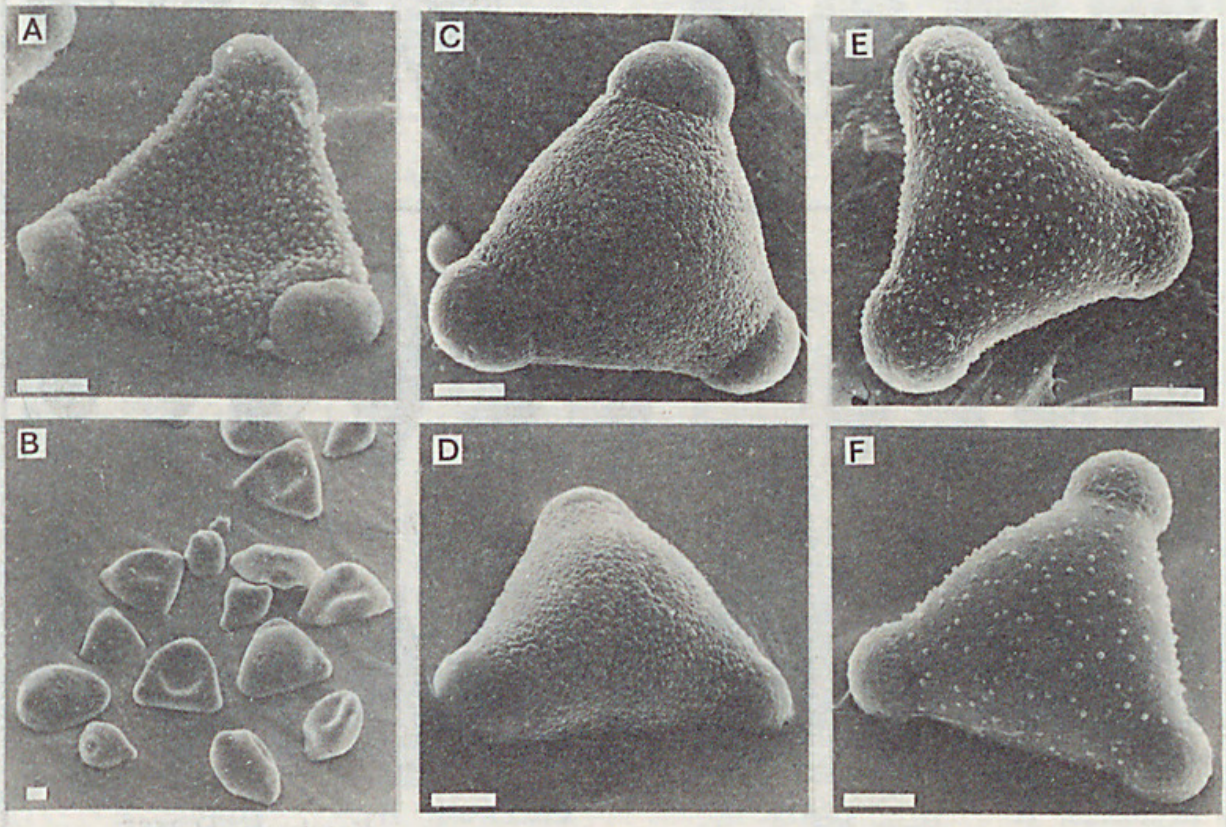

Fig. 4. Pollen morphology of species in the *H. ulicina* complex in southeastern Australia (scanning electron micrographs). A & B *H. aenigma* (pollen sterile, mostly collapsed: *Jackson 1212*); C, *H. repullulans* (*Muir 875*, 27.ix.1959, Mirranatwa Gap, Grampians, Victoria, MEL); D, *H. ulicina* (*Morrison*, s.n., 28.ix.1890, Frankston, Victoria, AD96412179); E, *H. carinata* (*Haegi 196*); F, *H. muelleriana* (*Wilson 1419*). Scales 10 μm.

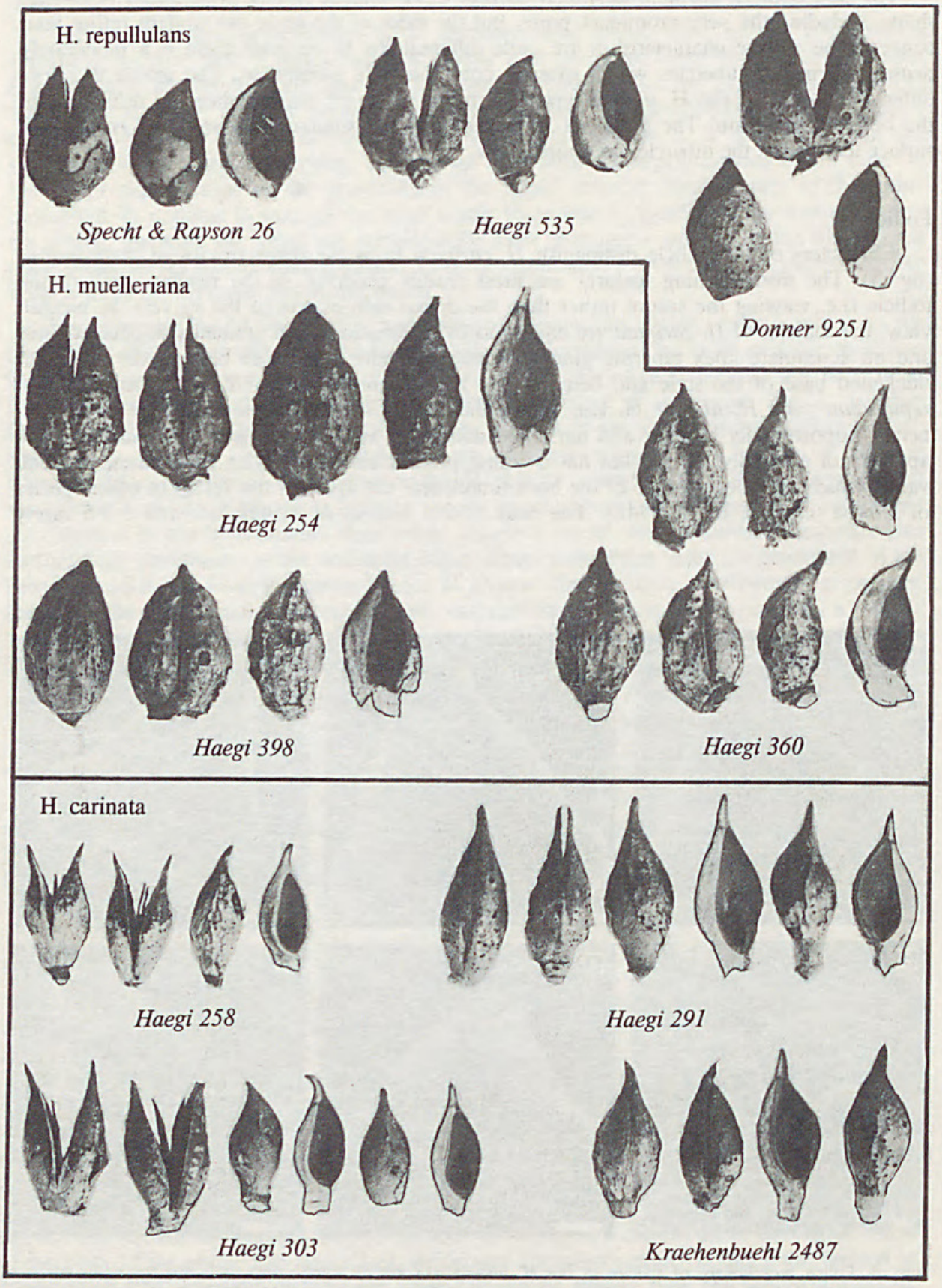

Fig. 5. Follicles (actual size) of the South Australian species allied to *H. ulicina*. Samples show median, lateral and inner views and are from single plants.

4 mm in *H. muelleriana*) is usually much shorter than in *H. carinata* (4-6.5 rarely only 3 mm) but care must be taken in using this as a distinguishing character because the beaks are frequently broken off. Fruit do not form in *H. aenigma*.

Seed

Useful diagnostic characters are found in the winged seeds (fig. 6). The seed-wings of *H. ulicina* and *H. repullulans* are indistinguishable and are uniformly blackish-brown, while those of *H. muelleriana* are pale grey-brown with blotches or streaks of darker pigmentation. The seed-wing in *H. carinata* is almost as dark as in *H. repullulans* but not quite as evenly pigmented; it is readily distinguished from *H. muelleriana*.

Two further features of the seed vary among the species. *H. carinata* has an almost globular to obovoid 'seed-body' (the solid part containing the embryo) with the testa extending as a ridge more than halfway towards the wing apex. This is readily seen in a longitudinal silhouette. The seed-body of *H. muelleriana* differs in being ellipsoid to ovoid-ellipsoid and the ridge extends scarcely more than a third of the way to the wing apex. It also begins higher up on the seed body than in *H. carinata*. In *H. repullulans* (and *H. ulicina*) the seed-body is usually larger than in the other species, and broadly elliptic in shape. The main ridge is very short or absent, being replaced by small narrow islands of hard tissue.

