A taxonomic revision of *Trachymene* sect. *Dimetopia* (Apiaceae)

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Abstract

Keighery, G.J. and Rye, B.L. A taxonomic revision of *Trachymene* sect. *Dimetopia* (Apiaceae). *Nuytsia* 13 (1): 33–59 (1999). The monotypic genus *Uldinia* J. Black (Apiaceae) is reduced to a synonym of *Trachymene* Rudge, resulting in the new combination *Trachymene ceratocarpa* (W. Fitzg.) Keighery & Rye. A further new combination, *Trachymene* sect. *Dimetopia* (DC.) Keighery & Rye, is made for the species group to which *T. ceratocarpa* belongs, and this section is revised. Sect. *Dimetopia* is endemic to mainland Australia and comprises five small ephemeral species with few-flowered umbels, few pollen grains per anther, fruits consistently with both monocarps developed, a reduced carpophore and probably a reduced chromosome number. *Trachymene moorei* Hiroe is reduced to a synonym of *T. cyanopetala* (F. Muell.) Benth. The single species previously placed in *Uldinia* produces natural hybrids with its closest relative *Trachymene cyanopetala*, but the hybrids are sterile. Although several other pairs of species from sect. *Dimetopia* are known to coexist, no other hybrids have been observed.

Introduction

South-western Australian members of the genus *Trachymene* Rudge (Apiaceae) belong to two species groups, one group with few-flowered umbels and the other with many-flowered umbels. These groups have been recognized as separate sections under two synonymous generic names, the few-flowered species in *Dimetopia* sect. *Dimetopia* (also known by the later name of *Didiscus* sect. *Oliganthon*) and the many-flowered species in *Didiscus* DC. ex Hook. sect. *Didiscus* (also known by the illegitimate name of *Didiscus* sect. *Polyanthon* (Domin) C.A. Gardner). Neither south-western group matches *Trachymene s. str.*, which is a group of perennial species occurring in eastern Australia. An accompanying paper (Rye 1999) revises Western Australian members of sect. *Didiscus* as well as members of another species group occurring in the north of the State. Sect. *Dimetopia*, a small group of species endemic to southern mainland Australia, is treated here, with the recombination made to recognize it formally as a section of *Trachymene*.

As in most other Apiaceae, *Trachymene* species have an inferior two-carpellate fruit, with the axis between the two fruitlets known as the carpophore. The fruitlets are monocarps, that is whole carpels.

More commonly, they have been referred to as mericarps, a term that should be restricted in use (Spjut 1994: 17) for true half-carpels such as those commonly found among the Lamiales.

Fruit characters have been used to differentiate *Trachymene* and its close relative, the monotypic genus *Uldinia*, which shows greatest similarity to sect. *Dimetopia*. Originally *Uldinia* was distinguished from *Trachymene* by its lack of a "free persistent carpophore" (Black 1922: 569). A more obvious distinguishing feature of *Uldinia*, used in keys such as Blackall & Grieve (1980: 262), Eichler (1986: 980) and Powell (1992: 88), is its rather bizarre fruit ornamentation. The *Uldinia* fruit has a very distinctive appearance, each monocarp bearing rows of retrorsely hooked spine-like bristles and two large terminal projections or wings. In *Trachymene* species the carpophore is usually much more substantial than in *Uldinia* and fruit ornamentation is very varied but never exactly as in *Uldinia*.

This paper presents morphological and genetic evidence supporting the inclusion of *Uldinia* in the genus *Trachymene* and the separation of sect. *Dimetopia* from the remainder of *Trachymene*. *Trachymene* sect. *Dimetopia* is fully revised for Western Australia, where all five of its species occur, and any additional variation found in those species extending to other parts of Australia is noted.

Materials and methods

A population in which natural hybrids had been produced between *Uldinia ceratocarpa* and *Trachymene cyanopetala* was sampled near Yuna in 1974. Fresh material of both parent species was obtained for pollination trials and a dried specimen (*G.J. Keighery* 940) of the hybrid was lodged at PERTH. Artificial cross-pollination was conducted on potted plants isolated with fine wire mesh covers in an insect-proof glasshouse. Pollen collected from the anthers of *Uldinia* plants was transferred to the stigmas of emasculated *Trachymene cyanopetala* flowers. Using the artifically derived hybrid seeds from this cross, F1 hybrid plants were grown to maturity for comparison with the natural hybrids. Germination trials using freshly harvested monocarps were conducted to compare the germination percentages of the parental species with F1 hybrid seeds as well as F2 hybrid seeds derived from the artificial hybrid plants.

Morphological measurements were taken from dried herbarium specimens located at PERTH. Distribution maps were drawn up with each symbol representing the occurrence of the taxon in a 0.25 degree latitude by 0.25 degree longitude area.

Comparison of *Uldinia* and the sections of *Trachymene*

Morphological evidence

Trachymene belongs to subtribe Hydrocotylinae together with three other large genera, *Centella* L., *Hydrocotyle* L. and *Platysace* Bunge, and the following five very small, mostly monotypic, genera: *Dickinsia* Franch., *Homalosciadium* Domin, *Micropleura* Lag., *Neosciadium* Domin and *Uldinia* (Pimenov & Leonov 1993). Pimenov & Leonov also included *Chlaenosciadium* C. Norman but this genus appears to belong in subtribe Xanthosiinae. Of the genera in the Hydrocotylinae, *Uldina* is quite clearly the closest to *Trachymene*. *Uldinia* shares with *Trachymene* all the main morphological

characters that collectively separate the latter from other genera of Apiaceae, particularly the following characters: stipules absent; leaves long-petiolate, with a shallowly lobed to deeply divided lamina; umbels simple; involucral bracts slightly united at the base into a single whorl; sepals reduced; styles free, slender, with a capitate stigma; stylopodium prominent, tuberculate, becoming concave in fruit; fruit without vittae, nearly always highly bilaterally compressed. Blue is a quite common flower colour in *Uldinia* and *Trachymene*, but is uncommon in the family as a whole. Indeed the blue flower colour of *Trachymene coerulea* Graham came as a surprise when the first specimens were seen by European botanists, who had not encountered this colour before in the family apart from in the thistle-like genus *Eryngium* L. (see Hooker 1828).

Within *Trachymene*, many infrageneric groups of unspecified level (under the synonymous name *Didiscus*) were published by Domin (1908) mainly on the basis of life forms, numbers of involucral bracts and flowers per umbel, and sepal characters. Sepal characters are not of any importance in distinguishing between the two south-western Australian species groups but the other characters are significant and are discussed in a later section on breeding systems. In sect. *Dimetopia*, the few involucral bracts are narrowly ovate to obovate. In other species groups the involucral bracts are usually fairly numerous and subulate, but occasionally are fewer and narrowly ovate.

Pollen grain numbers per anther are similar in sect. *Dimetopia* and *Uldinia*, but significantly lower than in other *Trachymene* groups that have been examined (Keighery unpublished data).

Although the schizocarps of *Trachymene* species do not have wings in the form of long terminal protrusions as in *Uldinia*, wings of other kinds are fairly common among the many-flowered species. For example *Trachymene bialata* (Domin) B.L. Burtt has two narrow wings encircling the body of each monocarp and *T. villosa* (F. Muell.) Benth. has a single broad wing along the outer margin. The origins of the *Uldinia* type of wing can possibly be seen in fruit variants of *T. cyanopetala* that have few bristles, the bristles mostly occurring along the outer margin and medial lines. Some monocarps have one or more of the bristles much more enlarged at the base than the other bristles, especially in *R. Ornduff* 9309–56, and occasionally an extra-large bristle is located in about the same position as a wing in *Uldinia*. In the *Uldinia–Trachymene* hybrid the reduced wing takes the form of an even more enlarged bristle, intermediate between the *T. cyanopetala* bristle and the *Uldinia* wing.

Many *Trachymene* species have bristles of various kinds on their fruits. Again, the closest approach to the usually very prominent spine-like bristles of *Uldinia* is probably to be seen in the sparsely bristly variants of *Trachymene cyanopetala*. Some specimens, such as *K.R. Newbey* 8931, have rows of retrorsely curved or uncinate bristles occurring in the same locations as in *Uldinia* but generally shorter, more slender and flexible.

Each species in sect. *Dimetopia* can be identified by its distinctive fruit and some of the many-flowered *Trachymene* species also have a unique fruit. Some species show great infraspecific variation in monocarp ornamentation, for example having rugose or tuberculate monocarps in some individuals or populations and bristly monocarps in others. *Trachymene pilosa* is a prime example of this kind of variation. In addition, plants of this species commonly have heteromorphic fruits, with the outer (abaxial) monocarp differing markedly in ornamentation from its sister monocarp in the adaxial position, as illustrated in Wheeler (1987: Figure 206A). Heteromorphic fruits have also been recorded in several African genera including *Heteromorpha* Cham. & Schlechtd. (Tilney & van Wyk 1995), and occasionally occur in a few Australian taxa of other genera. A notable example is an unnamed *Hydrocotyle* species from Western Australia that usually has one of the monocarps prominently winged and the other wingless.

While *Uldinia* certainly lacks a full-sized persistent carpophore, opinion differs as to whether *Uldinia* has no carpophore at all (e.g. Domin 1922), a fully deciduous carpophore (e.g. Black 1922) or a partially persistent carpophore (e.g. Fitzgerald 1904). Theobald (1967: 171) states that the carpophore is absent in *Uldinia* and that the persistent remains after the monocarps are shed are "lignified extensions from the pedicel into the base of the fruit".

The term carpophore is retained here in reference to *Uldinia* as there is no other obvious term to use for the tissue separating the monocarps. Certainly a structure of some kind, probably a reduced carpophore, does persist after the monocarps are shed in *Uldinia*. This persistent structure (Figure 1A) is similar to the carpophore in other members of sect. *Dimetopia* (Figure 1B) except that it is always shorter, never reaching the full length of the commissure of the fruit.

In *Uldinia* and *Trachymene* sect. *Dimetopia* the carpophore (Figure 1A,B) is usually highly dorsiventrally compressed and therefore much narrower than the pedicel from lateral view, triangular at the base in dorsal and ventral views and becoming very slender above. In sect. *Didiscus* the carpophore (Figure 1C) is more or less terete, thicker throughout its length and less flexible. Several of the perennial *Trachymene* species of eastern Australia have a carpophore that splits to the base before the monocarps are released, the two halves bending outwards. Considerable variation in carpophore characters may occur within other genera as well. The related genus *Hydrocotyle*, which shows a similar degree of variation in monocarp ornamentation to *Trachymene*, has the carpophore persistent in some species and deciduous in others.

