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CHROMOSOME NUMBER DETERMINATIONS IN *BRACHYSCOME* Cass. (ASTERACEAE: ASTEREAE) WITH COMMENTS ON SPECIES DELIMITATION, RELATIONSHIPS AND CYTOGEOGRAPHY

by

K. WATANABE[1] and P.S. SHORT[2]

ABSTRACT

Watanabe, K. and Short, P.S. Chromosome number determinations in *Brachyscome* Cass. (Asteraceae: Astereae) with comments on species delimitation, relationships and cytogeography. *Muelleria* 7(4): 457–471 (1992). — Chromosome number determinations from 145 populations attributed to 29 species or species complexes of *Brachyscome* are reported. First reports for *B. gracilis* (2n = 8), *B. muelleri* (n = 3, 2n = 6), *B. rara* (n = 6, 2n = 12), *B. readeri* (2n = 10), *B. riparia* (n = 9), and *B. tetrapterocarpa* (n = 4, 2n = 8), and new reports for the *B. diversifolia* (2n = 24) and *B. campylocarpa* complexes (n = 3, 2n = 6) are presented. Remaining counts support previously reported determinations and add to knowledge of chromosome number distribution. Polyploidy is common in the widespread *B. ciliaris* and *B. dentata* complexes. In the apomictic *B. ciliaris* group triploids and tetraploids are widespread, the diploids have restricted distributions. Problems with the delimitation of many species are discussed.

INTRODUCTION

Brachyscome Cass., a genus to which more than 70 species are currently attributed, exhibits a wide diversity of chromosome numbers, with Smith-White *et al.* (1970) reporting observations for 43 recognised taxa and for some undescribed entities. The work showed that the revision by Davis (1948) was inadequate, the group requiring a revision which took into account chromosome data and field observations. Since that time, further investigations within the genus have mainly concerned the elucidation of taxa and relationships within the *B. lineariloba* complex (e.g. Kyhos *et al.* 1977, Carter 1978b, Watanabe and Smith-White 1987). One of us (KW) is still carrying out cytological and molecular research in the genus, studying for example chromosome pairing in artificial hybrids and chloroplast DNA, while the other (PSS) has commenced a taxonomic revision of the genus which will incorporate cytological and molecular data, with data on breeding systems, fruit anatomy, etc. In this paper we extend the available chromosome data and briefly outline some of the taxonomic problems so far encountered, make observations on species relationships, and comment on the cytogeography of some species. Chromosome number determinations are primarily the work of Watanabe, taxonomic interpretation the work of Short.

There is also an additional need for this paper. Unfortunately many of the reports published by Carter (1978a) apparently lack extant voucher specimens and some of the specimens gathered by Smith-White *et al.* (1970), although usually identifiable, have been damaged by insects.

MATERIALS AND METHODS

Chromosome counts were obtained from either floral bud material fixed in the field, or from root tips obtained from seedlings grown, from fruit of known provenance, in the greenhouse of Kobe University. For the cultivation of specimens and the preparation of material for chromosome number determinations

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the procedures of Smith-White *et al.* (1970) and Watanabe *et al.* (1975) were followed. With the exception of *B. rara* (specimen in AD), two collections (*Short 3550* and *Short 3646*) of *B. dentata* (seed only), and two collections currently held in the private herbarium of the Australian Daisy Study Group (ADSG), a complete set of voucher specimens has been deposited in MEL. Following completion of a taxonomic revision duplicate voucher collections of non-Victorian populations will be deposited in the major government herbarium (AD, BRI, NSW, PERTH) of the State from which collections were gathered. An incomplete set has already been deposited with TNS.

Percentage pollen sterility was usually only estimated by using the double stain method (phloxine and methyl green; Owczarzak 1952). For each population (or collection) estimates were usually obtained from 15 florets, each of which came from a different plant. The material used for pollen sterility estimates was gathered in the field and stored in 70% ethanol. For members of the *B. dentata* complex, estimates of pollen sterility were also ascertained using 1% acetocarmine (for several plants only, a single value of percentage sterility being ascertained) as well as the double stain method.

RESULTS

All chromosome determinations are presented in Table I. The meiotic or mitotic chromosomes of some species are displayed in Fig. 1, and the distribution of the different ploidy levels in the *B. ciliaris* complex and *B. dentata* are shown in Figs 2 & 3.

Table I. Chromosome number determinations in *Brachyscome*

Species & locality	n	2n
B. basaltica F. Muell. var. **gracilis** Benth.		
Taylors Lake, 2 km SE of Sydenham, Vict., 12.i.1986, *Albrecht 2719*	6II	
4.2 km NW of Bearii, Vict., 14.xi.1988, *Short 3358*		12
B. breviscapis C.R. Carter		
19 km from Streaky Bay along Ceduna road and opposite Eba Island, S.A., 30.viii.1989, *Short 3738*	4II	
4.5 km from intersection with Elliston — Lock road along Mt Wedge — Colton road, S.A., 31.viii.1989, *Short 3742*	4II	
B. sp. aff. **campylocarpa** J.M. Black		
7 km N of Barringun, Qld, 15.viii.1989, *Short 3566*	3II	6
6.7 km E of Enngonia, N.S.W., 21.vii.1989, *Salkin s.n.* (ADSG 52)		12 or 12 + 2B
37 km N of Bourke, N.S.W., 15.viii.1989, *Short 3557*	3IV-6II	12
B. ciliaris (Labill.) Less. complex		
10 km W of Cockburn, S.A., 22.viii.1989, *Short 3657*		27
24.5 km SW of Olary, S.A., 22.viii.1989, *Short 3658*		27
77 km S of Pimba, S.A., 25.viii.1989, *Short 3664*		27
36 km E of Kimba, S.A., 29.viii.1989, *Short 3719*		27
8 km from Wirrealpa along Blinman road, Flinders Ranges, S.A., 1.ix.1989, *Short 3752*	27I (0–8II)	
24 km N of Wirrealpa, Flinders Ranges, S.A., 1.ix.1989, *Short 3756*		27
8 km from Broken Hill to Tibooburra road along road to White Cliffs, N.S.W., 19.viii.1989, *Short 3630*		27
16 km N of Barrier Hwy along road to Tilpa, N.S.W., 20.viii.1989, *Short 3639*		27
52 km W of Wilcannia, N.S.W., 21.viii.1989, *Short 3645*		27
4 km N of Pt Augusta, S.A., 25.viii.1989, *Short 3659*	36I (0–6II)	
8 km N of Glendambo, S.A., 26.viii.1989, *Short 3671*		36
8 km N of Glendambo, S.A., 26.viii.1989, *Short 3672*		36
54 km N of Glendambo, S.A., 26.viii.1989, *Short 3680*		36