Breeding System

The species of the *H. ulicina* complex exhibit a variety of breeding systems which are usefully considered in relation to regeneration following fire. Where fruits are produced, these are woody and fire-resistant; they persist on the plant unopened, dehiscing to release the protected seed only following the death of the branch on which they are held.

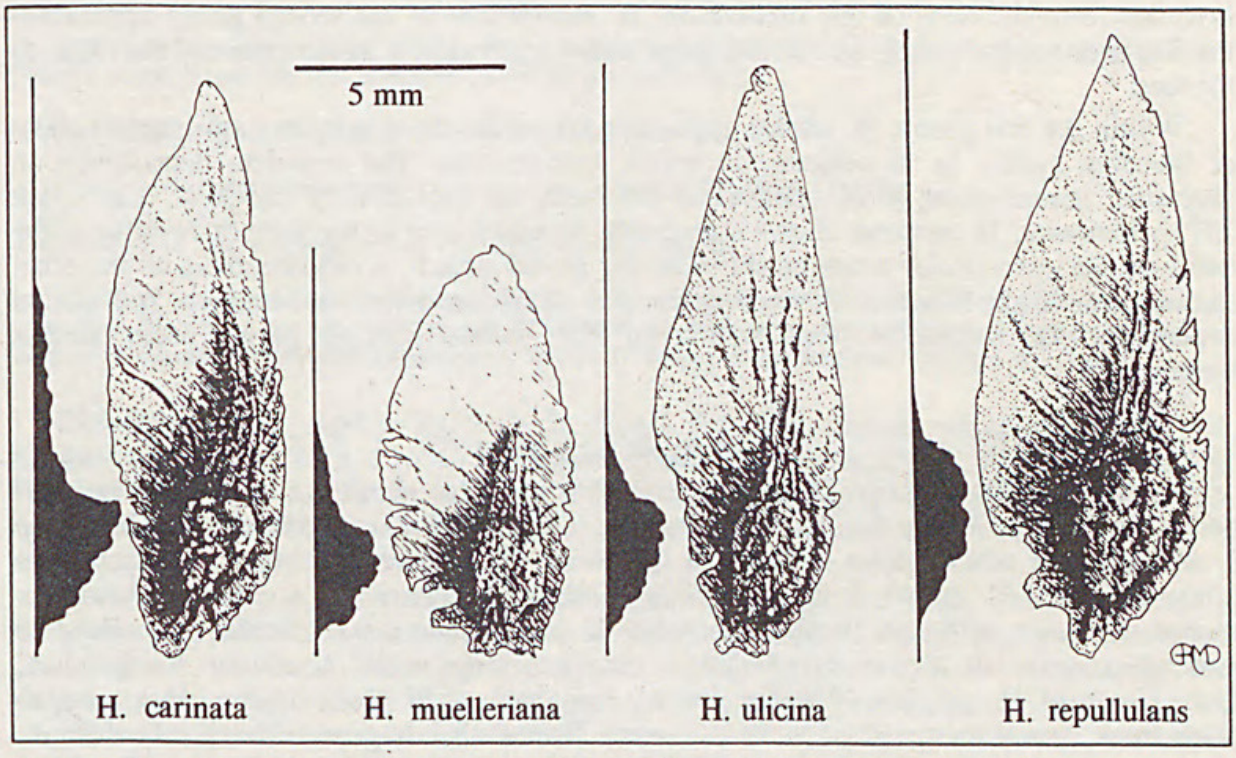

Fig. 6. Seeds of *H. carinata* (*Haegi 291*), *H. muelleriana* (*Haegi 274*), *H. ulicina* (*Czornij 473*, 9.xii.1971, Genoa Creek Track, c. 5 km W of Genoa, Gippsland, Victoria, AD) and *H. repullulans* (*Spooner 5380*) with longitudinal profiles showing shape of seed body and extent of ridge. Scale 5 mm.

At one extreme of the range of breeding systems is a strategy dependent entirely upon sexual reproduction involving bisexual entomophilous flowers. Fire kills such plants but promotes abundant seedling production, as in *H. ulicina* (Lee 1984) and *H. carinata*. At the other extreme is the complete dependence of *H. aenigma* on vegetative reproduction by means of horizontal subterranean roots from which suckers rise. A balance between these two reproductive strategies is found in *H. repullulans* which produces fruit but also regenerates from a lignotuber and horizontal roots (Lee 1984). The development of functionally male and female together with apparently bisexual plants in this species (Lee 1984) may function to maintain adequate variability within populations through outcrossing. This would compensate for the tendency for genetic uniformity through vegetative reproduction. Lee (1984) further observed that 'desert' or sand-heath populations of *H. repullulans* (based on material from Big Desert and Little Desert, Victoria) are consistently bisexual-flowered with all plants setting fruit. However, populations in South Australia which adjoin these same Victorian sand-heaths show highly malformed pollen (*Specht & Rayson 26*; *Symon 10781*).

Knowledge of the breeding system in *H. muelleriana* is far from complete. Judging from herbarium specimens and labels, most plants, particularly from mainland populations, produce abundant fruit and suckering has not been recorded, suggesting a strategy similar to that of *H. carinata*. However, as suggested above (see Leaf Shape) there is reason to investigate further the broad-leaved populations of *H. muelleriana* on Kangaroo Island. Pronounced differences in the abundance of fruit on different plants within populations has been observed but the reason for this is unknown.

Relationships

The *H. ulicina* complex in south-eastern Australia divides into two groups, the first comprising *H. ulicina*, *H. repullulans* and *H. aenigma*, the second *H. muelleriana* and *H. carinata*. Leaf venation characters, pollen morphology and indumentum persistence on the branches form the basis of this subdivision. *H. muelleriana* of the second group approaches the first group more closely by its fruit shape and is intermediate in the extent of the ridge on the seed.

Within the first group, *H. ulicina* appears to posses the more primitive attributes in terms of breeding system in its reliance on sexual reproduction. The complete dependence on vegetative reproduction in *H. aenigma* is obviously an evolutionary end-point (e.g. Grant 1971). However, *H. aenigma* shows a probably primitive trait in the lack of twisting of the leaf base. Its leaf vascular arrangement in having paired strands, is different from all the other species examined. Whether there is a parallel development of unisexuality and partial dependence on vegetative reproduction in the second species group needs further investigation.

Taxonomic Treatment

Bentham (1870) included *H. ulicina* and *H. carinata* (as *H. ulicina* var. *carinata*) in his Series *Nervosae* of *Hakea* Section *Conogynoides*. There is no reason to doubt that *H. ulicina* is related to the other species included in this series: *H. plurinervia* F.Muell., *H. dactyloides* (Gaertner)Cav., *H. falcata* R.Br. and *H. pycnoneura* Meissner, all non-South Australian species. However, although Bentham included *H. muelleriana* (as *H. flexilis*) with Western Australian species in Series *Teretifoliae* it clearly belongs with *H. ulicina*. Furthermore, species such as *H. ambigua* Meissner and *H. stenocarpa* R.Br. from nearby series seem to relate more closely to species of Series *Nervosae*. Bentham's infrageneric classification clearly needs re-appraisal. For the purposes of this account, a key distinguishing the *H. ulicina* complex from other *Hakea* found in South Australia and separating the species within the complex, is provided.

Key to Species of *H. ulicina* Complex in South Australia

1. Pollen presenter erect [inflorescences with 8-36 flowers, the rhachis 0.25-1 cm long; pistils 3-8.5 mm long; perianth glabrous outside; leaves simple].
   2. Leaves with usually 3-5 longitudinal veins (rarely only the midvein) on the upper side as prominent as the vein on the lower side; plant suckering; seed, if present, with ridge absent or very short.
      3. Leaves 5-35 cm, usually 9-23 cm long, not twisted; inflorescence-involucre 6-10 mm long, rhachis 2.5-4 mm long; pedicel 3-5 mm long; fruits never developing ..... *H. aenigma* 1.
      3. Leaves 4-10.5 cm, rarely to 14 cm long, twisted at the base; inflorescence-involucre 2.5-5 mm long, rhachis 1-2 mm long; pedicel 1.8-3.1, rarely to 3.6 mm long; fruits able to develop ..... *H. repullulans* 2.
   2. Leaves with the upper side excluding margins lacking prominent veins or midvein, rarely on broad leaves the veins of the lower side showing through faintly when dried; plant not suckering; seed with a ridge extending one-third to halfway to the apex of the wing.
      4. Fruit in median view elliptic to narrowly ovate-elliptic, gradually attenuated into narrow beak; beak fragile, 4-6.5 mm, rarely 3 mm long; seed wing evenly dark-brown ..... *H. carinata* 4.
      4. Fruit in median view oblong- to ovate-elliptic, often broadly so, usually with a protuberance on either side of the apex in median view below the beak; beak 1-2.5 rarely 4 mm long; seed wing light-brown with dark-brown streaks ..... *H. muelleriana* 3.
1. Pollen presenter oblique or erect [if erect then either inflorescences with 50-100 flowers, (the rhachis 2-9 cm long), pistils 14-19.5 mm long (*H. francisiana*, *H. laurina*, *H. minyma*), *or* perianth pubescent outside and leaves compound (*H. ednieana*)] ..... Other species of *Hakea* in South Australia.