Theobald (1967: 172) summarized the anatomical differences between *Uldinia* and *Trachymene* as "differences in floral venation at the commissure and in the upper portion of the mericarp" and "the orientation of fibres in the endocarp". Taking these differences together with the absence of a carpophore, the nature of the wings and the "retrorse barbs and papillae" on the fruit, he concluded that there was a "basis for the distinctiveness of the genus". His studies provided support for the close relationship between *Uldinia* and *Trachymene*, but he considered the differences between them

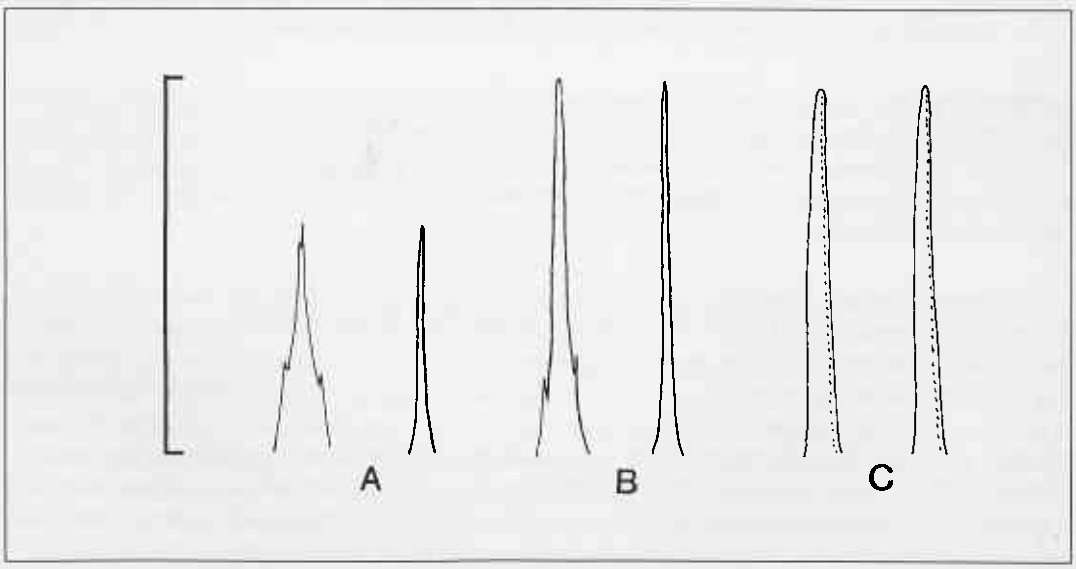

Figure 1. Adaxial and lateral views of carpophore, with magnifications varied to give all species the same commissure length, which is indicated by a bar line. A – *Uldinia*, B – *Trachymene cyanopetala*, C – *Trachymene coerulea*.

sufficient to maintain them as distinct genera. However, some of these 'differences' must be disputed; certainly papillae are common on the mature fruits of several members of *Trachymene* sect. *Dimetopia* and 'retrorse barbs', although not as well developed as in *Uldinia*, can also be present in sect. *Dimetopia*. It should also be noted that *Uldinia* shows much variation in these two characters, with the papillae often absent and the barbs sometimes rather poorly developed. As already discussed, carpophore characters are variable within *Trachymene* and might be useful for distinguishing some of the species groups within the genus, but do not seem to be sufficiently different in *Uldinia* to justify its recognition as a distinct genus.

All of the anatomical and gross morphological differences proposed above to separate *Uldinia* from *Trachymene* relate to the fruit. If bizarre fruits can be used as a sole basis for distinguishing genera, cases could be made for the recognition of further monotypic genera. For example, the Western Australian endemic species *Trachymene croniniana* F. Muell. has a fruit, illustrated in Rye (1999: Figure 6G,H), that is perhaps as highly modified and atypical of the genus as that of *Uldinia*. Only one monocarp develops and it is slightly to distinctly dorsiventrally compressed at maturity rather than being bilaterally compressed as is normal for the genus. The highly sculptured lateral extensions, including pits and narrowly winged ribs, are reminiscent of the fruit ornamentation found in some *Hydrocotyle* species. Two notable fruit developments within *Trachymene* sect. *Dimetopia* are the smooth swollen monocarps in *T. elachocarpa* and the woolly indumentum on the monocarps of *T. ornata*.

With such a high degree of variation in carpophore and fruit morphology within *Trachymene*, the fruiting characters observed in *Uldinia* do not seem very significant and are regarded here as insufficient reason to treat it as a separate monotypic genus. In *Trachymene* sect. *Dimetopia* two trends shown in fruit morphology are: (1) reduction of the carpophore to a highly compressed, fragile structure; (2) a tendency for the commissure to extend along a greater proportion of the length of each monocarp and to exceed the monocarp's width. *Uldinia* is regarded here as carrying these trends to their extreme, having the narrowest monocarps in relation to the commissure length and also the most reduced carpophores in the genus.

Hybridization

The occurrence of hybridization between species is evidence that they are closely related. A great majority of natural hybrids are produced between species belonging to the same species group within a genus; hybridization between members of different species groups within the same genus is much less common, and intergeneric hybidization is rare even under artificial conditions (e.g. Griffin, Burgess & Wolf 1988, Knobloch 1972).

Uldinia ceratocarpa hybridizes with the *Trachymene* species with which it shows the greatest morphological similarity, *T. cyanopetala*. Natural hybrids have been observed in mixed populations of *U. ceratocarpa* and *T. cyanopetala* near Yuna and near York, but not at a number of other mixed populations of these two species. Artificially produced hybrids bred from parent plants derived from the Yuna population matched the natural hybrids, confirming their origin. Germination percentages for the F1 seeds and non-hybrid seeds were similar. Although the F1 hybrids were as vigorous as the parent plants and produced a full crop of normal-sized monocarps, they showed reduced pollen fertility and the monocarps mostly lacked a fully formed seed. The F2 hybrid monocarps failed to germinate although monocarps from both parent species showed a greater than 90% germination rate.

Figure 2 illustrates a natural hybrid from the Yuna population and its parent species *Uldinia ceratocarpa* and *Trachymene cyanopetala.* Unfortunately there was no herbarium specimen of *T. cyanopetala* from the Yuna population, so the illustration of that parent was based on a specimen from the closest available population located closer to Murgoo and may therefore differ somewhat from the appearance of the species at Yuna. The hybrid is intermediate between the two parent species in its fruit morphology. Its monocarp is *c.* 3.4 x 1.9 mm, with two very reduced terminal wings *c.* 0.8 mm long (not including the apical hair or point) and with bristles present but reduced both in number and size. The bristles are mostly 0.5–0.7 mm long and are either widely distributed or concentrated along the outer margin and medial lines. The carpophore is full-sized as in *T. cyanopetala.*

Apart from the limited hybidization described above, no species of sect. *Dimetopia* have been observed to hybridize either with one another or with members of other sections of the genus. This does not result purely from spatial separation of the taxa as there are many mixed populations involving each of the possible combinations of three members of the section, *T. cyanopetala*, *T. ornata* and *T. pilosa.* It is improbable, although not impossible, that any member of sect. *Dimetopia* would be able to produce natural hybrids with a species of another genus, i.e. *Uldinia*, when all species in the section fail to hybridize even with closely related members of their own genus. An estimate obtained by Knoblock (1972) of the frequency of intergeneric hybridization in the Apiaceae was 2.5%, with only one out of the 40 reported cases of natural and artificial hybridization being between genera. Where intergeneric hybrids have been reported in the Apiaceae and other families, they always involve closely related genera and often occur in taxonomically difficult groups in which generic boundaries are uncertain. Inclusion of *Uldinia* within *Trachymene* sect. *Dimetopia* is therefore favoured by this genetic evidence.

Chromosome numbers

The base chromosome number for *Trachymene* is x=11, which is a fairly common base number in the family as a whole (Fedorov 1974; chromosome number indices up to Goldblatt & Johnson 1996). Among related genera, base chromosome numbers are known for several species of *Centella* with x=9, one species of *Micropleura* with x=10, one species of *Platysace* with x=8 (Keighery 1982a), and many species of *Hydrocotyle* with x=12, also some with x=11 and two with x=9.

Most of the many-flowered species of *Trachymene* in south-western Australia are diploid on n=11, one is tetraploid on n=22 and another shows infraspecific variation with both n=11 and n=22 recorded from different populations. Among the eastern Australian and New Guinea species, many of which are perennial, polyploidy is common, with tetraploid, hexaploid and octaploid levels recorded; see summary of previous counts in Keighery (1982a). In sect. *Dimetopia*, there is evidence of dysploidy to a base of x=10, as the only known number for the group is n=20 in *T. pilosa* (Keighery 1982a). Since this tetraploid chromosome number is unique in the genus as far as is known, perhaps it contributes to the reproductive isolation of *T. pilosa*, which fails to hybridize despite its fairly frequent co-existence with several closely related species. Chromosome number differences might, however, be more likely to result in hybrid infertility, such as occurs between *Uldinia ceratocarpa* and *Trachymene cyanopetala*, than in the prevention of hybridization.

Breeding systems

Trachymene sect. *Dimetopia* and *Uldinia* species are all small to medium-sized annuals, usually ephemeral, commonly either erect and 0.01–0.15 m high or decumbent to almost prostrate and with stems up to 0.3 m long. Rarely, especially in *Trachymene pilosa*, they are erect and 0.15–0.35 m high.