Species & locality	n	2n
119 km N of Glendambo, S.A., 26.viii.1989, *Short 3681*		36
10 km E of Evelyn Downs, S.A., 27.viii.1989, *Short 3698*		36
17 km S of Cadney Park, S.A., 28.viii.1989, *Short 3700*		36
17 km S of Cadney Park, S.A., 28.viii.1989, *Short 3701*		36
84 km N of Glendambo, S.A., 28.viii.1989, *Short 3703*		36
22 km NE of Iron Knob, S.A., 29.viii.1989, *Short 3709*		36
36 km E of Kimba, S.A., 29.viii.1989, *Short 3718*		36
4 km NW of Kyancutta, S.A., 29.viii.1989, *Short 3723*		36
19 km from Streaky Bay along Ceduna road, S.A., 30.viii.1989, *Short 3739*		36
20 km E of Cowell, S.A., 31.viii.1989, *Short 3746*		36
20 km E of Cowell, S.A., 31.viii.1989, *Short 3747*		36
4.5 km along road to Chambers Gorge from the Blinman to Arkaroola road, Flinders Ranges, S.A., 1.ix.1989, *Short 3758*		36
18 km from Murray Bridge along Karoonda road, S.A., 4.ix.1989, *Short 3765*		36
17 km S of Cunnamulla, Qld, 16.viii.1989, *Short 3575*		36
1 km S of Wyandra, Qld, 16.viii.1989, *Short 3582*		36
6 km N of Charleville, Qld, 17.viii.1989, *Short 3593*		36
8 km NNE of Noccundra, Qld, 18.viii.1989, *Short 3619*		36
11 km W of Bourke, N.S.W., 15.viii.1989, *Short 3553*		36
22 km N of Bourke, N.S.W., 15.viii.1989, *Short 3556*		36
4.5 km S of Tibooburra, N.S.W., 19.viii.1989, *Short 3624*		36
66 km S of Tibooburra, N.S.W., 19.viii.1989, *Short 3628*		36
28 km NE of Wilcannia along road to Tilpa, N.S.W., 20.viii.1989, *Short 3643*		36
20 km W of Wilcannia, N.S.W., 21.viii.1989, *Short 3644*		36
76 km W of Wilcannia, N.S.W., 21.viii.1989, *Short 3648*		36
200 m from S.A./Vict. border along Sturt Hwy, Vict, 4.ix.1989, *Short 3768*		36
31 km S of Ouyen, Vict., 5.ix.1989, *Short 3771*	36I (sometimes including II, IV)	
var. **lyrifolia** (J.M. Black) G.L. Davis		
Parachilna Gorge, Flinders Ranges, S.A., 1.ix.1989, *Short 3749*	9II	
B. ciliocarpa W.V. Fitzg.		
41 km E of Quilpie, Qld, 17.viii.1989, *Short 3607*	9II	18
B. curvicarpa G.L. Davis		
5 km W of Walgett, N.S.W., 15.viii.1989, *Short 3549*	4II	
18 km N of Bourke, N.S.W., 15.viii.1989, *Short 3554*	4II	
1.5 km SE of Wilcannia, N.S.W., 20.viii.1989, *Short 3633*	4II	
B. aff. **curvicarpa** (yellow ray florets)		
27 km N of Wyandra, Qld, 16.viii.1989, *Short 3587*	4II + BI	8 or 8 + 3B
0.7 km N of Charleville Post Office, Qld, 17.viii.1989 *Short 3592*	4II	8
43 km N of Charleville, Qld, 17.viii.1989, *Short 3597*	4II + BI	
B. debilis Sonder		
Mt Arapiles, Vict., 13.x.1990, *Short 3916*	3II	6
B. dentata Gaudich.		
24 km N of Wirrealpa, Flinders Ranges, S.A., 1.ix.1989, *Short 3755*	4II + BII or 2BI	8 & 8 + 2B
1.5 km SE of Wilcannia, N.S.W., 20.viii.1989, *Short 3634*	4II	
1.5 km S of Cunnamulla, Qld, 16.viii.1989, *Short 3577*	1IV + 6II or 8II	
27 km N of Wyandra, Qld, 16.viii.1989, *Short 3583*	1IV + 6II + BII or 8II + BII or 8II + 2BI	
21 km SW of Charleville, Qld, 17.viii.1989, *Short 3599*	8II + BII or 2BI	
53 km N of Coonamble, N.S.W., 14.viii.1989, *Short 3547*	8II	16 or 16 + 1B
47 km S of Walgett, N.S.W., 14.viii.1989, *Short 3548*		16
52 km W of Walgett, N.S.W., 14.viii.1989, *Short 3550*		16 + 1B
16.5 km N of Enngonia, N.S.W., 15.viii.1989, *Short 3564*	8II + BII	

Species & locality	n	2n
8 km from Broken Hill to Tibooburra road along road to White Cliffs, N.S.W., 19.viii.1989, *Short 3631*	1IV +6II or 8II	
52 km W of Wilcannia, N.S.W., 21.viii.1989, *Short 3646*	1IV + 6II or 8II	
76 km W of Wilcannia, N.S.W., 21.viii.1989, *Short 3649*	8II + BII	
50 km W of Broken Hill, N.S.W., 21.viii.1989, *Short 3650*	1IV + 6II + BII or 8II + BII or 8II + 2BI	
34 km S of Tibooburra, N.S.W., 19.viii.1989, *Short 3626*	12II + BI	
54 km S of Tibooburra, N.S.W., 19.viii.1989, *Short 3627*	12II + BI	
16 km N of Barrier Hwy along road to Tilpa, N.S.W., 20.viii.1989, *Short 3638*	1IV + 10II + BI or 12II + BI	
19 km N of Barrier Hwy along road to Tilpa, N.S.W., 20.viii.1989, *Short 3641*		24 + 1B
9 km S of Patchewollock, Vict., 5.ix.1989, *Short 3773*	12II	
4 km W of Hopetoun, Vict., 5.ix.1989, *Short 3774*	12II + BI	
B. dichromosomatica C.R. Carter		
var. **dichromosomatica** Cytodeme A1 (Watanabe *et al.* 1975)		
16 km N of Pt Augusta, S.A., 25.viii.1989 & 31.viii.1989, *Short 3662*	2II	
c. 12–17 km N of Simmonston along road to Yappala Homestead, S.A., 2.ix.1989, *Short 3761 p.p.*		4
18 km W of Pt Augusta, S.A., 29.viii.1989, *Short 3708*	2II	
22 km NE of Iron Knob, S.A., 29.viii.1989, *Short 3711*	2II	
var. **dichromosomatica** Cytodeme A2 (Watanabe *et al.* 1975)		
3 km S of Pimba, S.A., 25.viii.1989, *Short 3668*		4
65 km N of Hawker, S.A., 2.ix.1989, *Short 3760*		4
var. **dichromosomatica** Cytodemes A2 & A4 (Watanabe *et al.* 1975)		
c. 12–17 km N of Simmonston along road to Yappala Homestead, S.A., 2.ix.1989, *Short 3761 p.p.*		4
var. **alba** C.R. Carter		
16 km N of Barrier Hwy along road to Tilpa, N.S.W., 20.viii.1989, *Short 3637*	2II	
B. diversifolia (Graham) Fischer & C. Meyer var. **diversifolia**		
5 km W of Stawell, Vict., 12.ix.1988, *Short 3345*		24
B. eriogona (J.M. Black) G.L. Davis		
3 km S of Pimba, S.A., 25.viii.1989, *Short 3669*	4II	8
20 km N of Coober Pedy, S.A., 26.viii.1989, *Short 3684*	4II	
12 km N of Arckaringa Creek along the Coober Pedy to Oodnadatta road, S.A., 27.viii.1989, *Short 3687*	4II	
0.5 km N of Arckaringa Creek along the Coober Pedy to Oodnadatta road, S.A., 27.viii.1989, *Short 3693*	4II	
25 km W of Mt Barry Homestead, S.A., 27.viii.1989, *Short 3697*	4II	
8 km N of Evelyn Downs, S.A., 27.viii.1989, *Short 3699*	4II	
B. exilis Sonder		
Daly Head, Yorke Pen., S.A., 10.x.1990, *Short 3908*	9II	
B. goniocarpa Sonder & F. Muell.		
22 km W of Lock, S.A., 31.viii.1989, *Short 3743*	4II	8
Mt Arapiles, Vict., 5.ix.1989, *Short 3775*	4II	
B. sp. aff. **goniocarpa**		
Watson St., Cunnamulla, Qld, 11.viii.1989, *Salkin s.n.* (ADSG)		6
B. gracilis G.L. Davis		
Killawarra State Forest, Vict., 15.xi.1988, *Short 3361*		8