1. **Hakea aenigma** W.R. Barker & Haegi, sp. nov.

'*H.* near *H. multilineata*, Meisn.': Cleland & J. Black, Trans. Roy. Soc. S.Austral. 51 (1927) 35 (as to *Cleland AD 97111126*).

H. multilineata auct. non Meissner: J.Black, Fl. S.Austral. edn 2 (1948) 267, p.p. (as to 'Kangaroo Island (Flinders Chase)'); Wood, Trans. Roy. Soc. S.Austral. 54 (1930), p.p. (as to 'W').

?'*Hakea ulicina* .... var. nov.': Cleland, Plants of Kangaroo Island (Aug. 1967) 6.

'*H.* cf. *francisiana* FvM.': Maconochie, Trans. Roy. Soc. S.Austral. 97 (1973) 132, 133.

'*Hakea* sp.': W.R. Barker in Jessop, List. Vasc. Pl. S.Austral. (1983)75.

Frutex *H. ulicinae* sensu lato affinis surculis lignotubere et systemate horizontali radicum exorientibus floribus omnino sterilibus, fructibus haud evolutis, sed differt inter alia foliis longioribus (5-35 cm cf. 4-10.5 cm) basi non tortilibus, involucro inflorescentiae longiore (6-10 mm cf. 2.5-5 mm), rhache longiore (2.5-4 mm cf. 1-2 mm).

Holotypus: *W.R. Barker 4479 & L. Haegi*, 6.x.1982, 'South Australia. Region 12: Kangaroo Island. 35°49′S, 136°46′E. Flinders Chase; Shackle Road, ca. 2.8km by road S of Playford Highway, ca. 1.5 km by road NNE of N crossing of Bull Creek'. AD 98346065. *Isotypi*: MEL, NSW, K, CANB, PERTH.

Compact shrub to 2.5 m high, with ascending smooth branches, suckering from a lignotuber and a horizontal root system; *branchlets* with a more or less appressed tomentum persisting at least until flowering sometimes patchily glabrescent; *leaves* ascending, flat, narrow-linear to linear, 5-35 cm x 3-10 mm, not consistently twisted at the base, with 1-6 longitudinal veins above, 4-9 veins below, mucro 0.7-1.5 mm long; *involucral cone* ovoid, 6-10 mm long, apex and margins of bracts white-hirsute; *racemes* with 16-33 cream-white flowers; *rhachis* 2.5-4 mm long, white hirsute; *pedicel* 3-5 mm long; *perianth* 3-3.5 mm long, limb 0.8-1.1 mm long; *anthers* 0.5-0.6 mm long; *gland* absent; *pistil* 4.5-7.2 mm long;

pollen-presenter a narrow cone 0.5-0.8 mm long, dilated slightly at the base into a narrow flange 0.45-0.7 mm diam.; *fruits* never forming. Figs 7, 9.

Distribution and Ecology (fig. 10).

H. aenigma is confined to the western end of Kangaroo Island where it occurs on the upper parts of a lateritic plateau system. It is found in dense, heathy mallee-shrubland or sometimes on open sites regenerating after fire, on sandy to clayey loam soils of the Dy 5.41 type (Northcote 1960). Flowering occurs from late September to early November.

Conservation Status

Although *H. aenigma* is known from several populations, with one to in the order of one thousand individuals (R. Davies, pers. comm. 1983), none of these is extensive in area and the species is restricted to a relatively small region. With no sexual reproduction and propagation being solely by suckering the species is highly uniform genetically, as seen in its limited morphological variability. It therefore lacks the genetic resilience of sexually reproducing species. *H. aenigma* may be considered rare but does occur in the Flinders Chase Conservation Park. Applying the criteria of Leigh et al. (1981) it is assigned the conservation status 2RC.

Notes

1. The species epithet is from the Latin *aenigma*, a riddle, in reference to the puzzlingly unsuccessful repeated searches for fruits, the unusual life-history of the species and the long uncertainty about its identity and affinities.

2. In its fullest form the authority for this species is 'W.R. Barker & Haegi in Haegi & W.R. Barker, J. Adelaide Bot. Gard., etc.'

3. The restriction of *H. aenigma* with its solely vegetative mode of reproduction to an off-shore island begs the question why the capacity to reproduce sexually was lost. More work is required to answer this. Is there evidence of high polyploidy? Are pollinators such as work on *H. repullulans* present on Kangaroo Island?

With the closest of its nearest relatives, *H. repullulans*, occurring in the Upper South-East of mainland South Australia, *H. aenigma* or its progenitor must have arrived on the island during a period when the sea-level dropped sufficiently to allow a linking land bridge; such periods have occurred several times during the Pleistocene (Daily et al. 1979; Bowler 1982).

Despite the limited capacity of *H. aenigma* to spread because of its reliance on suckering from horizontal roots, it has attained a range of approximately 30 x 15 km. Effectively a single clone, the species could represent one of the oldest plants known.

Specimens examined

SOUTH AUSTRALIA. KANGAROO ISLAND: *Anon. per J.B. Cleland s.n.*, x.1965, Flinders Chase (AD); *W.R. Barker 4479 & L. Haegi*, 6.x.1982, Flinders Chase; Shackle Road, ca 2.8 km by road S of Playford Highway, ca 1.5 km by road NNE of N crossing of Bull Creek; ca 13 km direct NNE of Rocky River (AD, holotype); *C. Baxter A-C*, xii.1982, same locality as *Barker 4479* (AD.); *C. Baxter D-F*, xii.1982, same locality as *Haegi 2287* (AD); *C. Baxter G-H*, xii.1982, same locality as *Haegi 2288* (AD); *J.B. Cleland (Herb. J.M. Black) s.n.*, xi.1924, Flinders Chase (AD 97111126); *J.B. Cleland s.n.*, 27.xi.1954, Shackle Road, Flinders Chase (AD 96807235); *N. Coles 63*, 19.x.1965, Shackle Road, 2 miles (ca 4 km) in from Playford H[ighway] (AD); *B.J. Conn 1085*, 14.xi.1980, Watters' mail box, Western River headwaters (AD); *P. Copley s.n.*, i.1982, ridge W of Western River (West Branch), ca three-quarters km NNE of entry road to 'Yakilo' farm, ca 5 km direct NNE of turnoff from Playford Highway, on road to Waterfall Creek and Red Hill, (AD 98346066); *R. Davies 14 & W. Bushman*, 6.x.1983, 3.0 km east of West Bay Road along road to Larrikin Lagoon (AD); *L. Haegi 410-411*, 12.iv.1973, 25 km directly north of Karatta on a road running parallel to and situated 5 km north of the Playford Highway, near the source of Western River (AD); *L. Haegi 2287 & W.R. Barker*, 6.x.1982, Flinders Chase Conservation Park, 3 km WNW of Shackle Road turnoff along Playford Highway to Cape Borda (AD); *L. Haegi 2288, 2288A & W.R. Barker*,

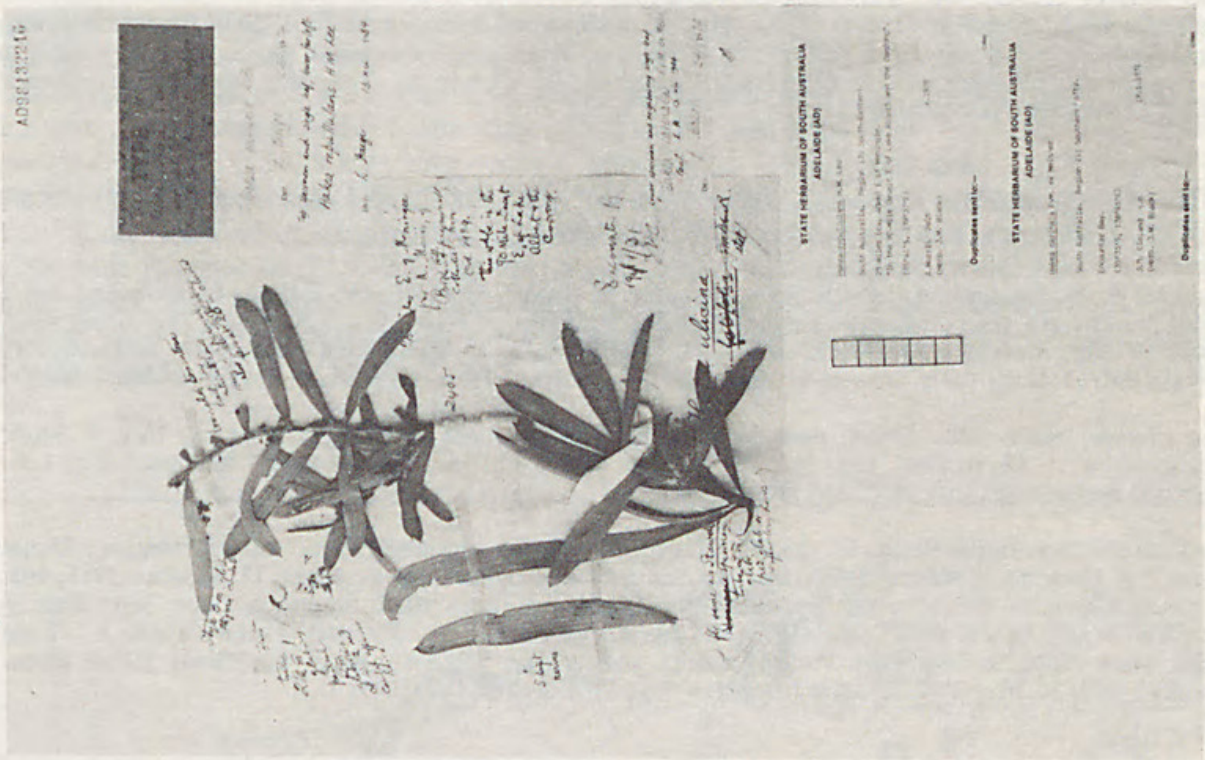

Fig. 8. Holotype of *H. ulicina* var. *latifolia* J. Black (*J.B. Cleland* per *A. Morris 2405*; scale 5 cm).