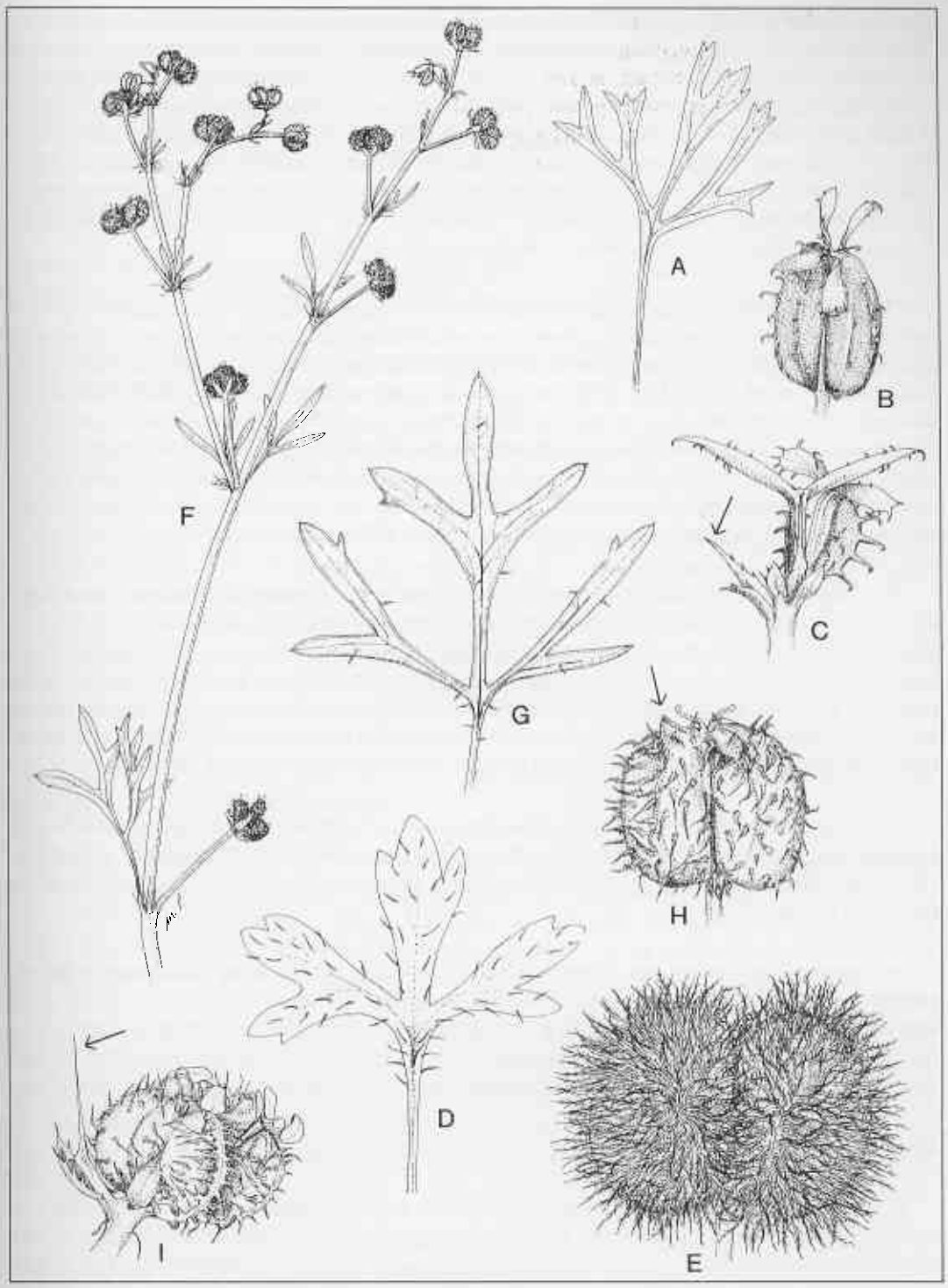

Figure 2. A–C. *Trachymene ceratocarpa*. A – leaf (x2.5), B – young fruit (x8), C – mature fruiting inflorescence with some fruits partially or fully shed, a carpophore arrowed (x6); D,E. *T. cyanopetala*. D – leaf (x2.5), E – fruit (x9); F–I. Natural hybrid between *T. ceratocarpa* and *T. cyanopetala*. F – fruiting branch (x1), G – leaf (x2.5), H – fruit with one of the reduced wings arrowed (x8), I – mature fruiting inflorescence with one fruit shed, a carpophore arrowed (x6). Drawn from *G.J. Keighery* 943 (A–C), *R.A. Saffrey* 1180 (D,E) and *G.J. Keighery* 940 (F–H).

Most have as few as 3–7 flowers and the same number of involucral bracts per umbel; however the most floriferous species, *T. pilosa*, produces usually 5–21 flowers and 5–10 bracts per umbel, but one variant has up to *c.* 50 flowers. In contrast, the *Trachymene* species in other sections of the genus are medium-sized to large annuals or perennials appearing annually from woody underground parts. Annual species in these groups are 0.1–2.5 m high, with large umbels of usually 30–200 flowers (but occasionally as few as *c.* 20 flowers in depauperate specimens), the flower number greatly exceeding the number of involucral bracts. A few of the perennial species regularly produce fairly low flower numbers per umbel, particularly the eastern Australian species *T. ochracea* L.A.S. Johnson with 20–45 flowers and *T. procumbens* (F. Muell.) Benth. with 12–30 flowers (Powell 1992).

Flowers of members of sect. *Dimetopia* and *Uldinia* are small and grouped into usually very small inconspicuous umbels. The outermost flowers are not differentiated from the inner ones except in the leafy coastal variant of *T. pilosa*. Plants occur in large numbers but do not normally mass flower after fires, although some populations of the leafy coastal variant of *T. pilosa* do so. Inflorescences are produced within the small plant or only shortly above the vegetative parts and generally attract few insect pollinators. A few small bees, wasps and flies have been recorded visiting the flowers, which appear to be primarily self-pollinated. The flowers are usually homogamous but sometimes slightly protandrous, produce negligible amounts of nectar, are fully self-compatible and self automatically on flower closure. Seed set in isolated plants approaches 100% (Keighery 1982b).

Members of the other annual *Trachymene* group of southern Australia (sect. *Didiscus*) have larger flowers grouped into large showy umbels with the outer petals of the outermost flowers often distinctly elongated, producing an effect similar to the ray florets of daisy inflorescences. Normally the plants mass flower after fires, prominantly displaying the inflorescences above the vegetative parts of the plants and attracting a large range of small to medium-sized insect pollinators, including bees, beetles, wasps, flies, butterflies and moths. Flowers are protandrous and produce noticeable amounts of nectar. Plants are almost fully self-compatible and seed set is usually high in isolated plants.

Perennial species of eastern Australia belonging to sect. *Trachymene* often produce male flowers as well as bisexual flowers, increasing the inflorescence size, food resources and pollen availability. For further details of breeding systems in *Trachymene* and a comparison with other members of the family see Keighery (1982b).

Among the *Trachymene* sect. *Dimetopia* and *Uldinia* species, the small schizocarps regularly produce two mature monocarps. In most of the many-flowered *Trachymene* species, 'asymmetric' fruits with one monocarp infertile and reduced are more common than those with bilateral symmetry (two full-sized mature monocarps). Some species, such as *Trachymene bialata*, invariably produce asymmetric fruits, the abaxial monocarp reduced to a persistent fleshy strip attached to the carpophore.

Seed dispersal

Developent of hooked bristles on the *Uldinia* fruit, and to a lesser extent in some variants of *Trachymene cyanopetala*, appears to be an effective adaptation for animal dispersal. The hairy bristles common in some *Trachymene* species, such as *T. pilosa*, also appear to be ideally suited to transport on animal fur. Strong evidence of the epizoochorous nature of the fruits is that two species in sect. *Dimetopia* have been recorded as wool aliens in the United Kingdom (Ryves 1975).

Uldinia has the added adaptation of wings, which might improve wind dispersal but perhaps are more useful in extending the hooks beyond the fruit body and so further increasing the likelihood of

animal dispersal. Few *Trachymene* species appear to have large enough wings for efficient wind dispersal, but even slight wings might significantly aid tumble-blowing.

Taxonomic treatment

Trachymene sect. *Dimetopia* (DC.) Keighery & Rye, *comb. nov.*

Dimetopia DC. (de Candolle 1830: 177) and sect. *Dimetopia* (automatically created by publication of *Dimetopia* sect. *Eriosciadium* in 1855). *Type: Dimetopia pusilla* DC. [= *Trachymene pilosa* Sm.].

Cesatia Endl. (Endlicher 1838: 11–12 [repaginated 1839: 200–201]). *Type: Cesatia ornata* Endl. [= *Trachymene ornata* (Endl.) Druce].

Dimetopia sect. *Eriosciadium* F. Muell. (Mueller 1855: 127). *Type: Dimetopia eriocarpa* F. Muell. [= *Trachymene ornata* (Endl.) Druce].

Didiscus A. *Oliganthon* Domin (Domin 1908: 27). – *Didiscus* sect. *Oliganthon* (Domin) C.A. Gardner (Gardner 1931: 100). *Type: Didiscus cyanopetalus* F. Muell. [= *Trachymene cyanopetala* (F. Muell.) Benth.], lectotype here chosen.

Maidenia Domin *nom. illeg.* (Domin 1922: 41–42) *non* Rendle (Rendle 1916: 316, t. 545). – *Dominia* Fedde (Fedde 1929: 272). *Type: Maidenia acroptera* Domin [as *M. macroptera* = *Trachymene ceratocarpa* (W. Fitzg.) Keighery & Rye].

Uldinia J. Black (Black 1922: 569–570, t. 37). *Type: Uldinia mercurialis* J. Black [= *Trachymene ceratocarpa* (W. Fitzg.) Keighery & Rye].

Annual herbs small, ephemeral. *Involucral bracts* 3–10; free portion narrowly ovate to obovate. *Umbels* 3–21(*c.* 50)-flowered. *Anthers* with few pollen grains. *Gynophore* dorsiventrally compressed, very narrowly triangular (or linear with an expanded base), flexible throughout or firm at base and flexible at apex, undivided. *Commissure* extending for most of the length of the monocarp and exceeding the width of the monocarp (except in *T. elachocarpa*).

Etymology. From the Greek *di* – two and *metopon* – brow or forehead, meaning two-browed. Presumably this refers to the different appearance of the two monocarps in the heteromorphic fruit variant of *Trachymene pilosa*, the only taxon included when the genus was originally named. The name seems appropriate for the section as a whole because the schizocarps regularly produce two mature monocarps and the word *di* implies only that there are two and not that they are necessarily different from one another.

Notes. A section of five species, occurring in southern mainland Australia, with the greatest representation in the south-west of Western Australia. These species are keyed out under couplets 7–10 in the key to all Western Australian members of the genus *Trachymene* in Rye (1999).

Domin (1908) did not indicate which taxonomic level he intended for his new infrageneric name *Oliganthon*. Presumably this is why Gardner (1931) did not cite Domin as author when he specified

sectional rank for the name. However, he included the same species as Domin, even listing them in the same order, and referred to Domin's work as the author of the combination *Didiscus junceus* (S. Moore) Domin. It therefore appears that the two names are equivalent and that Gardner's section should be regarded as a recombination of Domin's name.

Both Domin (1908) and Gardner (1931) misplaced *Trachymene elachocarpa* in the many-flowered species group *Polyanthon* [= *Didiscus*]. While *T. elachocarpa* differs from other members of sect. *Oliganthon* [= *Dimetopia*] in having a shorter commissure on the fruit, it otherwise has the typical characters of the section.

Sect. *Dimetopia* can generally be distinguished from other groups in the genus *Trachymene* by its expanded lamina (not subulate) on the bracts and more compressed carpophore, from the perennial species also by its annual life form, and from sect. *Didiscus* also by its smaller average habit and less exposed inflorescences with usually fewer flowers. It may also be the only group in the genus to have the commissure length usually exceeding the width of the monocarps. In *Trachymene* as a whole, sect. *Dimetopia* shows the greatest reduction in life cycle, bract and flower number, pollen grain number and also chromosome number, with all or some of these characters presumably being interrelated.

Trachymene ceratocarpa (W. Fitzg.) Keighery & Rye, *comb. nov.*

Hydrocotyle ceratocarpa W. Fitzg. (Fitzgerald 1904: 22–23). – *Maidenia ceratocarpa* (W. Fitzg.) Domin (Domin 1922: 42). – *Uldinia ceratocarpa* (W. Fitzg.) N.T. Burb. (Burbidge 1954: 452). *Type:* Wurarga, Western Australia, September 1903, *W.V. Fitzgerald* (*n.v.*).

Maidenia acroptera Domin (Domin 1922: 41–42). – *Dominia acroptera* (Domin) Fedde (Fedde 1929: 272). *Type:* Arrara–Lake Eliza, New South Wales, October 1912, *J.L. Boorman* (NSW, *n.v.*).

Uldinia mercurialis J. Black (Black 1922: 569–570, t. 37). *Type:* Ooldea, South Australia, 12 September 1920, *E.H. Ising* (*iso:* MEL).

Illustrations. Black (1926: Plate 40, p. 439); Eichler (1986: Figure 501A); Powell (1992: 96); Theobald (1967: Figures 1–15).