Species & locality	n	2n
B. aff. **gracilis**		
Kings Billabong State Game Reserve, near Mildura, Vict., 19.x.1987, *Browne 397*		24
B. halophila P.S. Short		
13 km N of Three Springs, W.A., 21.ix.1990, *Short 3855*		18
B. iberidifolia Benth. complex		
Karolin Rock, W.A., 16.ix.1990, *Short 3810*	9II	
Dookanooka Nature Reserve, W.A., 21.ix.1990, *Short 3860*	9II	
Tutanning Reserve, W.A., 25.ix.1990, *Short 3874*	9II	
8 km N of Glendambo, S.A., 26.viii.1989, *Short 3673*	9II	
119 km N of Glendambo, S.A., 26.viii.1989, *Short 3682*	9II	
27 km S of Hiltaba Homestead, S.A., 30.viii.1989, *Short 3733*	9II	
B. leariloba (DC.) Druce		
Cytodeme E (Carter 1978b)		
12.5 km W of Kimba, S.A., 29.viii.1989, *Short 3721 & 3722*	4II + 2I	
19 km from Streaky Bay along Ceduna road and opposite Eba Island, S.A., 30.viii.1989, *Short 3737*	4II + 2I	
22 km W of Lock, S.A., 31.viii.1989, *Short 3744*	4II + 2I	
Cytodeme B		
22 km NE of Iron Knob, S.A., 29.viii.1989, *Short 3710*	6II	
4 km NW of Kyancutta, S.A., 29.viii.1989, *Short 3724*	6II	
44 km NE of Minnipa, S.A., 30.viii.1989, *Short 3725*	6II	
10 km SE of Hiltaba, S.A., 30.viii.1989, *Short 3729*	6II	
4 km SSE of Halidon, S.A., 3.ix.1989, *Short 3766*	6II	
200 m from S.A./Vict. border along Sturt Hwy, Vict., 4.ix.1989, *Short 3769*	6II	
Cytodeme C		
2 km NE of vermin proof fence along Cleary to Paynes Find road, W.A., 16.ix.1990, *Short 3819*		16
10 km W of Cockburn, S.A., 22.viii.1989, *Short 3656*	8II	
7 km NE of Oodla Wirra, S.A., 22.viii.1989, *Short 3661*	8II	
Cutting Creek, 4.5 km S of Tibooburra, N.S.W., 19.viii.1989, *Short 3625*	8II	
76 km W of Wilcannia, N.S.W., 21.viii.1989, *Short 3647*	8II	
2 km NW of Yanco Glen, N.S.W., 21.viii.1989, *Short 3653*	8II	
B. melanocarpa Sonder & F. Muell.		
35 km S of Cunnamulla, Qld, 17.viii.1988, *Short 3164*		12
7 km N of Barringun, Qld, 15.viii.1989, *Short 3570*	6II	
1.5 km S of Cunnamulla, Qld, 16.viii.1989, *Short 3578*	6II	
16.5 km N of Enngonia, N.S.W., 15.viii.1989, *Short 3563*	6II	
B. muelleri Sonder		
Corunna Hill South, S.A., 29.viii.1989, *Short 3713*	3II	6
B. multifida DC.		
Clover Flat Power Station, Vict., 18.i.1988, *Short 3080*	9II	
2 km towards Zumsteins from the turn-off to MacKenzie Falls along the Halls Gap to Zumsteins road, Vict., 12.ix.1988, *Short 3347*	9II	18
B. oncocarpa Diels		
12 km N of turn-off to Bimbijy Stn along the Cleary to Paynes Find road, W.A., 17.ix.1990, *Short 3823*	9II	
B. perpusilla (Steetz) Benth.		
2 km NE of vermin proof fence along Cleary to Paynes Find road, W.A., 16.ix.1990, *Short 3818*		18
Corunna Hill South, S.A., 29.viii.1989, *Short 3715*	9II	
Mt Arapiles, Vict., 5.ix.1989, *Short 3776*	9II	
B. rara G.L. Davis		
Lake Apachirie, S.A., 18.v.1987, *Gillen & Reid 852*	6II	12