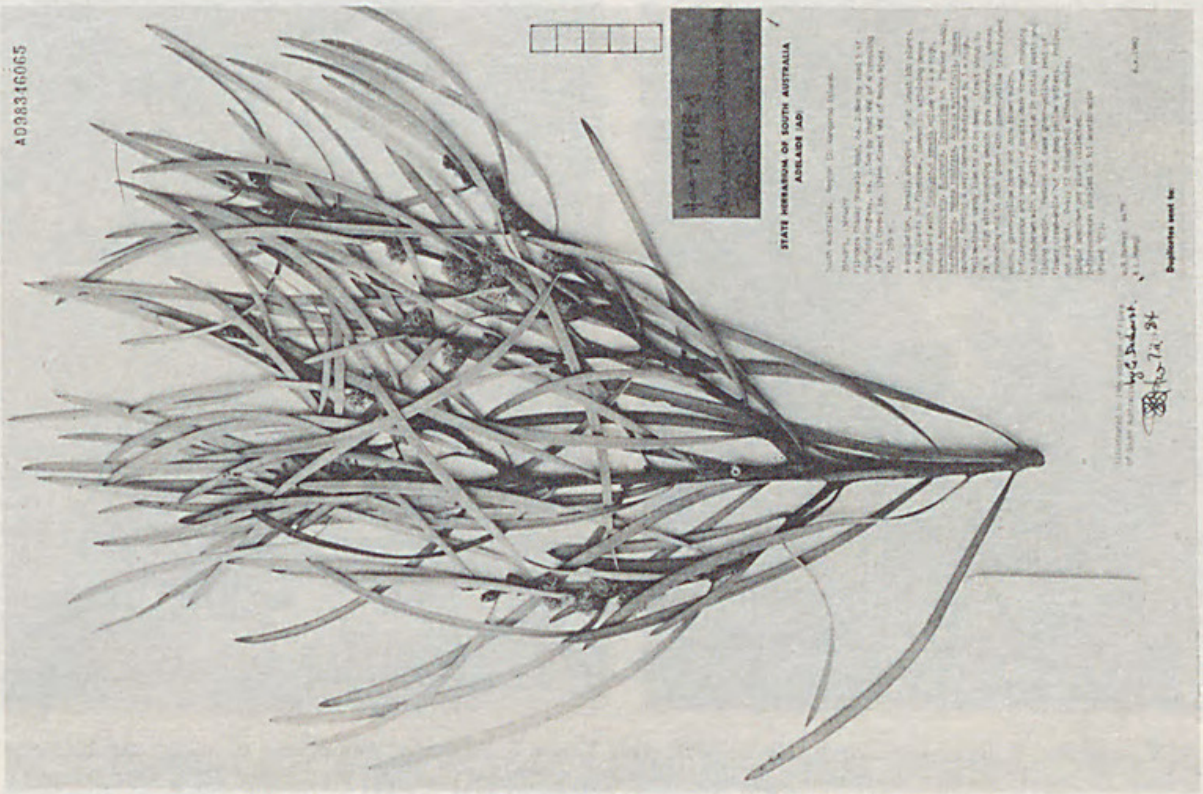

Fig. 7. Holotype of *H. aenigma*, sp. nov. (*Barker 4479 & Haegi*: scale 5 cm).

7.x.1982, Watters' mail box, on east-west road 3.2 km direct E of turnoff from Western River Cove road, ca 4.5 km direct NE of junction of Playford and West End Highways (AD); *G. Jackson 1081, 1082*, 7.xi.1976, Watters mail box near roadside, Western River Road (AD); *G. Jackson 1113*, 16.v.1977, on road to Western River Reserve about halfway between first farm, Yankillo Downs, and second farm, Colmar (AD); *G. Jackson 1143-1145*, 13.x.1977; *1212*, 23.ix.1979; 1506 1.xi.1981, Watters' mail box, road parallel to and north of Playford Highway, Hundred of Gosse (AD); *G. Jackson 1671*, 11.x.1984, Rex Ellis' property, Hundred of Borda, [up to ca 1 km E of trig T1/834 on 1:50,000 'Borda' Map] (AD); *G. Lonzar per J.B. Cleland s.n.*, 3.xii.1956, Flinders Chase; Shackle Road (AD 96225061, AD 98347057).

2. **Hakea repullulans** H.M. Lee, Austral. J. Bot. 32 (1984) 681. *Holotype*: *H.M. Lee 137*, 18.x.1979, Chimney Pot Gap, 40 km SW of Halls Gap, Grampians, Victoria (MEL, n.v.)

H. ulicina R. Br. var. *latifolia* J. Black, Trans. Roy. Soc. S. Austral. 54 (1930) 59; J. Black, Fl. S. Austral. edn 2 (1948) 266-267, p.p. (excl. 'Encounter Bay and near Goolwa'); Beek & Foster, Wildfl. S. Austral. (1972), p.p. (excl. 'Encounter Bay', 'Goolwa'); J.H. Willis, Handb. Pl. Victoria (1973) 49; Costermans, Native Trees & Shrubs S.E. Austral. (1981) 115, p.p. (as to 'Grampians', 'Deserts'), 155, p.p. (excl. 'Fleurieu Peninsula', Kangaroo Island—map).

Type citation: 'Ninety Mile Desert, near the Coorong; coll. E. Ashby.'—*Holotype*: *E. Ashby* [fide J. Black, protologue] *per A. Morris 2405*, Oct. 1929, 25 miles [c. 40km] E of Meningie, 'in the 90 mile desert E of Lake Albert and the Coorong'. (AD 98132246: top specimen).

H. ulicina auct. non R. Br.: Benth., Fl. Austral. 5 (1870) 524, p.p. (as to 'Glenelg River', 'Mount Sturgeon', 'Mount Abrupt'); J. Black, Fl. S. Austral. (1929) 161 p.p. (as to 'Eastern States' in part); Ewart, Fl. Victoria (1931) 408, p.p. (as to 'Grampians'); Specht, Veg. S. Austral. (1972) 250, p.p. (as to 'Heath Formation, Upper South East, in part); J.H. Willis, Handb. Pl. Victoria (1973) 49, p.p. (as to 'western .... Victoria', 'Lower Glenelg R.', 'Little Desert, Black Range & Grampians, Portland district' and, in part, 'Otways'); Haegi, Tax. Study *Hakea ulicina* Complex (1973) 56, p.p.; W.R. Barker in Jessop, List Vasc. Pl. S. Austral. (1982) 75.