Annual herb commonly 20–100 mm high, the larger plants decumbent to prostrate and with stems up to 300 mm long. *Stems* glabrous or rarely with scattered hairs; hairs retrorse, apparently non-glandular, mostly 0.4–1.0 mm long. *Cotyledons* very narrowly obovate to linear, 11–16 mm long, entire, glabrous. *Petioles* 5–40 mm long, long-ciliate on expanded base, glabrous or with very few hairs on narrow portion; expanded base 1.5–4 mm long; hairs mostly 1–2.5 mm long. *Leaf blades* deeply 3-lobed, the primary lobes simple or further divided into 2 or 3 secondary lobes, which may be slightly further lobed, 7–21 mm long, glabrous or with a few scattered hairs. *Involucral bracts* 3–5; free portion usually ovate, rarely obovate, 2–2.5 mm long, often toothed towards apex, with a few cilia mostly 0.3–0.6 mm long. *Inflorescence* 3–5-flowered. *Petals* white or blue. *Fruiting peduncles* 5–22 mm long; pedicels mostly 0.3–2 mm long, glabrous. *Fruit* homomorphic; carpophore about half as long as the commissure and ?usually exceeding the width of the monocarp, highly compressed, very flexible; styles 0.3–0.6 mm long. *Monocarps* very compressed, with a minute reticulate pattern or minutely papillate, 2-winged, with stout bristles in two rows along outer margin and 1–5 rows of smaller bristles on each face, including a row along each medial line; body 3.2–4.3 x 1.2–1.8 mm, with outer margin either extending horizontally for a short distance beyond outer edge of stylopodium or

immediately descending at an angle of up to 20 degrees; main bristles retrorsely uncinate, 0.3–1.2 mm long, greatly thickened and up to 0.5 mm wide at base, glabrous or minutely papillate; wings formed from a terminal protrusion of each medial line, 2–5.5 x 0.5–1.3 mm, with a few retrorsely uncinate bristles 0.2–0.4 mm long. (Figures 1A, 2A–C)

Selected specimens examined. WESTERN AUSTRALIA: 7.2 km E along Simpson Rd, from Morawa to Three Springs road, 19 Sep. 1991, *R.J. Cranfield & P. Spencer* 8092 (PERTH); Menzies–Diemals road 3.7 km NW of turnoff to Johnson Rocks, 12 Sep. 1982, *H. Eichler* 23002 (PERTH); Ivor Rocks, *c.* 1 km S of White Cliffs Station Homestead, 18 Sep. 1975, *G.J. Keighery* 528 (PERTH); 3 km S of Monkey Mia towards Denham, 28 Aug. 1989, *G.J. Keighery* 10880 (PERTH); 1.1 km SE of Crows Nest Well, 35 km NW of Mt Sandiman, 21 Aug. 1987, *K.R. Newbey* 11644 (PERTH); southern margin of Rason Lake, 13 Sep. 1984, *P.G. Wilson* 12122 (PERTH).

Distribution. Occurs in the south-west of Western Australia, extending from Kennedy Range and Peron Peninsula in the Eremean Botanical Province south to Watheroo National Park and near York in the South West Botanical Province and east to Rason Lake (east of Laverton) in the Eremean. Also occurs in South Australia and New South Wales. (Figure 3A).

Habitat. Commonly occurs on or between sand dunes, recorded in red or yellow soils, often in *Acacia* shrublands, sometimes in shrublands or woodlands dominated by *Callitris*, *Eucalyptus*, *Grevillea* or other genera. Sometimes associated with granite outcrops or salt lakes.

Phenology. Flowering and fruiting period: August to November.

Conservation status. Widespread and fairly common.

Common name. The common name Creeping Carrot has been applied to this species, but is not favoured here as the plant does not show much resemblance to a carrot plant.

Notes. A detailed comparison of the morphology of this species and other *Trachymene* species is given in an earlier section of this paper. *Trachymene ceratocarpa* differs from the other members of sect. *Dimetopia* in its narrower cotyledons and monocarps, the prominent projections on the monocarps and the more reduced carpophore.

In South Australia and New South Wales there do not appear to be any variants of the species that are significantly different from those found in Western Australia and no hybrids have been reported. All known occurrences of the hybrid between *T. ceratocarpa* and *T. cyanopetala* are shown in Figure 3B.

Trachymene cyanopetala (F. Muell.) Benth. (Bentham: 1867: 348). – *Dimetopia cyanopetala* F. Muell. (Mueller 1859: 231). – *Didiscus cyanopetalus* (F. Muell.) F. Muell. (Mueller 1875: 46). – *Didiscus cyanopetalus* var. *ciliatulus* Domin (Domin: 1908: 34). *Type:* Murchison River, Oldfield (*lecto:* MEL 679941, here chosen both for *Dimetopia cyanopetala* and *Didiscus cyanopetalus* var. *ciliatulus.*)

Trachymene moorei Hiroe (Hiroe 1979: 887). – *Trachymene juncea* S. Moore *non* Bunge *nom. illeg.* (Moore 1899: 194). – *Didiscus junceus* (S. Moore) Domin (Domin 1908: 35). *Type:* Gibralter, [Western Australia], September 1895, *S. Moore* (BM, *n.v.* but photograph PERTH 01597337).

Annual herb either erect and 15–150 mm high, or decumbent to semi-prostrate and with spreading stems up to 220 mm long. *Stems* glabrous or hairy; hairs retrorse or somewhat so, 0.3–0.7 mm long, usually appearing non-glandular but sometimes obviously glandular, perhaps losing glandular apex and appearing non-glandular with age. *Cotyledons* usually narrowly obovate, 6–19 mm long, entire, glabrous. *Petioles* 2–50 mm long, long-ciliate on expanded base, glabrous or with few to many hairs on narrow portion; expanded base 1–9 mm long, sometimes with scattered hairs on outer surface; hairs mostly 0.4–1.8 mm long. *Leaf blades* deeply 3-lobed, the primary lobes simple or further divided into 2 or 3 secondary lobes, which may be slightly further lobed, 3–26 mm long, glabrous or with scattered hairs. *Involucral bracts* 3–6; free portion usually ovate or obovate,1.4–3.5 mm long, sometimes toothed at apex, with cilia mostly 0.3–1 mm long. *Inflorescence* 3–6(7)-flowered. *Petals* blue or white. *Fruiting peduncles* 5–60 mm long; pedicels mostly 1–3 mm long, glabrous or rarely with a few hairs towards apex. *Fruit* homomorphic; carpophore as long as commissure and exceeding the width of the monocarp, highly compressed, flexible; styles 0.5–0.8 mm long. *Monocarps* very compressed, 2.6–3.4 x 1.5–2.3 mm, with a distinct medial line, usually densely bristly and shaggy-looking, sometimes sparsely bristly to glabrous, smooth or minutely papillate between the bristles, pale to medium brown at first, the surface (often hidden by bristles) becoming dark brown to almost black; outer margin extending horizontally beyond outer edge of stylopodium before curving downwards; bristles (0.2)0.4–2.5 mm long, either glabrous or with minute patent side branches up to 0.1 mm long, white to deep purple, usually *c.* 0.1 mm wide at base at maturity, if broader then compressed. (Figure 1B)

Distribution. Widespread in the south-west of Western Australia, except for the most humid portion (including the Perth Region). Occurs in the South West Botanical Province from Nerren Nerren Station and Kalbarri National Park south-east to Stirling Range, and extends inland to Koonmarra Station and near Agnew in the Eremean Botanical Province and to Uraryie Rock (south-west of Zanthus) in the South-western Interzone. Also occurs in South Australia, New South Wales and Victoria. (Figure 3C)

Habitat. Occurs in sandy soils, on granite outcrops or other rocky sites, often in *Acacia* shrublands or *Eucalyptus* woodlands.

Phenology. Flowering and fruiting period: mainly August to November.

Conservation status. Widespread and common but variants with non-bristly or sparsely bristly fruits are found in only a few localities.

Common name. A rather inappropriate common name, Purple Parsnip, has been applied to this species, which has blue not purple petals and does not resemble a parsnip plant. When in fruit, however, the plant's inflorescences may have a more purplish or pinkish appearance.

Notes. According to the protologue, this species has densely 'ciliate' bristles on the fruit. Actually the hairs or lateral branches arise and radiate from all positions on the bristles rather than being strictly marginal or in rows as implied by the term ciliate. The specimen chosen here as the lectotype for *T. cyanopetala* has uniform fruits with bristles of the densely hairy kind. Further advantages of this specimen are that it has both a definite locality and collector, and it is the first of the specimens cited by Mueller. The other material examined was:

1. Murchison River, *Oldfield* (MEL 66987) – two plants mounted on the sheet, one with densely hairy bristles and one with glabrous bristles.

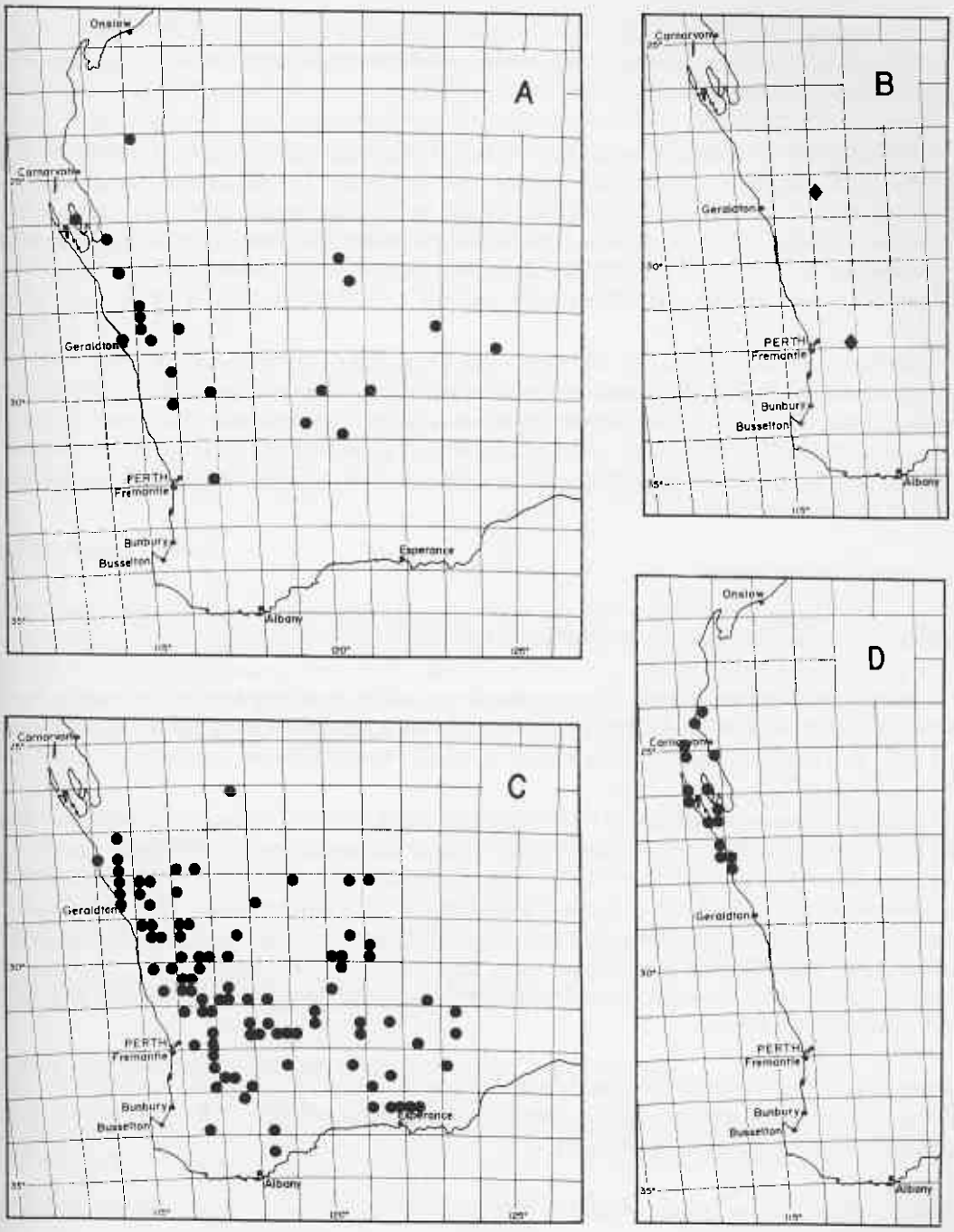

Figure 3. Distribution in Western Australia. A – *Trachymene ceratocarpa*, B – Hybrid between *T. ceratocarpa* and *T. cyanopetala*, C – *T. cyanopetala*, D – *T. elachocarpa*.