Species & locality	n	2n
B. readeri G.L. Davis		
Tallagiera Forest, Vict., 2.xi.1990, *Short 3917*		10
B. rigidula (DC.) G.L. Davis		
Quartz Ridge, Bogong National Park, Vict., 18.i.1988, *Short 3086*	9II	
B. riparia G.L. Davis		
Tulach Ard Gorge, Vict., 15.xi.1988, *Walsh 2409*	9II	
B. tetrapterocarpa G.L. Davis		
30 km E of Eromanga, Qld, 18.viii.1989, *Short 3609*	4II or 4II + 1B	8
30 km SW of Eromanga, Qld, 18.viii.1989, *Short 3611*	4II	8
B. whitei G.L. Davis		
41 km S of Charleville, Qld, 16.viii.1988, *Short 3159*	5II	10
27 km S of Cunnamulla, Qld, 16.viii.1989, *Short 3574*	5II	
1 km S of Wyandra, Qld, 16.viii.1989, *Short 3581*	5II	
6 km N of Charleville, Qld, 17.viii.1989, *Short 3594*	5II	
43 km N of Charleville, Qld, 17.viii.1989, *Short 3596*	5II	
13 km W of Charleville, Qld, 17.viii.1989, *Short 3598*	5II	
80 km SW of Charleville, Qld, 17.viii.1989, *Short 3601*	5II	
25 km W of Parroo River along Charleville to Quilpie road, Qld, 17.viii.1989, *Short 3602*	5II	
34 km S of Bourke, N.S.W., 17.viii.1988, *Short 3167*	5II	10
51 km S of Enngonia, N.S.W., 15.viii.1989, *Short 3561*	5II	

Chromosome number determinations from 145 populations attributed to 29 species or species complexes of *Brachyscome* are reported. First reports for *B. gracilis* (2n = 8), *B. muelleri* (n = 3, 2n = 6), *B. rara* (n = 6, 2n = 12), *B. readeri* (2n = 10), *B. riparia* (n = 9), and *B. tetrapterocarpa* (n = 4, 2n = 8), and new reports for the *B. diversifolia* (2n = 24) and *B. campylocarpa* complexes (n = 3, 2n = 6) are presented. The presence of B chromosomes are newly reported for members of the *B. dentata* complex, i.e. *B.* aff. *curvicarpa* (yellow ray florets) and *B. tetrapterocarpa*.

Data pertaining to pollen sterility are summarised in Table II.

DISCUSSION

The taxonomic revision of *Brachyscome* is in its infancy. It has not been possible as yet to view all type material or literature, and few species have been satisfactorily sorted. This work will not be completed for some years. Therefore, in this paper, reference to species and species complexes largely follows the concepts of Smith-White *et al.* (1970), their work in turn having been strongly based on that by Davis (1948). This is not an entirely desirable step to take, particularly in regard to the species complexes, where morphological and chromosomal evidence suggests that members of the ill-defined *B. campylocarpa*, *B. diversifolia* and *B. lineariloba* complexes are closely related. Nonetheless, this approach maintains continuity with past papers, and still provides a useful framework for discussion of the taxonomic problems encountered, probable new taxa, species relationships and cytogeography. However, we have refrained from referring to Davis's super-species, and also to the invalidly published subgeneric names (Davis 1948). All, or nearly all, such categories are likely to prove artificial.

Brachyscome campylocarpa Complex (including *B. eriogona*)

Smith-White *et al.* (1970) recognised three species within *B. campylocarpa* (sp. A, n = 4; sp. B, n = 5; sp. C, n = 6), which they noted, 'is morphologically rather

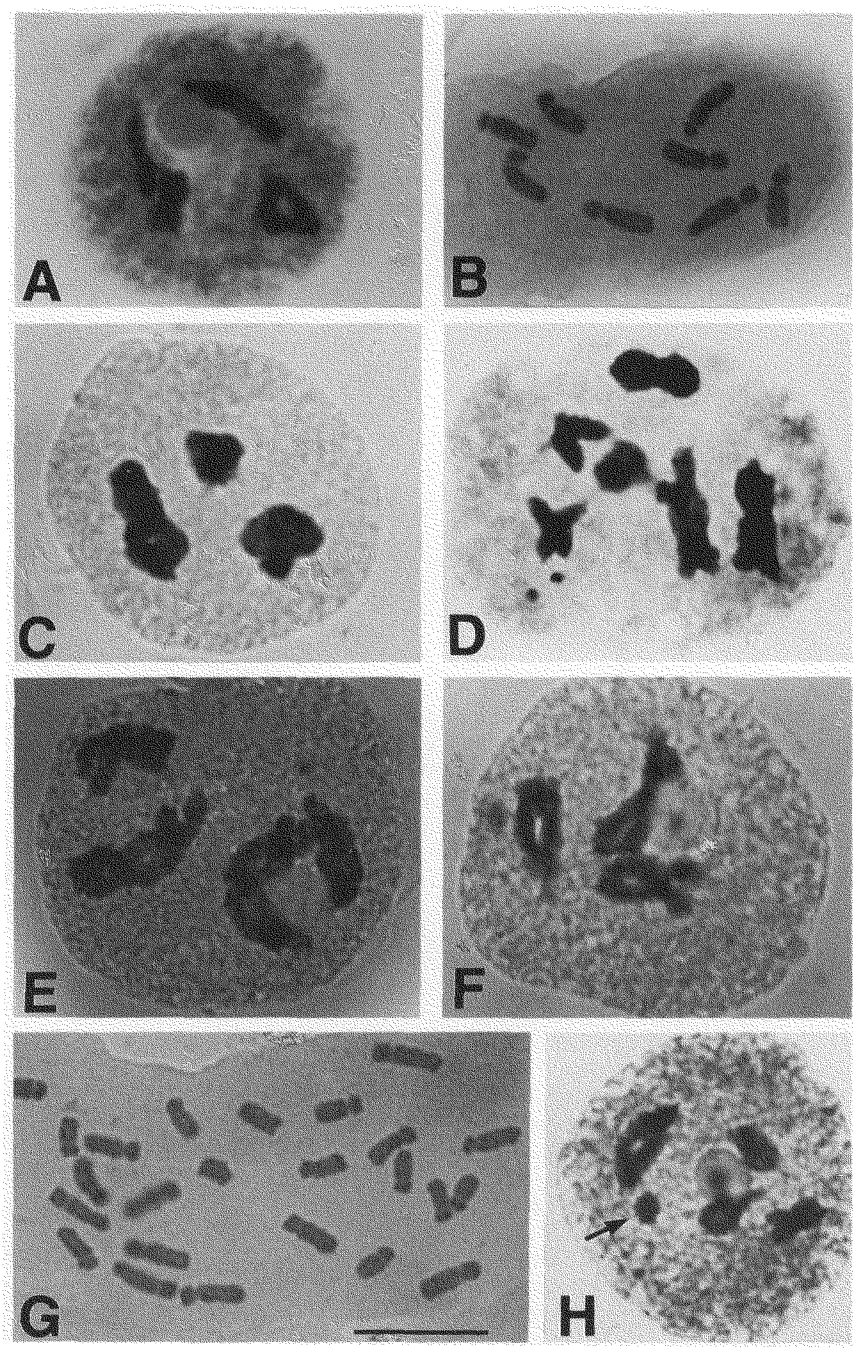

Fig. 1. Mitotic and meiotic chromosomes in *Brachyscome*. A — *B. goniocarpa* n = 4II (*Short 3743*). B — *B. gracilis* 2n = 8 (*Short 3361*). C — *B. muelleri* n = 3II (*Short 3713*). D — *B. rara* n = 6II (*Gillen & Reid 852*). E — *B. tetrapterocarpa* n = 4II (*Short 3611*). F — *B.* sp. aff. *campylocarpa* n = 3II (*Short 3566*). G — *B. diversifolia* 2n = 24 (*Short 3345*). H — *B.* aff. *curvicarpa* (yellow rays) n = 4II + 1B (*Short 3587*), arrow indicates B chromosome. Scale: 10 µm