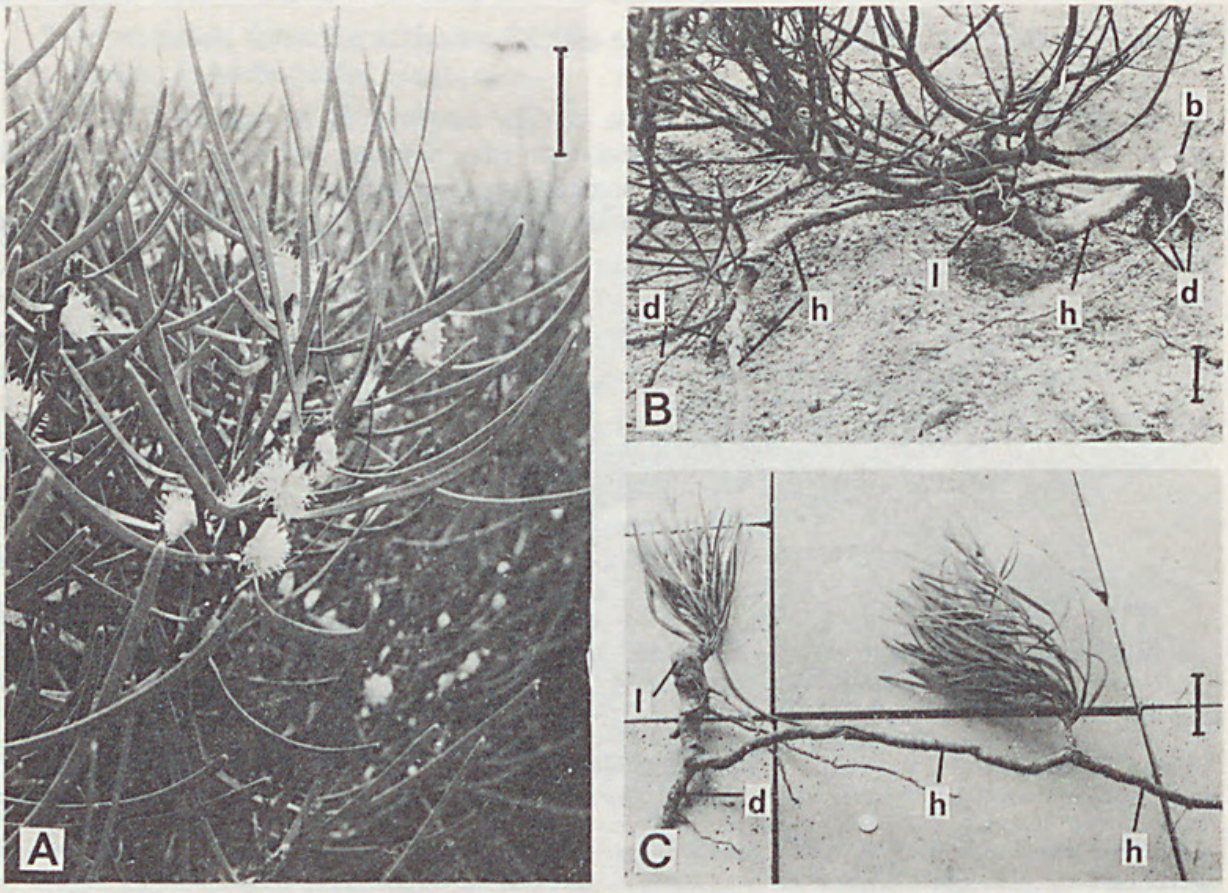

Fig. 9. *H. aenigma*. A, flowering branch (*Haegi 2288*; scale 5 cm); B, excavated root-system of mature shrub (*Haegi 2287*; scale 10 cm); C, suckers developed from lignotuber and horizontal root after fire (*Haegi 2287*; scale 10 cm); l, lignotuber; h, horizontal root; d, downturned root; b, base of earlier shrub.

Erect open shrub c. 2 m high, producing suckers; *branches* ascending; *branchlets* with tomentum persistent at least until flowering; *leaves* widely spreading, linear, 4-14 cm x 1.5-12 mm, twisted through 90 degrees at base, with 1-5 longitudinal veins above and below, mucro 1-4 mm long; *involucral cone* ovoid to spherical, 2.5-5 mm long, bracts with the apex woolly-tomentose and margin ciliate; *racemes* with 10-28 flowers; *rhachis* 1-2 mm long, white-hirsute; *pedicel* 1.8-3.6 mm long, rarely pubescent; *perianth* 1.7-4 mm long, limb 0.9-1.2 mm diam.; *anthers* 0.4-0.6 mm long; *gland*0.1-0.5 mm high; *pistil* 4-5.7 mm long; *pollen-presenter* a cone 0.5-0.9 mm long, with a basal flange 0.3-0.6 mm diam.; *fruit* ellipsoid to ovoid, often broadly so, 1.6-2.5 cm long, in lateral view 1-1.3 cm wide, in median view 1.3-1.8 cm wide, often black-pusticulate, with a slight protuberance on either side in median view near the base of the 1-2.5 mm long fragile beak; *seed* obliquely ovate, 10-16 x 3.5-6.5 mm, body broad-elliptic to ovate-elliptic, c. 1.9 mm thick, ridge inconspicuous, almost absent, wing decurrent further and more broadly down one side of the body, evenly blackish-brown. Figs 5, 6, 8.

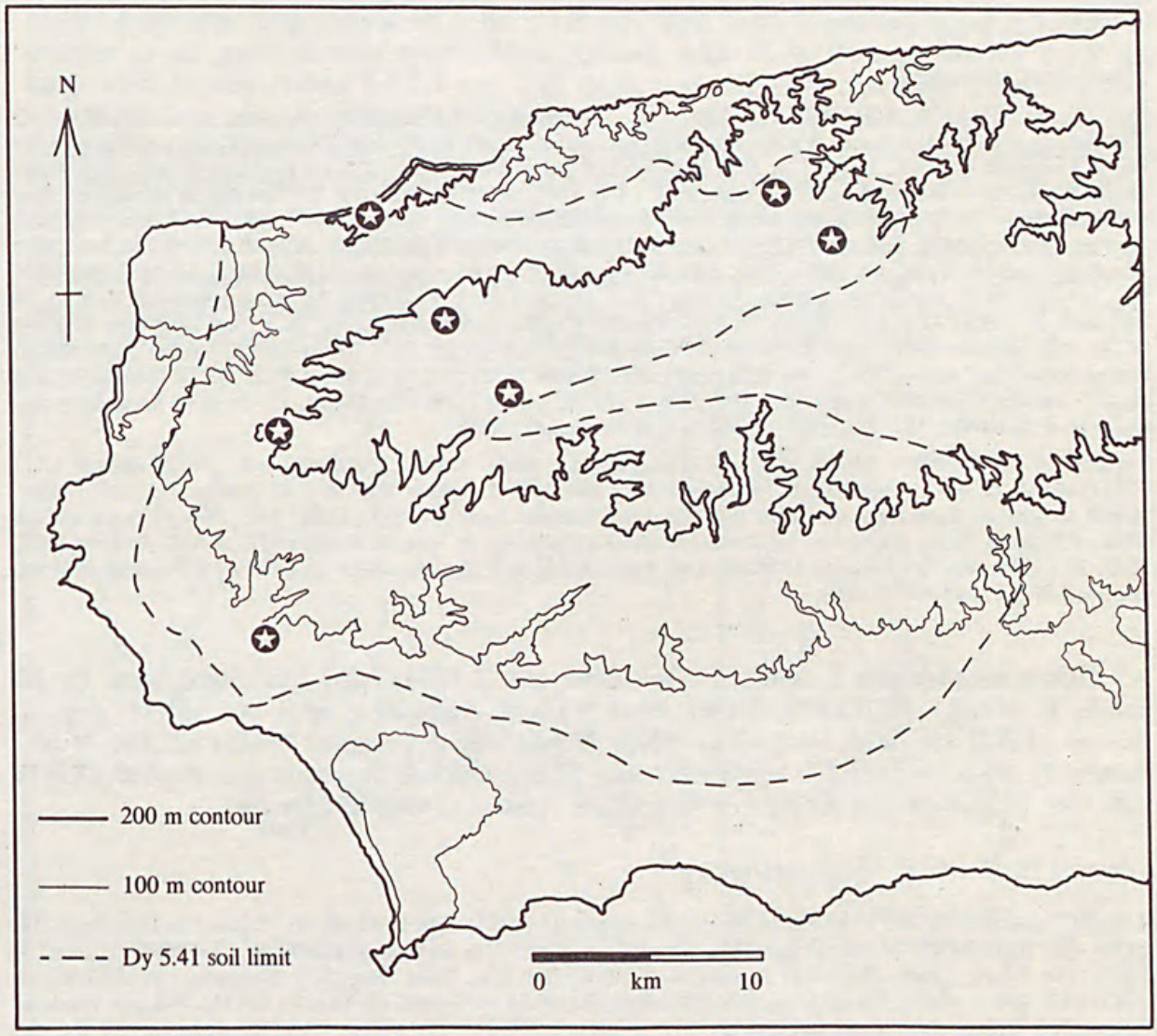

Fig. 10. Distribution of *H. aenigma* on western Kangaroo Island showing confinement to lateritic uplands, particularly on duplex soils of the Dy 5.41 type (limit after Northcote 1960).

Distribution and Ecology (fig. 11)

The major part of the distribution of *H. repullulans* is in sclerophyllous forest and mallee-heath in central and western Victoria. In South Australia its occurrence is restricted to mallee-heath on sandy soils of the South-Eastern region, where populations are small and somewhat scattered. Flowering occurs during September and October.

Note

The holotype of *H. repullulans* has not been seen but that of the taxonomic synonym *H. ulicina* var. *latifolia* has (fig. 8). The latter is cited by Black (1930) as having been collected by E. Ashby. This name, however, does not appear on the only specimen from Black's herbarium in AD labelled by Black as *H. ulicina* var. *latifolia* and from the type locality. The relevant specimen is labelled 'per A. Morris of Broken Hill and presumably collected by him' and bears the number 2405, presumably Morris's. It seems likely that Black ascertained that Morris had acquired the specimen from Ashby (who was the collector) but failed to annotate the specimen, which is regarded as the holotype. No duplicate of the specimen has been found in the Morris herbarium which is housed at ADW (D.E. Symon, pers. comm. Dec. 1984).