2. "Mononuka" [probably Moonymooka, Victoria], *P. Walcott* (MEL 36988) – material with densely hairy bristles.

3. Murray River, collector unknown (MEL 36986) – with mixed specimens, some having glabrous or sparsely hairy bristles and others densely hairy bristles.

Domin (1908: 34) evidently meant his *Didiscus cyanopetalus* var. *typicus* Domin *nom. inval.* to be the typical variant of *T. cyanopetala*, but included type material of this species instead under the variant he named var. *ciliatulus*. His description of var. *typicus* as having glabrous bristles also conflicts with the protologue of *T. cyanopetala*. Since Domin clearly intended one of his varieties to be equivalent to the species and cited *Oldfield* material from Murchison River, the same lectotype is chosen for his var. *ciliatulus* as for the species.

Western Australian specimens are much more variable than those from other states, showing significant differences in the number, arrangement and size of the bristles as well as in the hairiness of the bristles. Of the three main variants given below, only the first one extends to other regions of Australia. In South Australia both the hairy and glabrous kinds of bristle occur in this variant, but it appears from the description given for the species in New South Wales (Harden 1992) that only the hairy kind of bristle occurs there.

a. Densely bristly variant

Illustrations. Eichler (1986: Figure 500C); Powell (1992: 103).

Monocarps bristly throughout, pale to medium brown at first, becoming dark brown or rarely almost black; bristles slender, (0.7)1–2.5 mm long, either glabrous or with few to numerous minute patent hairs up to 0.1 mm long, the base *c.* 0.1 mm wide at maturity. (Figure 2D,E)

Selected specimens examined. WESTERN AUSTRALIA: 48 km W of Coonana near Coardonia Rocks, 18 Sep. 1973, *R.J. Chinnock* 1112 (PERTH); 1 km S of Truslove Reserve Rd on Swan Lagoon Rd, Truslove Nature Reserve, 22 Sep. 1992, *C.F. Craig* 2169 (PERTH); *c.* 2 km N of Morawa, 25 Sep. 1976, *L. Haegi* 1128 (PERTH); 9 miles [14.5 km] S of Koorda to Wyalkatchem, 6 Sep. 1974, *G.J. Keighery* 66 (PERTH); 50.7 km E of Kalbarri, 20 Sep. 1973, *G.J. Keighery* 1768 (PERTH); Dryandra State Forest, 3 Nov. 1987, *D.M. Rose* 459 (PERTH).
NEW SOUTH WALES: southern end of Narrandera Range, W of summit of Mt Bogolong, 1 Oct. 1978, *T.B. Muir* 6091 (PERTH).

Distribution. The Western Australian distribution is as described for the species as a whole but with few records in the general area where the other two variants are found (Figure 3C). Also occurs in South Australia, New South Wales and Victoria.

Habitat. Occurs in sandy soils, on granite outcrops or other rocky sites, often in *Acacia* shrublands or *Eucalyptus* woodlands.

Notes. The fruit bristles are slender, usually long and giving a shaggy appearance to the fruit, but sometimes shorter, for example in specimens from Comet Vale (*R.D. Royce* 4411, 4498) and south of Zanthus (*K.R. Newbey* 7234).

b. Intermediate variant

Monocarps with 3–5(8) rows of bristles along the medial and other lines or intermediate between the lines, usually absent between the medial line and the commissure; bristles rather stiff, patent or retrorsely curved, compressed, narrowly or very narrowly triangular, 0.3–0.6 mm long, with numerous minute hairs up to 0.1 mm long, usually *c.* 0.1 mm wide at base at maturity but sometimes 0.15–0.2 mm wide, with occasional bristles *c.* 0.3 mm wide, the broad bristles much compressed at the base.

Selected specimens examined. WESTERN AUSTRALIA: 6 km E of Beechina Hill, 27 Oct. 1980, *R.J. Cranfield* 1268 (PERTH); Boyagin Rock, 12 Sep. 1983, *R. Ornduff* 9299–22 (PERTH); Boyagin Rock, 15 Oct. 1983, *R. Ornduff* 9299–101 (PERTH); The Humps, 4 Oct. 1983, *R. Ornduff* 9309–56 (PERTH).

Distribution. Known from a few scattered localities including Boyagin Rock and The Humps, north-east of Hyden in the South West Botanical Province of Western Australia.

Habitat. Occurs in soil pockets on granite outcrops or sheets of granite, also recorded from laterite.

c. Non-bristly variant

Monocarps non-bristly or often with a few small hair-like bristles along the abaxial line or in two rows along the submarginal lines on either side of the abaxial line, occasionally also with 1 or 2 bristles on each medial line, becoming almost black (appearing very deep reddish brown when viewed with a strong light source); bristles rather stiff, patent or retrorsely curved to retrorsely uncinate, 0.2–0.4 mm long, glabrous or papillate or with patent hairs *c.* 0.05 mm long, the base becoming up to 0.2 mm wide and very compressed at maturity. (Figure 4A–C)

Selected specimens examined. WESTERN AUSTRALIA: Tutanning Reserve, 21 Sep. 1974, *A.S. George* 12867 (PERTH); Wallaroo Rock, WNW of Coolgardie, 17 Sep. 1981, *K.R. Newbey* 8931 (PERTH).

Distribution. Endemic to south-western Australia, known from a few records extending from the Menzies area of the Eremean Botanical Province south-west via the South-western Interzone to Tutanning Reserve in the South West Botanical Province.

Habitat. Occurs in soil pockets on granite outcrops or sheets of granite.

Conservation status. Previously listed under the name *T. moorei* as Priority Two of the CALM Conservation Codes for Western Australian Flora, but removed from the list because it is now considered to be a variant of *T. cyanopetala*.

Notes. This extreme variant of *Trachymene cyanopetala* was previously regarded as a distinct species, named *T. moorei*, because its dark-coloured non-bristly fruits give it a distinctive appearance. In typical *T. cyanopetala* the fruits may be just as darkly coloured on the surface at maturity but this is largely or totally hidden by the bristles so that the fruit appears to be a less dark colour. In the area where typical *T. moorei* occurs and nearby, many specimens are intermediate between typical *T. cyanopetala* and typical *T. moorei*, having sparsely bristly fruits with relatively short bristles.

Trachymene elachocarpa (F. Muell.) B.L. Burtt (Burtt 1941: 44). – *Didiscus elachocarpus* F. Muell. (Mueller 1892: 58). *Type:* between Murchison River and Shark Bay, [Western Australia], F. Mueller (*n.v.*).

Annual herb erect or decumbent, 15–50 mm high; indumentum of patent glandular hairs, those on leaf blades and bracts sometimes losing glandular apex. *Stems* rather densely hairy; hairs patent, 0.1–0.4 mm long. *Cotyledons* narrowly obovate, 3.5–6 mm long, entire, glabrous. *Petioles* 1–17 mm long, ciliate on the expanded base and sparsely to densely hairy above; base often only slightly expanded, up to 2 mm long; hairs mostly 0.3–0.6 mm long. *Leaf blades* shallowly to deeply 3-lobed, the primary lobes entire or with 2 or 3 secondary lobes, which may be further lobed, 2.5–16 mm long, with a few scattered hairs or sometimes more densely hairy. *Involucral bracts* 5–9; free portion narrowly obovate to more or less elliptic, 2–3.5 mm long, sparsely hairy on outer surface or with a few hairs along midvein, ciliate on margins; hairs mostly 0.2–0.5 mm long. *Inflorescence* 5–15-flowered. *Petals* white. *Fruiting peduncles* 5–34 mm long; pedicels mostly 0.5–4 mm long, often with a few hairs towards summit. *Fruit* homomorphic, apparently succulent; carpophore as long as commissure but shorter than width of monocarp, 0.4–0.6 mm long, highly compressed, flexible; styles 0.3–0.4 mm long. *Monocarps* swollen especially towards outer margin, 0.7–1.1 x 0.5–0.8 mm (up to 1.1 mm across the diagonal), smooth (but shallow bumpy shrinkage marks often visible on dried material), the medial line not visible; outer margin extending horizontally beyond outer edge of stylopodium before curving downwards. (Figure 4D–F)

Selected specimens examined. WESTERN AUSTRALIA: *c.* 1.4 km WSW of Red Cliff Point, Bernier Island, 26 Aug. 1998, *S.J. Claymore & A.S. Weston* 151; Herald Bay outcamp, Dirk Hartog Island, 3 Sep. 1972, *A.S. George* 11462 (PERTH); Quobba, 11 Aug. 1976, *G.J. Keighery* 830 (PERTH); Little Lagoon, 1 km from Denham, 29 Aug. 1989, *G.J. Keighery* 11308 (PERTH); Tamala Station, 20 July 1988, *G.J. Keighery & J.J. Alford* 1992 (PERTH), Dorre Island, 16 July 1959, *R.D. Royce* 5915 (PERTH); Denham, 29 Sep. 1985, *P.G. Wilson* 12232 (PERTH).

Distribution. Endemic to Western Australia, extending from near Cape Cuvier and Bernier Island in the Eremean Botanical Province south to Kalbarri National Park in the far north of the South West Botanical Province. (Figure 3D)

Habitat. Occurs in sandy soils near the coast, sometimes on dunes or overlying limestone, in low coastal shrublands or herbfields.

Phenology. Flowering and fruiting period: July to September.

Conservation status. Not considered to be at risk at present.

Notes. This was the first species of Apiaceae to have been collected in Australia, being one of the plants brought back by William Dampier after his expedition to the Shark Bay area in 1699 (George 1971). It is one of the very few *Trachymene* species in which the monocarps are not greatly compressed and possibly has the smallest fruits in the genus; certainly its fruits are smaller than those of any other Western Australian species.