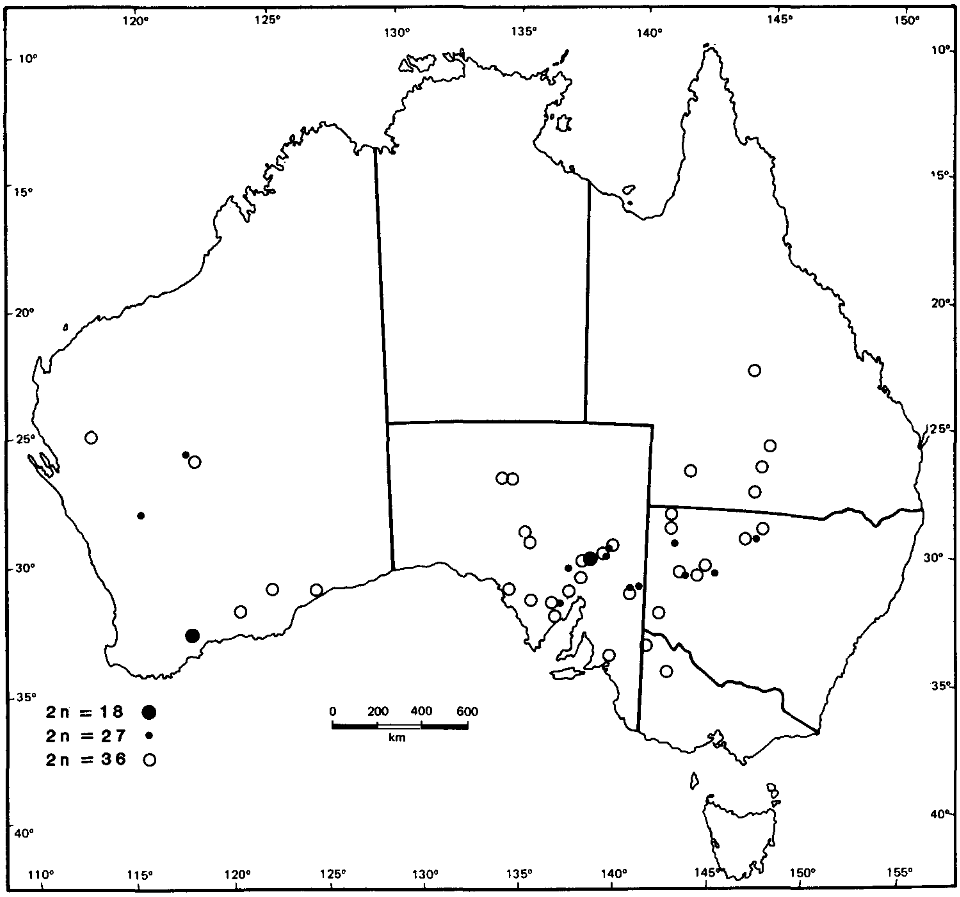

Fig. 2. Distribution of populations of *B. ciliaris* of known chromosome number.

similar to *B. leariloba* but is readily distinguishable from the latter on the bases of its pronounced stem development, its curved fruits, and its conical rather than hemispherical fruiting heads'. Subsequently Watanabe *et al.* (1976) recorded that hybridization was possible between '*B. campylocarpa* (n = 4)' and several members of the *B. leariloba* complex. Khyos *et al.* (1977) and Watanabe & Smith-White (1987) further discussed the affinities of the taxa in papers concerning relationships and phylogeny of the *B. leariloba* complex.

Herbarium studies of members of this complex are incomplete. However, some type specimens, and extant voucher specimens used by Smith-White *et al.* (1970) have been examined. There is no doubt that the taxon referred to as '*B. campylocarpa* (sp. A, n = 4)' is *B. eriogona*, a species widespread in northern South Australia. This species is characterised by strongly curved, brown fruit in which the margins of the more or less entire wings are ciliate throughout their length.

B. campylocarpa s. str. occurs in SW Queensland and NE South Australia, extending south to at least Maree and Mt Lyndhurst. The mature fruit of this species are curved, dark brown to black, and have prominently lobed wings, each lobe having a few long hairs. Their voucher specimens lack mature fruit, which are desirable for positive identification, but it appears that '*B. campylocarpa* (sp. B,

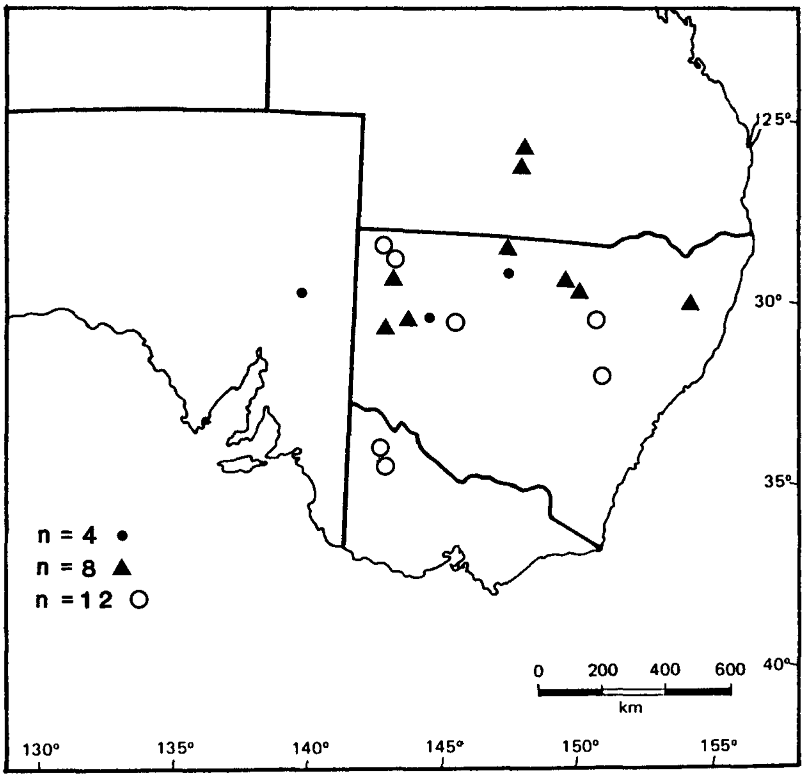

Fig. 3. Distribution of populations of *B. dentata* of known chromosome number.