Specimens examined

SOUTH AUSTRALIA. SOUTH-EASTERN: *A.C. Beauglehole 7366*, 12.x.1963, Hundred of Coles (AD); *J.B. Cleland s.n.*, 9.iii.1963, Reserve, 5 miles (ca 8 km) east of Salt Creek (AD); *N.N. Donner 9251*, 9.x.1982, ca 8 km NE of Lucindale (AD); *L. Haegi 534, 535*, 22.ix.1973, 6 km east of Woods Well on Culburra-Woods Well Road, ca 0.5 km north of the road (AD); *D. Hunt 917*, 14.vii.1962, north of The Gap, Bordertown to Naracoorte road (AD); *D. Hunt 1212*, 6.x.1962, Bordertown to Naracoorte road (AD); *D. Hunt 2477*, 19.ix.1965, east of Penola Durradong road (AD); *E.H. Ising s.n.*, 13.xii.1934, Lucindale (AD); *R.H. Kuchel 2733*, 8.ix.1968, Messent Wild Life Reserve (AD); *A. Morris 2405 (Herb. J.M. Black)*, x.1929, 25 miles (ca 40 km) E of Meningie (AD 98132246 p.p., holotype of *H. ulicina* var. *latifolia* J. Black); *A.E. Orchard 1013*, 8.viii.1968, Mt Rescue National Park, ca 16 km north of Keith (AD); *R.L. Specht 26 & P. Rayson*, x.1950, Dark Island heath, ca 15 km north-east of Keith (AD); *A.G. Spooner 5380*, 10.x.1977, Messent Conservation Park (AD); *D.E. Symon 10754*, 2.x.1977, Mt Shaugh Conservation Park near 35°49′S, 140°56′E (AD); *D.E. Symon 10781*, 3.x.1977, about 3 km NE of 'Tamboore' and about 7 km due S of Mt Rescue (AD); *D.E. Symon 10928*, 8.x.1977, 90 Mile Desert, 10 km N of Kirra boundary (AD); *R.M. Welbourn 191*, 25.x.1964, ca 40 km N of Naracoorte (AD).

VICTORIA. WESTERN HIGHLANDS (GRAMPIANS): *Anon. (Herb. J.M.Black) s.n.*, 1927, Stawell (AD 97337146); *E. & A.K. Ashby 153*, xi.1940, Grampians (AD); *W.R. Barker 4601 & R.M. Barker*, 1.ix.1983, below turnoff to Sundial Peak from the main Wartook-Lake Bellfield road (AD); *L. Haegi 641*, 18.iv.1975, ca 10 km NNE of Victoria Valley Hamlet on road running along eastern side of Victoria Range (AD); *E.N.S. Jackson 1494, 1518*, 25.x.1969, near Mt Difficult on Roses Gap Road (AD); *A.G. Spooner 4865*, 24.x.1976, on Dunkeld to Hall's Gap road 37°22′S, 142°25′E, AD.

3. **Hakea muelleriana** J. Black, Fl. S.Austral. edn 2 (1948) 267 (substitute name for *H. flexilis* F. Muell.); H. Eichler, Suppl. Black's Fl. S. Australia (1965) 96; Specht, Veg. S. Austral. (1972) 250, 274; Haegi, Tax. Study *Hakea ulicina* Complex (1973) 62; J.H. Willis, Handb. Pl. Victoria 2 (1973) 53; Costermans, Native Trees & Shrubs in S.E. Austral. (1981) 110, 156; W.R. Barker in Jessop List Vasc. Pl. S. Austral. (1982) 75.

Type: see *H. flexilis* F. Muell. below

H. flexilis [auct. non R. Br.: F. Muell. ex Meissner, Linnaea 26 (1854) 359; F. Muell. ex Meissner in DC. Prodr. 14 (1856) 415 'flexibilis'] F. Muell., Fragm. Phyt. Austral. 6 (1868) 216, nom. illeg. non R. Br.; Benth., Fl. Austral. 5 (1870) 530; Tepper, Trans. Roy. Soc. S. Austral. 3 (1880) 39; Tate, Trans. Roy. Soc. S. Austral. 3 (1880) 68, 6 (1883) 138, 160; J. Black, Trans. Roy. Soc. S.Austral. 40 (1916) 59; Ewart, Fl. Victoria (1931) 408, p.p. (excl. S. Victoria; N.S.Wales record not substantiated).

Type citation (Meissner 1856): 'In deserto ad flum. Murray crescens.' *Type material*: to be searched for in the Meissner herbarium, NY. *Possible duplicates of the type*: *F. Mueller*, River Murray (MEL 55874, 55876, s.n.); *F. Mueller*, In the Murray Desert (MEL 55875); *F. Mueller*, 1849, Murray Scrub (MEL).

H. ulicina R. Br. var. *flexilis* (F. Muell.) C. Moore & Betche, Handb. Fl. New South Wales (1893) 243; J. Black, Trans. Roy. Soc. S. Austral. 41 (1917) 42, 42 (1918) 42, 43 (1919) 29, 350; Wood, Trans. Roy. Soc. S. Austral. 54 (1930) 130, p.p. (as to 'W', 'C' 'E.Aust.'; Ising, Trans. Roy. Soc. S. Austral. 59 (1935) 244; J. Black, Fl. S. Austral. (1924) 161, p.p. (excl. 'Southern part of Flinders Range').

H. ulicina auct. non R. Br.: Tate, Trans. Roy. Soc. S. Aust. 12 (1889) 90, p.p. (as to 'Y', 'L', 'K' and, in part, 'T'); Tate, Fl. Extratrop. S. Austral. (1890) 94, 228, p.p. (as to 'Y', 'K' and, in part, 'T'); Wood, Trans. Roy. Soc. S. Austral. 54 (1930) 130, p.p. (as to 'W', 'C', 'Pt. L.'); Baldwin & Crocker, Trans. R. Soc. S. Austral. 65 (1941) 273, 274; Specht, Veg. S. Austral. (1972) 274.

H. ulicina var. *carinata* auct. non (F. Muell. ex Meissner) Benth.: Tepper, Trans. Roy. Soc. S. Austral. 9 (1887) 115.

H. marginata auct. non R. Br.: Tepper, Trans. Roy. Soc. S. Austral. 10 (1885) 291.

H. corymbosa auct. non R. Br.: Tate, Trans. Roy. Soc. S. Austral. 12 (1889) 63.

Erect rounded shrub 1-4 m high, not suckering; *branchlets* appressed-pubescent initially, glabrous by the time of flowering (apart from new shoots); *leaves* widely spreading, rarely ascending, terete with no veins apparent to 3-angled, narrow-linear, with marginal veins and mid-vein on lower side conspicuous, rarely flat and obovate-linear, 3.5-12 cm x 1-10 mm, mucro 1-2.5 mm long; *involucral cone* 2-4.5 mm long, with bracts appressed-pubescent all over or at the apex, densely white-ciliate; *racemes* with 16-36 flowers; *rhachis* 1-2.5 mm long, white-hirsute; *pedicel* 1.5-2.7 mm long, pink; *perianth* 2.1-4 mm long, white to yellow, limb 0.9-1.2 mm diam.; *anthers* 0.35-0.7 mm long; *gland* 0.1-0.5 mm high; *pistil* 4.5-6.2 mm long; *pollen-presenter* a cone 0.5-0.7 mm long, basal flange 0.3-0.7 mm diam.; *fruit* ellipsoid to ovoid-ellipsoid, often broadly so, 1.2-2.5 cm long, in lateral view 0.5-1.3 cm wide, in median view 0.7-1.6 cm wide, black-pusticulate, with a slight protuberance on either side in median view below the 1-3.5 (-4) mm long fragile beak; *seed* obliquely elliptic, 8-15 x 3.5-6 mm, body elliptic to ovate-elliptic, c. 1.6 mm thick, ridge at the base half the thickness of the body, extended a third way to the wing apex, wing decurrent more broadly and further down one side of the body, light-brown with dark streaks, rarely dark-brown. Figs 3, 6.