Compared with other members of sect. *Dimetopia*, *T. elachocarpa* is unique in having swollen monocarps with no medial line visible and in having the commissure shorter than the width of the monocarp.

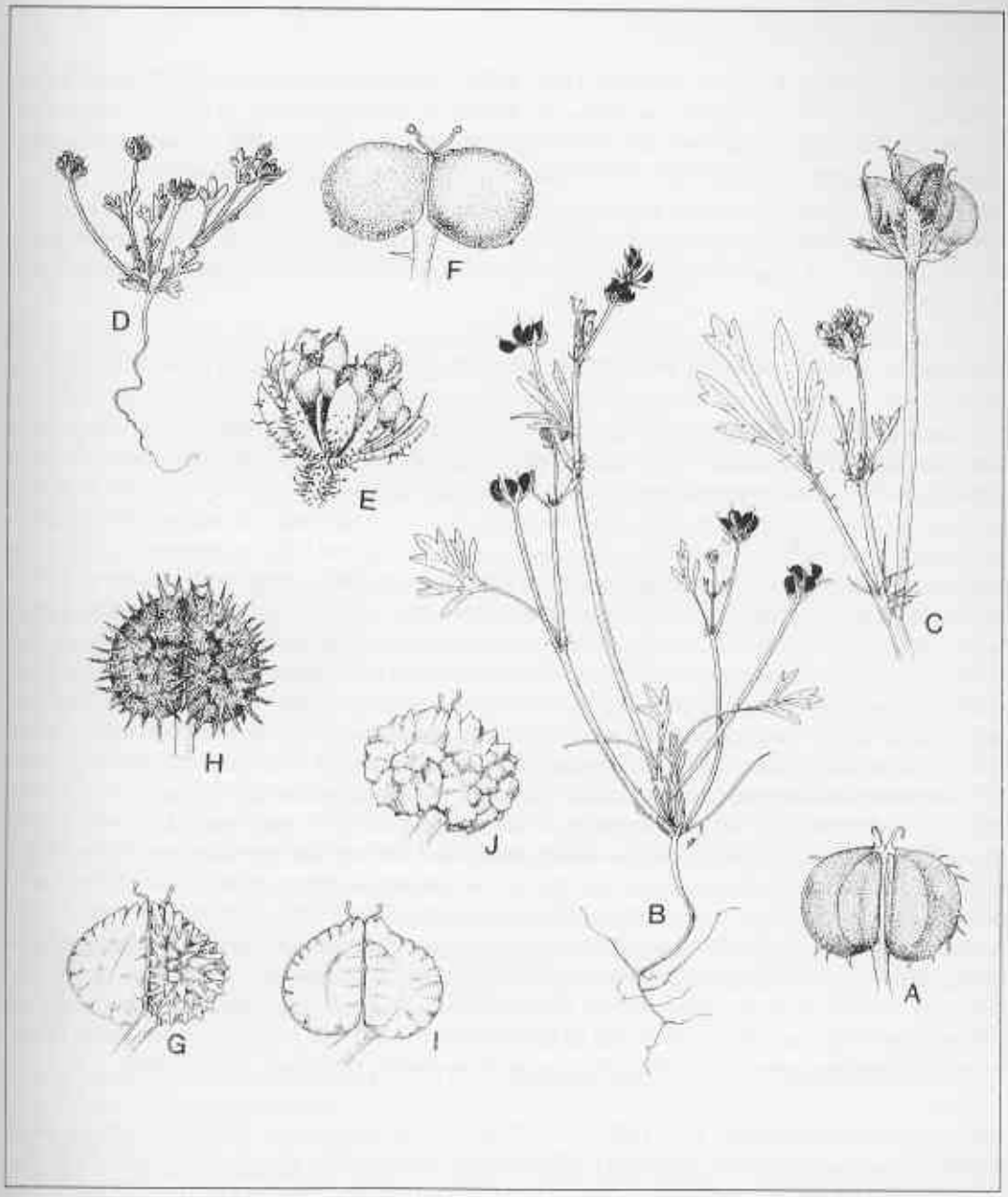

Figure 4. A–C. Non-bristly variant of *Trachymene cyanopetala*. A – fruit with a few hair-like bristles (x6), B – whole plant of specimen with fruits completely lacking bristles (x1), C – flowering and fruiting branch from B (x3.5); D–F. *Trachymene elachocarpa*. D – whole plant (x1), E – inflorescence (x5.5), F – fruit (x15); G–J. *Trachymene pilosa*. G – heteromorphic fruit, the inner monocarp shallowly tuberculate and the outer one with short bristles (x6.5), H – homomorphic fruit, both monocarps with long bristles (x8.5), I – homomorphic fruit with shallowly tuberculate monocarps (x6.5), J – homomorphic fruit with deeply tuberculate monocarps (x6.5). Drawn from *K.R. Newbey* 8931 (A–C), *G.J. Keighery* 11308 (D–F), *K.R. Newbey* 8868 (G), *G.J. Keighery* 5895 (H), *G.J. Keighery* 11485 (I) and *K.R. Newbey* 7589 (J).

Trachymene ornata (Endl.) Druce (Druce 1917: 650). – *Cesatia ornata* Endl. (Endlicher 1838: 200 or 63–64). – *Didiscus ornatus* (Endl.) Domin (Domin 1908: 35–37). *Type:* interior of western Australia, *Roe* (*n.v.*).

Dimetopia eriocarpa F. Muell. (Mueller 1855: 127). – *Trachymene eriocarpa* (F. Muell.) Benth. (Bentham 1867: 348). – *Didiscus eriocarpus* (F. Muell.) F. Muell. (Mueller 1875: 46). *Type:* near Cudnaka, in the neighbourhood of Lake Torrens, [South Australia] (*?holo:* MEL not numbered.). Also numbered specimens MEL 679943, 679944 from Cudnaka, Herbarium O.W. Sonder.

Trachymene ornata var. *semilanata* (J.M. Black) H. Eichler (Eichler 1963: 297). – *Didiscus ornatus* var. *semilanatus* J.M. Black (Black 1926: 438). *Type:* between Maree and Strangways Springs, South Australia (*n.v.*).

Illustrations. Eichler (1986: Figure 500E); Erickson *et al.* (1979: Figure 438); Powell (1992: 103).

Annual herb 20–250 mm high; indumentum (where present on vegetative organs) of glandular or non-glandular hairs, sometimes with minute lateral branches. *Stems* sparsely to densely hairy or rarely glabrous; hairs retrorse or patent, mostly 0.3–1.4 mm long. *Cotyledons* narrowly obovate, 7–24 mm long, entire, glabrous. *Petioles* 4–46 mm long, long-ciliate on expanded base and sparsely to rather densely hairy above; base sometimes only slightly expanded, 1–5 mm long, sometimes hairy on outer surface; hairs mostly 0.3–1.7 mm long. *Leaf blades* deeply 3-lobed, the primary lobes simple or further divided into 2 or 3 secondary lobes, which may be further lobed, 4–36 mm long, with more or less patent hairs. *Involucral bracts* 3–6, usually purple- or red-tinged to deeply red-purple throughout; free portion narrowly ovate to narrowly obovate, 1.8–4.5 mm long, with cilia mostly 0.2–1.0 mm long and often scattered hairs on outer surface. *Inflorescence* 3–7-flowered. *Petals* white or pale blue. *Fruiting peduncles* 10–68 mm long; pedicels mostly 2–6 mm long, glabrous or hairy. *Fruit* homomorphic, white throughout or pale purple to deep reddish purple at summit, sometimes also with a dark central portion (if indumentum shorter and less dense there); carpophore as long as commissure and exceeding the width of the monocarp, very compressed, flexible; styles 0.6–0.9 mm long. *Monocarps* very compressed, 2.0–2.7 x 1.2–1.8 mm, covered by many hairs (or very fine hair-like bristles) forming a dense woolly indumentum over whole surface or concentrated on the margin, 2.4–7 x 1.6–4.5 mm including woolly covering, with a distinct (often pale) medial line or slight to prominent medial ridge beneath the woolly layer, often prominently rugose at maturity, sometimes with a reticulate pattern of large pits to the outside of the medial ridge and a furrow to the inside of the medial ridge, sometimes distinctly beaked at apex; outer margin descending at 30–45 degrees from the outer edge of stylopodium; hairs curved or twisted into an indumentum 0.4–2.5 mm long, with a number of lateral branches; branches patent, 0.2–0.4 mm long, sometimes further branched. **Spongefruit**

Selected specimens examined. WESTERN AUSTRALIA: N of Ajana, 1 Sep. 1959, *N.T. Burbidge* 6436 (PERTH); 6 miles [10 km] E of White Cliffs Station, 18 Sep. 1975, *G.J. Keighery* 530 (PERTH); Quarderwardup Lake, SE margins of Stirling Range, 15 Oct. 1983, *G.J. Keighery* 6657 (PERTH); Ponier Rock, *c.* 65 km S of Balladonia Motel, 13 Sep. 1980, *K.R. Newbey* 7303 (PERTH); 17.5 km W of Lyons River Homestead, 19 Aug. 1987, *K.R. Newbey* 11580 (PERTH); Hyden Rock, 13 Sep. 1983, *R. Ornduff* 9307–14; York, 14 Oct. 1954, *G.G. Smith* (PERTH).
SOUTH AUSTRALIA: upper slopes of Mt John, Wilpena, 14 Sep. 1960, *D.E. Symon* 582 (PERTH).

Distribution. Widespread in the south-west of Western Australia, extending from Lyons River and Wooramel Stations in the Eremean Botanical Province south-east to Stirling Range in the South West Botanical Province and Ponier Rock in the South-western Interzone and inland to Windidda Station and Yamarna in the Eremean. Also occurs in South Australia and New South Wales. (Figure 5A)

Habitat. Commonly occurs in soil pockets or crevices on granite and other types of rocks, in moss mats and herbfields or in shrublands or low woodlands, these often dominated by *Acacia* species or *Eucalyptus* species with a mallee habit.

Phenology. Flowering and fruiting period: mainly July to October.

Conservation status. Widespread and common.

Common name. Spongefruit is accepted here as the common name for this species as it well describes its odd fruit. The dense woolly indumentum on the fruits increases their apparent size and hides the beak on the monocarps and the whitish medial line from view.

Notes. The vegetative indumentum is extremely variable. Throughout the species range and almost exclusively in some areas, the upper peduncles have long retrorse hairs, often with minute lateral branches and with the apical gland (when present) fairly inconspicuous. In many specimens from the more humid south-western part of the species range, from Wickepin and Hyden southwards, the peduncles have short prominently glandular hairs tending to be more patent, with the apical gland deep purple. Specimens with a mixture of both main kinds of hairs are also common through most of the species range.

There are two main fruit variants, one with the woolly indumentum densely covering the whole surface of the monocarp and the other with long woolly indumentum around the margin and shorter indumentum on the lateral faces of the monocarp, giving the fruit a somewhat winged appearance. The latter variant occurs in South Australia, where it has been treated as var. *semilanata* (e.g. Eichler 1986: 1007) and is apparently known only from the type locality. In Western Australia many specimens (e.g. *D.J. Pearson* 2140) have the young fruits sparsely hairy and dark in the centre, with much longer denser indumentum around the margin giving the fruits a winged appearance. Mature fruits invariably appear to be densely hairy throughout except where the indumentum has been rubbed off the medial ridges. The South Australian taxon does not appear to be any more significant than the many fruit variants of *Trachymene cyanopetala* and *T. pilosa* and shows no other morphological differences, so is not recognized here as a distinct variety.