Table II. Percentage pollen sterility in *Brachyscome*

B. ciliaris (Labill.) Less. complex
Short 3352, 3575, 3582, 3671, 3698 (all *c.* 100%)
Short 3556 (range 56–100%), *Short 3643* (75–100%)
B. curvicarpa
Short 3554 (0–9%, 11 of 15 plants showed no sterility)
**Short 3554* (0.9%), *Short 3549* (0.9%), *Short 3633* (9%)
B. aff. **curvicarpa** (yellow rays)
Short 3155 (20–41%), *Short 3587* (0–72%)
**Short 3587* (9.5%), *Short 3597* (12.6%)
B. dentata Gaudich.
Short 3755 (0–37%; n = 4), *Short 3650* (0–34%; n = 8) and *Short 3626* (0–77%; n = 12)
B. tetrapterocarpa
Short 3609 (0–49%), *Short 3611* (0–21%)
**Short 3609* (2.4%), *Short 3611* (0.9%)

* Pollen stained with aceto-carmine. (Other results are from phloxine/methyl green double stain.)

n = 5)', recorded by Smith-White *et al.* (1970) from William Creek, is *B. campylocarpa s. str.*

The further species recognised by Smith-White *et al.*, '*B. campylocarpa* (sp. C, n = 6)', has also been re-examined. Smith-White *et al.* recorded the frequent occurrence of rings or chains of four and suggested that the species may have a basic x = 3. This is the case. We have now recorded n = 3 (*Short 3566*), as well as n = 6 (*Salkin s.n.*, *Short 3557*), and the respective voucher specimens are morphologically indistinguishable. This common species, referred to in Table I as *B.* sp. aff. *campylocarpa*, is found in arid areas of southern Queensland and New South Wales. The limited data suggest that diploids are found in the north of the range, our report being for specimens gathered near Barringun in Queensland. All tetraploids have been reported from New South Wales, collections having come from the vicinity of Booligal, Bourke, Brewarrina, and Menindee (Smith-White *et al.*). The species has curved, brown to almost black mature fruit. A prominent, ciliate wing is developed in the upper, curved portion of the fruit and there are two prominent tufts of hair at the base of the fruit.

BRACHYSCOME CILIARIS COMPLEX

Brachyscome ciliaris is usually readily distinguished from all other brachyscomes as it is the only one which has heteromorphic fruit, cypselas of the ray florets being non-winged, those of the disc florets having a prominent wing. Within the species Davis (1948) recognised four varieties, i.e. var. *ciliaris*, var. *lanuginosa* (Steetz) Benth., var. *lyrifolia* and var. *subintegrifolia* G. L. Davis. Subsequently Davis (1964) reported that both var. *ciliaris* and var. *lanuginosa* were agamospermous and displayed the *Antennaria*-type of diplospory. De Jong (1963) reported var. *ciliaris* to be diploid with n = 9. Turner (1970) recorded both var. *ciliaris* and var. *lanuginosa* to be tetraploid and presumably apomictic. Smith-White *et al.* (1970) and Carter (1978a) reported 2x, 3x, 4x, 6x and 9x for *B. ciliaris*. Except for var. *lyrifolia* Carter refrained from applying any of the varietal names available. He also recorded that diplospory was supported by the cytological observations, i.e. the failure of some plants to enter meiosis at all, with disintegration of the pollen mother cells, or virtually complete asynapsis and a failure to finish meiotic division. All polyploids examined by Carter were pollen sterile. Only diploid var. *lyrifolia* from the Flinders Ranges, South Australia and a different diploid entity from the Ongerup region in Western Australia were found to exhibit regular pollen formation. Carter further noted that ploidy levels do not necessarily correspond to the morphological varieties formally recognised by Davis.

We also observed severe male meiotic irregularities in most members of this complex. Their apomictic nature is also reflected in the estimates of percentage pollen sterility for various populations (Table II).

Our observations on the morphological variation exhibited within *B. ciliaris* are in agreement with Carter's observations. In eastern Australia it is not uncommom to find two very different forms growing together. Comparatively more robust, clearly perennial plants with wholly or partly white, cottony stems are frequently found growing with less robust, probably annual plants which have reddish-brown, often glandular pubescent stems. Following Davis, members of the former group are referrable to var. *lanuginosa*, the latter to var. *ciliaris*. However, closer examination reveals that specimens referrable to both var. *lanuginosa* and var. *ciliaris* may exhibit considerable variation in features such as leaf shape, the type and extent of the indumentum on the stem, leaves and bracts, and in fruit morphology. The same is true for Western Australia, where the morphological variation seems more complex than in the east. Clearly, the recognition of the aforementioned varieties is artificial, their circumscription being based on features which are readily apparent, but not consistent, for circumscribing taxa.

We have also found that morphologically identical populations may exhibit different ploidy levels, e.g. *Short 3630 & 3645* (n = 27I or 2n = 27) and *Short 3556 & 3643* (n = 36I or 2n = 36).

Within the *B. ciliaris* complex variation is such that attempts at delimitation may prove to be an impracticable exercise and, as discussed by authors such as Löve (1960) and Stebbins (1971), for an apomictic, polyploid group it may not be necessarily desirable to formally describe and name taxa. *Brachyscome ciliaris* var. *brachyglossa* Gauba (Gauba 1948), published soon after the revision by Davis (1948) is an example where the formal naming of an entity is not justifiable. The key attribute of this variety is the possession of reduced ray florets. However, specimens with reduced rays have a sporadic occurrence in populations which are otherwise morphologically distinct from one another. For example, *Short 3758* is vegetatively distinct from the type specimen of var. *brachyglossa* but has reduced ray florets. There can be no doubt that specimens with reduced ray florets are mutant forms undeserving of formal recognition.

With the exception of var. *lyrifolia*, no attempt has been made in Table I or Fig. 2 to assign collections to the varieties recognised by Davis.

The distribution of diploid and higher ploid entities of *B. ciliaris* illustrated in Fig. 2 incorporates our data plus that provided by Turner (1970), Smith-White *et al.* (1970) and Carter (1978a). Turner's unnamed collection, *Turner 5266*, belongs to this complex. Although vouchers pertaining to Carter's paper seem to be no longer extant it is unlikely that his chromosome determinations would pertain to any other species. However, we have excluded the determinations of 6x and 9x recorded by him. We found no evidence of such numbers and Carter has since indicated that they are likely to be erroneous (Dr Carolyn Leach, pers. comm. 1991). The distribution pattern is similar to that often found in apomictic, polyploid complexes, i.e. the sexual diploids have restricted distributions, the apomictic higher ploids, in this case 3x and 4x, are widely distributed and frequently occur in disturbed habitats such as roadsides (e.g. Stebbins 1971, Watanabe 1986).