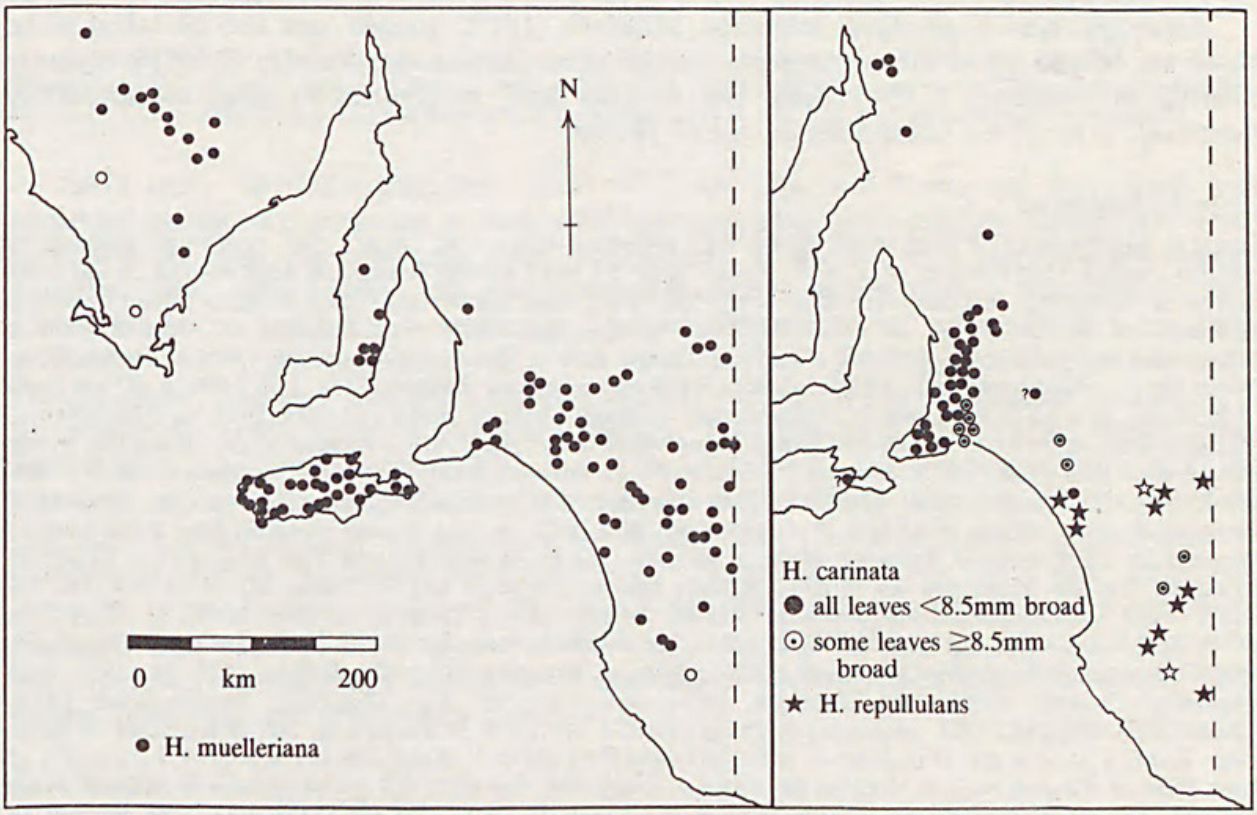

Fig. 11. Distributions of *H. muelleriana*, *H. carinata* and *H. repullulans* in South Australia. Hollow symbols indicate imprecise localities.

Distribution and Ecology (fig. 11)

The distribution of *H. muelleriana* extends from Eyre Peninsula to north-western Victoria and Kangaroo Island. It occurs in dry though not arid regions, bounded approximately by the 250 mm and 500 mm isohyets. Records of the occurrence of *H. muelleriana* in New South Wales (e.g. Willis 1973) are apparently in error. This species is found in mallee-heath vegetation, often as a moderately common, conspicuous component, on sandy soils. On Kangaroo Island it has also been recorded from dry sclerophyll forest. On the mainland flowering occurs principally in November, beginning in late October and extending only a few days into December. On Kangaroo Island, where many species flower later than on the mainland, the flowering season is December and January.

Note

The name *H. muelleriana* is based on '*H. flexilis* F.v.M. (1853)' (Black 1948). This reference is evidently to the observation by Meissner in Linnaea volume 26 (published during 1853 and 1854) of what he believed to be the misidentification by Mueller of a specimen as *H. flexilis* R. Br. No description appears at this place and therefore Black's reference may be taken as an indirect one to a subsequent mention by Meissner (1856) of Mueller's specimen, where the earlier observation is cited and a Latin description is provided (satisfying the requirements of the International Code).

A complication arises through Meissner's (1856) use or at least the appearance in the text of the spelling '*H. flexibilis* Ferd. Mull.' Whether this is a printing error (as it is taken as by Bentham, 1870 and Eichler, 1965), an error on Meissner's part, or even the partly intentional proposal by Meissner of a provisional name for what he believed to be possibly a new species, it is at best an invalid name, not validated before the publication of *H. muelleriana*. In a brief note Mueller (1868) was the first to decide firmly that the material from the Murray River region, originally misidentified as *H. flexilis* R.Br., was a distinct species and took up the name *H. flexilis* F. Muell. for it, not using Meissner's spelling '*flexibilis*'.

Although there is no direct reference, Mueller's (1868) '*flexilis*' can also be taken to be based on Meissner's (1856) description. In the same publication, Mueller (1868) frequently referred to Meissner's (1856) work, but saw no need, in contrast to other species newly described, to provide a full description for *H. flexilis*.

Selected specimens

SOUTH AUSTRALIA. EYRE PENINSULA (47 specimens seen): *C.R. Alcock 582*, 6.vii.1965, Hundred of Wanilla, Section 125 (Reserve) (AD); *C.R. Alcock 4049*, 3.x.1972, Gawler Ranges, off main road ca 25 km south of Yardea Homestead, ca 1 km north of Scrubby Peak (AD); *W.R. Barker 3556*, 23.ix.1978, ca 32 km by road S of Kimba on the Cleve road, ca 1 km WNW of Mt Bosanquet (AD); *H.C. Robjohns s.n.*, 24.x.1967, Point Bolingbroke (AD); *K.D. Rohrlach 693*, 18.x.1959, County Buxton, Hundred Pinkawillinie, south of Section 95, ca 24 km west-north-west of Kimba (AD). MURRAY (43 specimens): *Hj. Eichler 12368*, 12.iv.1956, ca 37 km north of Pinnaroo, on road from Loxton to Pinnaroo, near Peebinga (AD); *L. Haegi 260*, 30.iii.1973, ca 5 km south of Monarto South on road to Ferries McDonald Conservation Park (AD); *E.N.S. Jackson 2322*, 14.xi.1972, Billiatt Conservation Park (AD); *M.C.R. Sharrad 1239*, 31.x.1961, 6 miles (ca 9 km) west of Coomandook (AD). YORKE PENINSULA (14 specimens): *B. Copley 2881*, on boundary road between Hundred of Wiltunga and Hundred of Cameron, south of railway line (AD); *B. Copley 4647*, 20.x.1974, on road running east-west from 2 km south of Weetulta to 1 km south of Arthurton (AD); *E. Giankos per B.Copley 4193*, near Pine Point (AD); *T.Hall 46*, 26.x.1982, Cut Line Road, (on the 34°53'S, parallel), between Stansbury and Hardwicke Bay (AD). SOUTHERN LOFTY (19 specimens): *J.B. Cleland s.n.*, xi.1921, Goolwa, AD 97210017, AD 966130111.-*L. Haegi 265*, 9.ii.1973, 8.5 km north-east of Two Wells and 4 km south-south-east of Reeves Plains (AD); *L. Haegi 274*. 20.ii.1973, 4 km NW of Currency Creek P.O. on track to Mosquito Hill (AD); *D.Hunt 3425*, 30.x.1972, road connecting Currency Creek and Middleton (AD); *A.G. Spooner 972*, 18.xi.1970, Finniss Scrub (AD). KANGAROO ISLAND (111 specimens): *L. Haegi 322-323*, 7.iv.1973, 34 km by road SW of Kingscote on South Coast Road., 2 km due east of intersection with Birchmore Hwy (AD); *L. Haegi 336-343*, 8.iv.1973, 1.2 km NW of Point Ellen on Vivonne road, at Vivonne Bay (AD); *L. Haegi 360*, 9.iv.1973, 3.2 km W of Karatta (AD); *L. Haegi 395-398*, 11.iv.1973, roadside near Remarkable Rocks (AD); *L. Haegi 404-406*, 11.iv.1973, near entrance to Lighthouse Station at Cape Borda (AD); *L. Haegi 422*, 13.iv.1973, 4 km W of Cape Willoughby, Dudley

Peninsula (AD). SOUTH-EASTERN (63 specimens): *D. Hunt per R.M. Welbourn 176*, 12.xii.1963, Lucindale (AD); *L.Haegi 250, 251, 253*, 5.xii.1972, ca 3 km east of Meningie on road to Coonalpyn (AD); *L. Haegi 254*, 5.xii.1972, ca 16 km W of Coonalpyn on road to Meningie (AD); *T. Roach 60*, 21.xi.1970, ca 32 km south of Keith near Willalooka Store (AD); *J.G. West 2233*, 2.x.1977, Mt Shaugh Conservation Park, 2 km south-east of Mt Shaugh and 2 km west of Victorian border (AD);*P. Wilson 1419*, 22.xi.1959, Ashville, ca 20km N of Meningie.

VICTORIA (14 specimens): *A.C. Beauglehole 25239*, 28.v.1968, Grampians, Black Range, 2 mls S of Mt Talbot, 1.1 mls W of road junction [which is] at a point 2 mls SSE of Mt Talbot (AD); *A.C. Beauglehole 28711*, 1.x.1968, Wyperfeld National Park, Dattuck Track, 2 miles ENE of Eastern Lookout (AD); *E. & G. Gardiner s.n.*, 27 km S of Murrayville (AD 98151113).

4. **Hakea carinata** F. Muell. ex Meissner, Linnaea 26 (1854) 360 (incl. *α planifolia* Meissner and *β trigonophylla* Meissner); Meissner in De Candolle, Prodr. 14 (1856) 418; F.Muell., Fragm. Phyt. Austral. 4 (1868) 315; Haegi, Tax. Study *H. ulicina* Complex (1973) 49; W.R.Barker in Jessop, List. Vasc. Pl. S.Austral. (1982) 75.