Trachymene pilosa Sm. (Smith 1819). – *Didiscus pilosus* (Sm.) Domin (Domin 1908: 31–33). – *Trachymene pilosa* Sm. var. *pilosa* (created by publication of var. *preissiana* in 1867). *Type:* King George Sound, [Western Australia], *Menzies (n.v.).*

Dimetopia pusilla DC. (de Candolle 1830: 177). – *Didiscus pusillus* (DC.) F. Muell. (Mueller 1875: 47). *Type:* New Holland [Western Australia] (*holo:* G, *n.v.*, microfiche seen).

Dimetopia hirta Benth. (Bentham 1837: 54). *Type:* King George Sound, [Western Australia], *Huegel (n.v.)*

Trachymene pilosa var. *preissiana* Benth. (Bentham 1867: 348). – *Dimetopia preissii* Bunge (Bunge 1845: 284–285). – *Didiscus pilosus* var. *preissii* (Bunge) Domin (Domin 1908: 33). *Type:* Rottnest Island, [Western Australia], 21 August 1839, Herb. Preiss. No. 2089 (*n.v.*).

Annual herb 20–350 mm high. *Stems* usually sparsely to densely glandular-hairy, sometimes glabrous; hairs patent, 0.3–0.8(1.3) mm long. *Cotyledons* elliptic to obovate or narrowly obovate,

5–11 mm long, entire, glabrous or rarely sparsely glandular-hairy. *Petioles* 6–78 mm long, long-ciliate on expanded base, glabrous or with few to many cilia on narrow portion; expanded base 2.5–9 mm long; hairs mostly 0.5–1.5 mm long. *Leaf blades* usually very deeply 3-lobed, the primary lobes further divided into usually 3 secondary lobes, which are often further lobed, 4.5–40 mm long, with a uniform sparse indumentum or with few hairs. *Involucral bracts* (5)7–10; free portion narrowly ovate to obovate or rarely almost narrowly oblong, 1.8–4.3 mm long; cilia mostly 0.1–0.6 mm long. *Inflorescence* (5)11–21(*c.* 50)-flowered. *Petals* white. *Fruiting peduncles* 14–92 mm long; pedicels 1–7 mm long. *Fruit* heteromorphic or homomorphic (commonly bristly on outer monocarp and tuberculate-rugose to fairly smooth on inner monocarp, less commonly bristly or tuberculate on both monocarps); carpophore as long as commissure and exceeding the width of the monocarp, compressed or very compressed, stiff in basal half, somewhat flexible towards apex; styles 0.4–0.8 mm long. *Monocarps* very compressed, 1.7–3.3 x 1.4–2.4 mm, with a distinct medial line, slightly beaked at apex; outer margin usually immediately descending at a shallow angle of 10–30 degrees from the outer edge of styopodium, rarely almost horizontal; bristles up to 1.0 mm long, terete or only slightly compressed at the base at maturity and 0.1–0.4(0.5) mm wide at maturity, often very solid, minutely retrorsely barbed; tubercles (when present) prominent to reduced but always two apical ones visible on a slight beak even when the surface is otherwise rather smooth. (Figures 4G–K, 6)

Distribution. Widespread in the south-west of Western Australia. Occurs in near-coastal areas and off-shore islands around the coast of the South West Botanical Province from Bernier Island (west of Carnarvon) to Middle Island, Recherche Archipelago, with an isolated coastal record from near Eyre near the border between the South-western Interzone and Eremean Botanical Province. Extends inland to Canning Hill (north of Paynes Find) in the Eremean and to Mt Walter (east of Koolyanobbing) and Jyndabinbin Rocks (south-west of Norseman) in the Interzone. Also occurs in South Australia and Victoria. (Figure 5B)

Habitat. Occurs on coastal sand dunes and inland dunes, or associated with salt lakes, or on granite outcrops, often in *Banksia*- or *Eucalyptus*-dominated vegetation.

Chromosome number. n=20 (Keighery 1982). Voucher specimens: *G.J. Keighery* 493, 2053, 2177.

Phenology. Flowering and fruiting period: August to October.

Conservation status. Widespread and common.

Common name. Hartley (1979) records the common name Dwarf Parsnip for this species but this was not followed by Wheeler (1987) and is not favoured here either.

Affinities. Trachymene pilosa has often been confused with *T. cyanopetala* but can be distinguished by having one or more of the following characters: stems with patent glandular hairs, flowers more than 7 per umbel, fruits with one or both monocarps tuberculate at least at apex and bristles with retrorse hairs, and monocarps shortly but distinctly narrowed at the apex into a slight beak. Another difference in the bristles of the two species is that the *pilosa* bristle is terete or only slightly compressed at the base, which is usually distinctly enlarged and solid at maturity, whereas the *cyanopetala* bristle is either very slender at the base or broad but very compressed.

Notes. Some other synonyms of *Trachymene pilosa* are listed by Bentham (1867: 348) and Domin (1908: 31) as follows: *Didiscus pilosus* var. *glaberrimus* Domin, *Dimetopia isocarpa* Bartl., *Dimetopia*

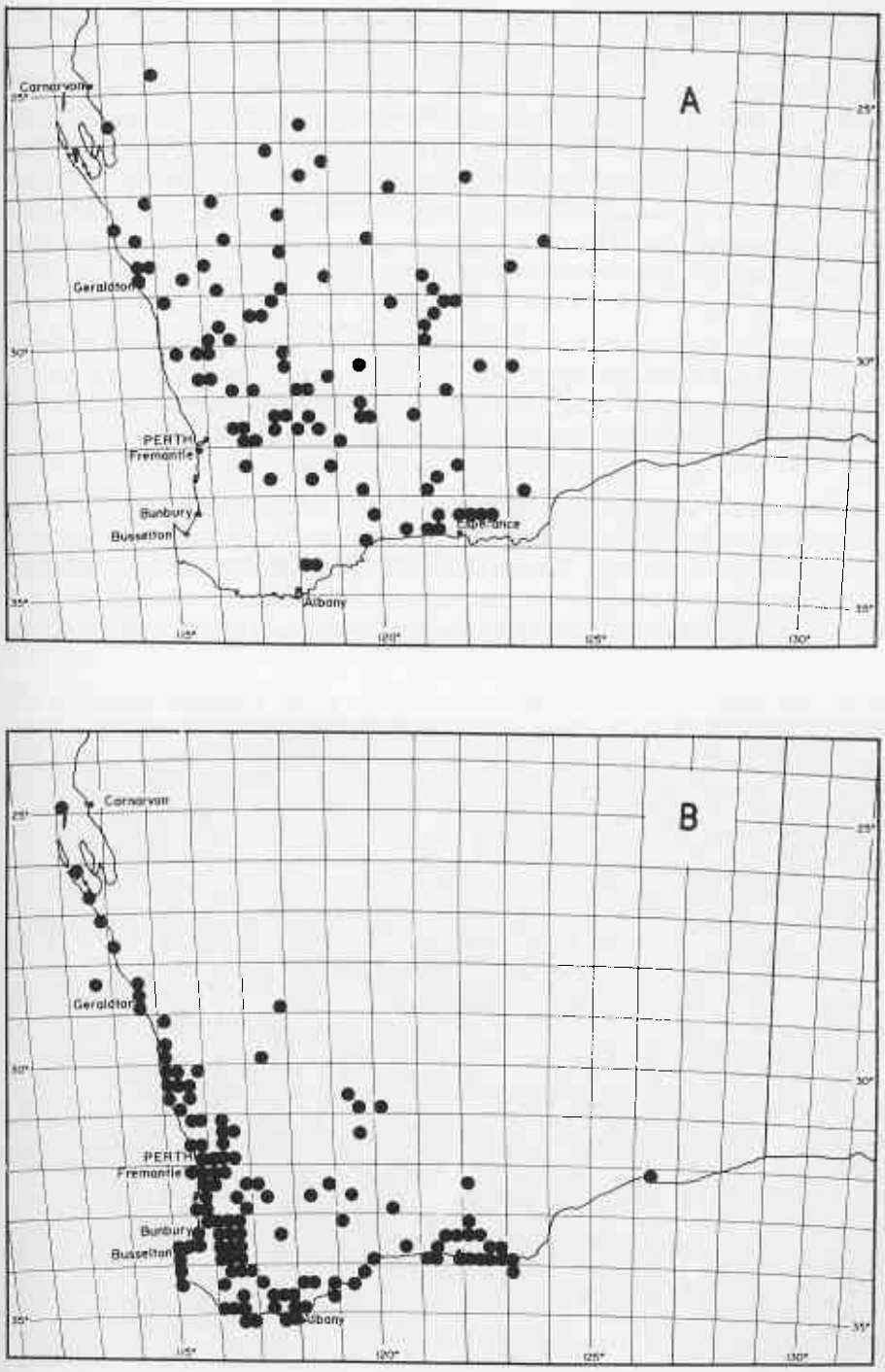

Figure 5. Distribution in Western Australia. A – *Trachymene ornata*; B – *T. pilosa*.

homocarpa Bunge, *Dimetopia walpersii* Bunge and *Pritzelia didiscoides* Walp. No type material of these taxa has been seen as they all either lack type citations or were named from cultivated material.

Trachymene pilosa is an extremely variable taxon which appears to be in the process of evolution into a number of species. A leafy variant with numerous long radical leaves forming a dense tuft equalling or exceeding the stems and with relatively long involucral bracts, is distributed from the Abrolhos islands southwards along the west coast probably to near Bunbury. Its dense domed habit is shown from top view in Figure 6. The leafy variant occurs on islands and on the Quindalup dunes system of the mainland, in relatively exposed locations including the sandy margins of saline lakes, its unusual domed growth form presumably an adaptation to its harsh environment. It has been named var. *preissiana* but is not recognized here as it appears to completely intergrade with specimens with the typical growth form.

A few plants (e.g. *G.J. Keighery* 2572 and *P.G. Wilson* 8128) have glandular hairs on the cotyledons and also on the stems just below the cotyledons. The great majority of specimens have glabrous cotyledons and the stem below them also glabrous. *T. pilosa* tends to have its leaves more divided than other species in sect. *Dimetopia* but there is considerable overlap in this character.

Inland specimens of *T. pilosa* tend to be smaller plants than the coastal specimens, with fewer flowers per umbel and with bristles either shorter or absent, the coastal specimens always having bristles on the outer monocarp or both monocarps. Coastal plants sometimes have large umbels with dimorphic flowers, the outermost flowers having the outer petal enlarged. This species shows the closest approach to the members of sect. *Didiscus*, which regularly produce large or very large umbels with dimorphic flowers.

Figure 6. Photograph of *Trachymene pilosa* taken by G.J. Keighery at Lake Coolongoolup.