BRACHYSCOME DEBILIS

Smith-White *et al.* (1970) noted that the karyotype of *B. debilis* and *B. leptocarpa* F. Muell. were similar and further suggested that the presence or absence of a wing on the mature fruit, the only means of distinction, may have a simple genetic determination. This has not been experimentally tested but both entities are frequently found growing together. If they prove to be conspecific then *B. debilis*, the earlier name (and with unwinged fruit), has priority.

It was not possible to decide from the bud material of *Short 3916* whether the chromosome number determination was referable to *B. debilis* or *B. leptocarpa* and mature plants from the same population gathered in November 1990 revealed that both entities were present. Unfortunately it was not noted whether subsequent determinations of 2n = 6 were from root tips emergent from winged, or unwinged, fruit.

BRACHYSCOME DENTATA COMPLEX (including *B. chrysoglossa*, *B. curvicarpa*, *B.* aff. *curvicarpa*, *B. papillosa* & *B. tetrapterocarpa*)

Davis (1948) adopted the name *B. marginata* Benth. for a species which is 'very variable in vegetative characters' but with fruit 'relatively constant in character' (Davis *l.c.*, pp. 189, 190). Within the species she recognised two varieties, var. *marginata* and var. *chrysoglossa* (F. Muell.) Davis, the latter having 'orange-yellow' ray florets but otherwise said to be identical to the white-rayed var. *marginata*. The name *B. marginata* was also used by Smith-White *et al.* (1970) whereas others (e.g. Eichler 1965; Cooke 1986) adopted the name *B. heterodonta* DC., a name previously, and incorrectly, cited by Davis as a synonym of *B. marginata*. However, Burbidge (1982) found *B. dentata* Gaudich. to be the earliest legitimate name available for members of this complex and it is adopted here.

In the key to species, which is based on differences in fruit morphology, the winged fruit of this taxon were described by Davis as having a body with short glandular hairs or finger-like, cylindrical tubercles. The fruit wing was found to be completely and irregularly dissected. We, and presumably Smith-White *et al.*, used these features to determine a name for the voucher collections, all of which have white ray florets, and therefore fit Davis's concept of '*B. marginata* var. *marginata*'. However, as with Davis, we note that specimens may be vegetatively quite variable. It should also be noted that the hairs on the body of the fruit are apparently eglandular, not glandular as indicated by Davis.

In their paper Smith-White *et al.* (1970) reported chromosome number determinations of n = 4, 8, 9 and 12 for this species. In view of a supposed close affinity of *B. dentata* and the *B. aculeata* (Labill.) Less. group, the latter with x = 9, they were not convinced that the higher numbers were polyploid derivatives. However, determinations of n = 9 for several collections are likely to have been due to the presence of B chromosomes, of which one or more are frequently found in this species. They are large (the largest so far detected in any species of *Brachyscome*), being nearly the same size of autosomes, and metacentric. There is no evidence of pairing affinity with chromosomes of the normal complement although two B chromosmes can pair with each other at diakinensis and metaphase I. Stace (1981) has also noted that the Carlton Bay (Tasmania) collection with n = 9 that was attributed to *B. dentata* by Smith-White *et al.* is in fact *B. sieberi* DC. var. *gunnii* DC., a member of the *B. aculeata* group. Thus, there can be no doubt that this is a polyploid sequence based on x = 4.

According to Davis (cited in Smith-White *et al.* 1970), in the Armidale district of New South Wales, *B. dentata* is, or may be, a facultative apomict. No evidence was presented to support this statement. Although it may be correct it is generally at variance with our findings. In this study all of the plants examined, including tetraploids and hexaploids which frequently formed a single quadrivalent, displayed reasonably regular male meiosis. The formation of seemingly good pollen was observed. Estimates of pollen sterility obtained (Table II) suggest that this is not always the case but florets displaying no pollen sterility were found in each population and high estimates of percentage pollen sterility were rare: 18 of the 45 individual florets examined for this species displayed no pollen sterility, and a further 9 exhibited less than 5% sterility. It was also found that isolated, tetraploid plants grown in the greenhouse did not set seed. These observations suggest that, at least for most of its range, *B. dentata* is a sexual outbreeder.

It is evident from herbarium specimens that there are not only problems with the circumscription of *B. dentata* but also with *B. curvicarpa*, *B. papillosa* and *B. tetrapterocarpa*, all taxa with x = 4. For example, *Corrick 7332* displays fruit similar to that usually attributable to typical *B. dentata* but has a leaf morphology resembling the more typical form of *B. papillosa*. Furthermore, *B. curvicarpa*, as circumscribed by Davis (1948), is an exceedingly variable taxon in relation to fruit colour and morphology, leaf morphology, and the colour of the ray florets (white or yellow). Vegetatively, many collections with the typical fruit of *B. curvicarpa* are not dissimilar to *B. dentata*. It has also been noted that, were it not for the four-winged fruit, *B. tetrapterocarpa* would probably be indistinguishable from typical *B. curvicarpa*.

Cytological observations in *B. curvicarpa*, *B.* aff. *curvicarpa* and *B. tetrapterocarpa* were mainly made at diakinensis or metaphase I. The chromosomes displayed regular pairing but univalent B chromosomes were often found in *B.* aff. *curvicarpa* (yellow rays) and *B. tetrapterocarpa*. Smith-White *et al.* (1970, fig. 53, voucher not seen) have also recorded B chromosomes for *B. curvicarpa s. str.* although they were not observed by us, which may reflect the small sample of pollen mother cells examined. In contrast to *B. dentata*, the B chromosomes found in all three of the aforementioned taxa are minute and distinct from the chromosomes of the normal complement.

Populations of the aforementioned taxa were tested for pollen sterility (Table II) using both double stain and aceto-carmine. All such staining methods are only an estimate of sterility and adverse environmental conditions can affect pollen development. This may explain why, with the double stain method, marked variation in percentage pollen sterility was sometimes found between individuals of the one population, e.g. in *Short 3554* eleven of the 15 individuals displayed no sterility but in one floret a value of 9% sterility was obtained. It is also noticeable that results from staining with aceto-carmine suggest lower levels of sterility although this may reflect the smaller sample and different method of sampling. Despite these problems with the interpretation of data the observations suggest that pollen sterility may be associated with the presence of B chromosomes. With the exception of *Short 3633* (*B. curvicarpa*), an increase in the percentage of sterile pollen grains tended to correlate with an increase in the number of pollen mother cells observed to have B chromosomes.