Type citation: 'Lofty Range, Adelaide, Octob. Brighton, Austr. fel., Octob.'—*Lectotype* (here designated): F.Mueller, 1851-52, Lofty Range, Adelaide, ex Herb. W. Sonder (NY: Meissner Herb., specimen on far left side; mounted with 2 other *syntypes*—no further locality data on sheet). Probable isosyntypes including possible isolectotype(s): MEL 55892, 55907, 55908, 55911, 55913; S.

H. ulicina R. Br. var. *carinata* (F. Muell. ex Meissner) Benth., Fl. Austral. 5 (1870) 24.

H. ulicina auct. non R. Br.: Tate, Trans. Roy. Soc. S. Austral. 3 (1880) 68; Anon., Trans. Roy. Soc. S. Austral. 9 (1887) 278; Tate, Trans. Roy. Soc. S. Austral. 9 (1887) 278; Tate, Trans. Roy. Soc. S. Austral. 12 (1889) 90, p.p. (as to 'A', 'N' and, in part, 'T'); Tate, Fl. Extratrop. S. Austral. (1890) 84, 228, p.p. (as to 'A' and, in part, 'T'); J. Black, Fl. S. Austral. (1924) 161, p.p. (excl. 'Eastern States', var. *flexilis*), (1929) 682; Wood, Trans. Roy. Soc. S. Aust. 54 (1930) 130, p.p. (as to 'Fl', 'Fl G'; Ewart, Fl. Victoria (1931) 408, p.p.; J. Black, Fl. S. Austral. edn 2 (1948) 266, p.p. (excl. 'Murray Lands', 'Eastern States'); Specht, Veg. S. Austral. (1972) 250, p.p. (excl. 'Heath formation, Upper South East' in part); J.H. Willis, Handb. Pl. Victoria 2 (1973) 49, p.p. (as to 'S.A. (as far west as Mt Lofty)' in large part).

H. ulicina R. Br. var. *latifolia* auct. non J.Black: J. Black, Fl. S. Austral. edn 2 (1948) 266-267, p.p. (as to 'Encounter Bay and near Goolwa'); Beek & Foster, Wildfls S. Austral. (1972), p.p. (as to 'Encounter Bay and near Goolwa'); Costermans, Native Trees & Shrubs in S.E. Austral. (1981) 115, 155, p.p. (as to 'Fleurieu Peninsula').

Erect often unevenly branched shrub 1.5-3 m high, not suckering; *branchlets* with appressed-pubescence persisting at least until flowering, sometimes patchily glabrescent; *leaves* narrow-linear to narrow-trigonous, rarely broad-linear, 5-24 cm x 1-12 mm, base not twisted, marginal veins conspicuous, mid-vein prominent below, rarely with 3 longitudinal veins prominent below and faintly conspicuous in dried material above, mucro 0.5-2.5 mm long; *involucral cone* 3.5-5 mm long, with the apex of the bracts appressed-white-pubescent, densely ciliate; *racemes* with 8-24 flowers; *rhachis* 1-2 mm long, white-hirsute; *pedicel* 1.5-3.5 mm long, rarely sparsely pubescent, pinkish; *perianth* 1.9-2.8 mm long, cream-white, limb 0.9-1.4 mm diam.; *anthers* 0.4-0.6 mm long; *gland* 0.1-0.4 (-0.8) mm high; *pistil* 3-6 mm long, cream-white; *pollen-presenter* a cone 0.5-0.8 mm long, with a basal flange 0.5-0.8 mm diam.; *fruit* ellipsoid to narrowly ovoid-ellipsoid, 1.3-2.6 x 0.6-1.1 cm, smooth or minutely verrucose, gradually attenuated into a fragile beak (3-) 4-6.5 mm long; *seed* obliquely ovate to elliptic-ovate, 10-18 x 4-6.5 mm, body almost globular, c. 2.4 mm thick, ridge at base a third of the thickness of the body, extended halfway to the wing apex, wing decurrent more broadly and further down one side of the body than the other, evenly dark-brown, rarely unevenly pigmented. Figs 5, 6.

Distribution & Ecology (fig. 11)

H. carinata is endemic in South Australia where its principal occurrence is in the Mount

Lofty Ranges, from the Barossa Valley to Cape Jervis. The distribution extends north with occurrences in the Tothill Ranges and the southern Flinders Ranges from near Gladstone to Mt Remarkable and vicinity. South of the Mt Lofty Ranges, it is found in small, scattered populations as far south as Padthaway in the South-Eastern region. In the main part of its distribution, *H. carinata* is common at several sites as an understorey plant in sclerophyll forest and heathy scrub, on sands and loams. Flowering occurs during September and October.

Notes

1. A single collection bearing the locality Woods Point, 15 km SSE of Murray Bridge (*Anon. AD 97732763*) represents a disjunction which requires substantiation. *H. carinata* is doubtfully recorded for Kangaroo Island on the basis of only one specimen, reputedly collected at Muston (*Cooper AD 96229335*). Collecting in recent years has failed to confirm its occurrence there.

2. Meissner (1854) described *H. carinata* from material in the Sonder herbarium. Only one sheet from Meissner's herbarium (in NY) bears this name. It consists of three pieces and has a single label indicating among other things that the material, collected by Mueller in the Mt Lofty Ranges near Adelaide, is from the Sonder herbarium. This agrees in part with the protologue, but there a second locality, 'Brighton, Austr. fel. [Australia Felix, i.e. the State of Victoria (see Wells 1848)]' is also given. The only specimen of *Hakea* in the Meissner herbarium bearing the locality 'Brighton Austr. fel.' is the type of *H. semiplana* F.Muell. ex Meissner (described in the same publication by Meissner (1854), and a synonym of *H. nodosa* R.Br., which is known to occur at that locality). Although no specimen bearing this locality known to have been seen by Meissner has been traced, specimens of *H. carinata* labelled 'Australia felix' collected by Mueller are to be found in the Sonder herbarium at MEL. Since *H. carinata* is not otherwise known from Victoria, the locality is treated as an error rather than as indicating the existence of syntypes from another species.

3. Although Meissner described the varieties *planifolia* and *trigonophylla*, these names do not appear on the type sheet or any other specimens traced. Since no infraspecific classification is proposed, the complicated typification of these names is not attempted.

Selected specimens

SOUTH AUSTRALIA. FLINDERS RANGES (18 specimens seen): *J.B. Cleland s.n.*, 28.vi.1965, Alligator Gorge (AD 96536154); *H.M. Cooper s.n.*, 15.viii.1954, Mt Remarkable (AD 97834128, AD 97834160); *P. Martinsen 57*, 8.ix.1974, Mambray Creek (AD). NORTHERN LOFTY (4 specimens): *B. Copley 3071*, 10.ix.1970, c. 8 km W of Gladstone (AD); *D.N. Kraehenbuehl 2487*, 8.ix.1973, Central Tothill Range (AD); MURRAY (5 specimens): (*Anon. School) s.n.*, 15.x.1925, Wood's Point (AD 97732763); *Schodde 1107, 1108*, 20.iv.1959, In Wirra Wirra Scrub, c. 6 km W of Springton on road to Williamstown (AD); *Tepper s.n.*, ix.1927, Keyneton (AD 97732773). SOUTHERN LOFTY (204 specimens): *H.M. Cooper s.n.*, 3.x.1943, Taperoo (AD 96608283); *L. Haegi 196*, 27.ix.1971, ½km NE of Upper Sturt Post Office (AD); *L. Haegi 228, 229, 231*, 2.xii.1972, 5.5 km west of Kangarilla on road to Blewitt Springs (AD); *L. Haegi 276, 278-283, 285, 291, 292, 295, 299, 301-303*, 1.iv.1973, an area between 4 km and 5 km south of Ashbourne along the Ashbourne to Goolwa road, more or less adjacent to the eastern boundary of Cox's Scrub Conservation Park (AD); *L. Haegi 552-554*, 23.ix.1973, Mt Barker Road near the Eagle on the Hill (Safety Ramp) (AD); *L. Haegi 2703*, 13.ix.1984, Cox's Scrub Conservation Park (seedlings; all mature plants seen killed by fire—no suckering) (AD); *L.D. Williams 10309, 10311*, 7.v.1979, 2.3 km N of W of Williamstown (AD). KANGAROO ISLAND (in need of confirmation): *H.M. Cooper s.n.*, vi.1941, Muston (AD 96229335). SOUTH-EASTERN (15 specimens): *P. Canty s.n.*, 23.x.1980, Padthaway [Conservation Park] (AD, 2 specimens); *T.J. Fatchen, A. McDonald & A.C. Robinson s.n.*, 1.x.1976, Padthaway Conservation Park (AD); *L. Haegi 256-258*, 5.xii.1972, ca 16 km west of Coonalpyn on road to Meningie (AD); *L. Haegi 532*, 22.ix.1973, at the intersection of a fourth class road running south from Field and the Culburra-Woods Well Road; ca 30 km south-west of Coonalpyn (AD); *J.R. s.n.*, 11.viii.1965, Archibald & Makin Wild Life Reserve (AD); *M.C.R. Sharrad 544*, 27.iii.1960, 5 miles east of Malinong Hall (AD).

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Material in the herbaria AD, MEL and NSW, as well as selected types from BM, K and NY have been studied.

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