In coastal areas where the species is most common, the fruit is most often heteromorphic with long bristles on the outer monocarp and the inner monocarp prominently rugose-tuberculate to fairly smooth with a few marginal tubercles. Less commonly in coastal populations the fruit is bristly on both monocarps and plants of this and the more common kind frequently occur in mixed populations. There are also populations with a mixture of two different sorts of heteromorphic fruits, some with the inner monocarp prominently tuberculate and others with the inner monocarp largely smooth, sometimes also with intermediate fruits. These variants become replaced inland by variants with shorter bristles or with both monocarps tuberculate. In heteromorphic fruits on specimens from far inland, the bristles are very short. One specimen from Lake Seabrook (*K.R. Newbey* 5872) has the bristles so reduced as to resemble a very prominent type of rugose patterning rather than bristles.

Bristle thickness is greater in southern than in north-eastern populations. In areas from Perth northwards the bristles are commonly 0.1–0.3 mm wide at the base at maturity whereas those from southern areas are mostly 0.2–0.4(0.5) mm wide.

The main fruit variants in Western Australia are listed below. Judging from the descriptions in the most recent floras for South Australia and Victoria (Eichler 1986, Willis 1972), only the variant of *T. pilosa* with the highly heteromorphic fruits occurs in those states. This is also the most common variant in Western Australia.

a. Heteromorphic variant with long bristles

Illustrations. Eichler (1986: Figure 500F); Wheeler (1987: Figure 206D).

Fruit with outer monocarp bristly and inner monocarp tuberculate; bristles 0.6–1.0 mm long.

Selected specimens examined. WESTERN AUSTRALIA: East Wallabi Island, Abrolhos Islands, 3 Oct. 1987, *J.J. Alford* 654 (PERTH); Boonanarring proposed nature reserve, off Wannamal road, 21 Sep. 1987, *J.J. Alford* 715 (PERTH); *c.* 1.7 km W of Wedge Rock, Hospital Landing area, Bernier Island, 28 Aug. 1998, *S.J. Claymore & A.S. Weston* 148; 2.5 km N of Scadden East Rd on Dempster Rd, 25 Sep. 1992, *G.F. Craig* 2221 (PERTH); S of Tamala homestead, 27 Aug. 1969, *A.S. George* 9599 (PERTH); 7.9 km N of Eyre, 1 Oct. 1984, *G.J. Keighery* 7566 (PERTH); below Jilakin Rock, 24 Oct. 1959, *C.V. Malcolm* (PERTH); Middle Island, Recherche Archipelago, 11 Feb. 1960, *R.D. Royce* 6267 (PERTH); Gibraltar Rock, Porongurup Range, 10 Nov. 1960, *G.G. Smith* (PERTH); Cape Naturaliste, 5 Nov. 1974, *D.J.E. Whibley* 5022 (PERTH).

Distribution. A very common variant in coastal and near-coastal areas of Western Australia from Bernier Island to near Eyre, and extending inland to Jilakin Rock. Also occurs in South Australia and Victoria. (Figure 7A)

Notes. As far as is known, this fruit variant includes all the leafy domed specimens that have been named var. *preissiana* and one specimen (*J.J. Alford* 654) of that is cited above.

b. Heteromorphic variant with short bristles

Fruit with outer monocarp bristly and inner monocarp tuberculate; bristles up to 0.6 mm long. (Figure 4G)

Specimens examined. WESTERN AUSTRALIA: southern end of Lake Seabrook, 11 Sep. 1979, *K.R. Newbey* 5872 (PERTH); Mt Walter, *c.* 88 km NE of Station, 16 Sep. 1981, *K.R. Newbey* 8868 (PERTH); Lake Deborah East, 26 Sep. 1981, *K.R. Newbey* 9060 (PERTH).

Distribution. A rare inland variant known from only three localities in the area south and south-east of Koolyanobbing, Western Australia. (Figure 7A)

c. Homomorphic bristly variant

Fruit with both monocarps bristly. (Figure 4H)

Selected specimens examined. WESTERN AUSTRALIA: off Talbot West Rd, 3.2 km S of Mt Talbot, 12 Nov. 1996, *M.G. Allen* 580; Spalding Park, 3 miles [5 km] N of Geraldton, 7 Sep. 1965, *A.C. Burns* 9 (PERTH); Cape Riche, 28 Oct. 1987, *E.J. Croxford* 5884 (PERTH); Middleton Beach, Albany, 1923, *Goadby* (PERTH); Tagon Bay, Cape Arid National Park, 16 Oct. 1991, *W. Greuter* 22876 (PERTH); Lake Walyungup, Rockingham, 23 Oct. 1993, *G.J. Keighery* 12779 (PERTH); Steep Point, Shark Bay, 22 Sep. 1997, *A. Markey* 1327; E boundary of Watheroo National Park, 14 Sep. 1971, *R.D. Royce* 9716 (PERTH).

Distribution. Widespread around the coast from Shark Bay to Cape Arid National Park, restricted to the coast in southern areas but extending inland on the Darling Range near Perth and progressively further inland northwards to Watheroo National Park. (Figure 7B)

d. Homomorphic tuberculate variant

Fruit with both monocarps tuberculate. (Figure 4I,J)

Selected specimens examined. WESTERN AUSTRALIA: Marramburup Rock, Porongurup Range, 15 Dec. 1986, *G.J. Keighery* 8430 (PERTH); *c.* 20 km ESE of Grass Patch, 12 Sep. 1984, *P. van der Moezel* 480 (PERTH); Condarning Rock, 3 km S of Yellowdine, 19 Sep. 1979, *K.R. Newbey* (PERTH); Nettleton Rd, 7.8 km SE of Byford, 8 Oct. 1983; *R. Ornduff* 9300–65 (PERTH); *c.* 2 km S of Newdegate, 16 Sep. 1985, *K. Schmidt* 771 (PERTH).

Distribution. Absent from the coast but a few records in near-coastal areas, extending from Darling Range, Porongurup Range and near Grasspatch inland to near Yellowdine. (Figure 7B)

e. Mixed variant.

Fruit with outer monocarp long-bristly; inner monocarp varying from long-bristly to tuberculate or smooth, often bristly only on margin or outer half.

Specimens examined. WESTERN AUSTRALIA: Canning Hill, 12 Aug. 1969, *M.I.H. Brooker* 1989 (PERTH); Goodlands Reserve, *c.* 66 km NE of Kalannie, 3 Sep. 1995, *M. Hislop* 150B *& E. Hudson* (PERTH).

Distribution. Recorded from two inland localities in the Paynes Find area, one at Canning Hill (on Wydgee Station) and the other from west of Lake Moore. (Figure 7A)

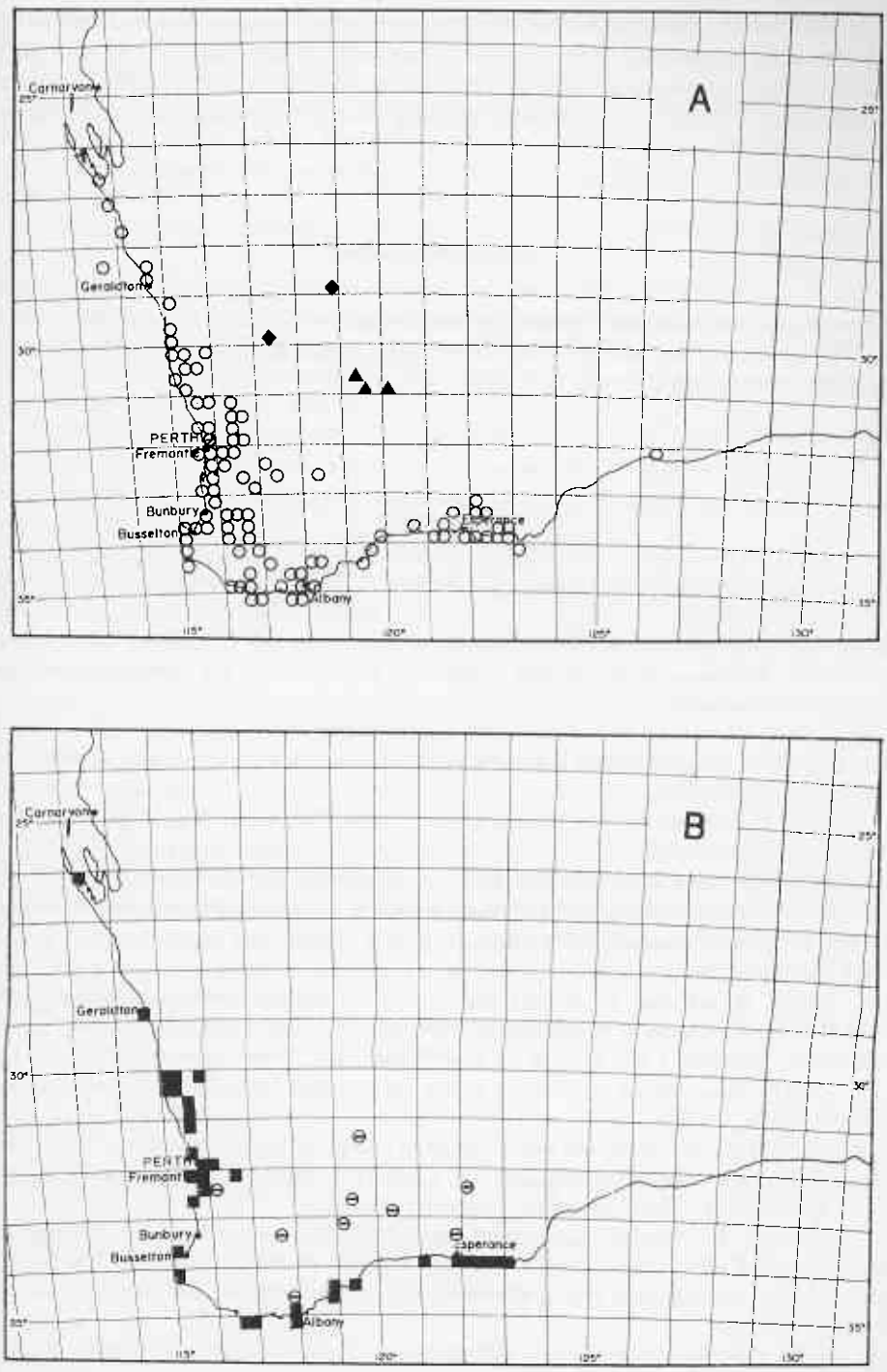

Figure 7. Distribution of variants of *Trachymene pilosa* in Western Australia. A – heteromorphic variants with long bristles ○ or short bristles ▲, and mixed variant ◆; B – homomorphic variants with fruits bristly ■ or tuberculate ⊖.

Notes. Unlike other variants of *Trachymene pilosa* this variant sometimes shows significant variation in the fruits borne on the same plant. The Canning Hill collection (*M.I.H. Brooker* 1989) has some specimens with homomorphic long-bristly fruits only, some specimens with the typical heteromorphic fruits only and some specimens with more than one type of fruit including intermediate fruits in which the inner monocarp is bristly on its outer half and smooth on its other half. The Goodlands Reserve collection is of a single plant, in this case the fruits all heteromorphic but some with the inner monocarp smooth and others with the inner monocarp partially bristly, the bristles occurring mainly on the margin.

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