The specimens referred to above as *B.* aff. *curvicarpa* (yellow rays) are not the same as *B. marginata* var. *chrysoglossa*. Specimens referred to the former taxon have fruit resembling those of typical *B. curvicarpa*. The combination to accomodate var. *chrysoglossa* under *B. dentata* is also wanting. Because of the problems in circumscribing taxa the combination is not made here. At least for the time being we suggest that the name *B. chrysoglossa* F. Muell. be adopted, as in Ross (1990), for this taxon.

Figure 3 displays the distribution of populations of *B. dentata* (*sensu B. marginata* var. *marginata* of Davis) of known chromosome number, incorporating our data and that of Smith-White *et al.* (1970). It shows that the tetraploids and hexaploids are more widely distributed than the diploids which are only known from a few isolated localities. Again, this is consistent with the distribution pattern that is frequently observed in polyploid taxa. However, the poor delimitation of this taxon and its obvious close affinities with the aforementioned group of species should not be forgotten. If chromosome data for the entire *B. dentata* complex were incorporated in the figure then diploids would be found to be the most widespread.

BRACHYSCOME DIVERSIFOLIA COMPLEX (including *B. goniocarpa*, *B. gracilis* & *B. readeri*)

The collection *Short 3345*, here tentatively attributed to *B. diversifolia* var. *diversifolia*, 2n = 24 would appear to be a hexaploid with a base of x = 4. Three other levels, 2x, 8x and 10x have been reported for this variable species (Smith-White *et al.* 1970).

Smith-White *et al.* (1970) reported n = 3 for *B. goniocarpa*. However, more recent work has revealed that *B. goniocarpa s. str.*, a species with inconspicuous ray florets, and restricted to Western Australia, South Australia and western Victoria, has n = 4.

The name *B. goniocarpa* has been misapplied in Queensland and New South Wales to at least two distinct entities. Much of the material from southern New South Wales is apparently of another closely related species, *B. gracilis*, whereas the records of n = 3 by Smith-White *et al.* seemingly apply to an undescribed taxon referred to herein as *B.* sp. aff. *goniocarpa*. In the latter taxon at least the outer fruit in each capitulum are characterised by having a prominent knob-like projection at the apex.

Herbarium specimens suggests that, as defined by Davis, *B. readeri* may prove to constitute two taxa which have similar fruit but differ vegetatively. One of these, i.e. *B. readeri s. str.*, is confined to south-west Victoria and south-east South Australia, the other is confined to north-west Victoria and adjoining areas in New South Wales. Further work is required to substantiate this view and *Short 3917* is here referred to *B. readeri*.

There can be little doubt that taxa referred to this complex, i.e. *B. diversifolia* (x = 4), *B. goniocarpa* (n = 4, 2n = 8), *B.* sp. aff. *goniocarpa* (2n = 6), *B. gracilis* (2n = 8), *B.* aff. *gracilis* (2n = 24), and *B. readeri* (2n = 10) are closely related to each other. However, the complex is not readily delimited from some other species groups. Experimental hybridization work (Watanabe *et al.* 1992) suggests a close relationship of *B. goniocarpa* and *B. dichromosomatica* (a member of the *B. lineariloba* complex) and, as noted by Davis (1955), the fruit morphology of *B. gracilis* suggests a strong affinity with *B. campylocarpa s. str.*

BRACHYSCOME IBERIDIFOLIA COMPLEX

Herbarium material referred to by various botanists as *B. iberidifolia* exhibits considerable vegetative and floral diversity but is as yet unsorted. Sharma & Murty (1977) have previously noted that the species is a casual apomict and this may partly explain the observed variation. *B. bellidioides* Steetz, *B. exilis*, *B. eyrensis* G.L. Davis and *B. pusilla* Steetz are all closely related and the circumscription of each of these species is also problematic. In this paper, of the aforementioned species, only *B. exilis* is recognised as a distinct entity, all other collections being referred to *B. iberidifolia s. lat.*

All members of this group so far examined exhibit a haploid number of n = 9 (De Jong 1963, Carter 1978a).

BRACHYSCOME LINEARILOBA COMPLEX (including *B. breviscapis* & *B. dichromosomatica*)

Smith-White *et al.* (1970) recognised five unnamed species within *B. lineariloba* (sp. A, n = 2; sp. B, n = 6; sp. C, n = 8; sp. D, n = 4; sp. E, 2n = 10). Further work, pertaining to such features as the frequency of B chromosomes, race relationships and meiosis in natural hybrids, was carried out (e.g. Watanabe *et al.* 1975, Khyos *et al.* 1977) and subsequently Carter (1978b) formally recognised 'sp. A' as *B. dichromosomatica* and 'sp. D' as *B. breviscapis*. The remaining three 'species' proved to be morphologically indistinguishable and were treated as cytodemes B, C and E within *B. lineariloba*. The distribution of the various cytodemes, as presented by Kyhos *et al.* (1977) and Carter (1978b), are confirmed by the data presented in Table I.

Surprisingly the karyotype obtained for the Western Australian collection, *Short 3819*, of cytodeme C (2n = 16) is identical with that of Variant V_{17} (C_1) which until now has only been found in New South Wales (east of the Darling River localities 1, 2 & 3; see Watanabe *et al.* 1985). It differs from the standard C_1 in having a longer short arm of the satellited 3 and 4 chromosomes. In Watanabe *et al.* (1985) plants with this karyotype were in the minority and this variant (V_{17}) was regarded as being derived from the majority 'standard' karyotype.

BRACHYSCOME ONCOCARPA COMPLEX (including *B. cheilocarpa*, *B. ciliocarpa* & *B. halophila*)

Currently four species are generally recognised within the complex, i.e. *B. cheilocarpa* F. Muell, *B. ciliocarpa*, *B. halophila* and *B. oncocarpa*. This complex is most distinct, each constituent taxon so far examined having fruit with two large secretory canals in the pericarp, a feature which, at least in combination with the lack of terminal anther appendages, is unique to this group. However, the component taxa, named and unnamed, are not always so clearly delimited. Preliminary sorting of herbarium specimens has revealed the existence of several distinctive, unnamed taxa of uncertain rank. Each of these tends to have a limited geographical range and they differ from each other in fruit morphology and/or the vestiture of the leaves, scapes and bracts. The true application of the names *B. ciliocarpa* and *B. clementii* Domin are also yet to be ascertained. In keeping with current usage, in this paper the name *B. ciliocarpa* is used for the eastern Australian collection, *Short 3607*. The name is, however, likely to be either reduced to synonymy under *B. oncocarpa* or, if retained, apply to a western taxon.

BRACHYSCOME RARA

Until recently this species was only known by the type collection from southwest Queensland. It has since been established that the name *B. coongiensis* Munir is synonymous and that *B. rara* is probably restricted to the Cooper River drainage basin (Short 1990). Its affinities are seemingly with *B. basaltica* F. Muell. var. *gracilis* Benth., also n = 6.

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