

## Insect Communities on *Berkheya* Flower Heads: A Southern Hemisphere Analogue for Cardueae (Asteraceae)

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Insect herbivore communities in the flower heads of 26 species of the South African asteraceous genus *Berkheya* are compared with those from the European Cardueae, the flower heads of which are very similar in structure. The patterns of species packing are similar in the 2 communities: flower head size and other aspects of plant morphology have no effect, nor does extent of geographical range. On the other hand, both show some associations between species packing and resource utilization, and they share genera and families of specialist feeders. In *Berkheya* there is evidence for a double radiation within the genus and this appears to have parallels in the associated fauna. Overall, similarities between the 2 insect/plant associations are great, and this suggests shaping by similar evolutionary pressures.

### Introduction

The genus *Berkheya* (Asteraceae: Arctoteae) has a predominantly South African distribution. It consists of medium-sized herbaceous plants whose morphologies, particularly their flower head structures, are very similar to European thistles and knapweeds (Asteraceae: Cardueae), amongst which are numerous agricultural weeds.

Zwölfer (1985, 1987, 1988) has drawn attention to a number of particular features characterizing the evolutionary and ecological dynamics of the herbivorous insects feeding on Cardueae. Clark (1988, 1990) set out to determine the extent to which similar patterns could be found in herbivore relationships on *Berkheya*, which has radiated independently of the Cardueae.

Clark's studies involved intensive sampling of a small number of *Berkheya* species in limited areas. We report here on a survey designed to supplement Clark's work by an extensive survey, involving a much larger part of the geographical area occupied by *Berkheya*, and greatly increasing the number of species involved. The number of samples per species,

however, is low, and we regard our conclusions mainly as pointers to useful areas for further study.

### The Host Plants

Roessler (1959) reviews the genus *Berkheya*, which contains over 70 species, most of which occur in southern Africa. Roessler divides the genus into 8 species groups, and gives details of their distribution. Table 1 shows the patterns of distribution by species group, using 5 arbitrary regions delimited in Fig. 1. Table 1 also shows the levels of affinity between the *Berkheya* floras of each region, using the Jaccard Index (Southwood 1966).

The south-east region (3) is the centre of diversity for *Berkheya*, but there is clear evidence for a secondary centre of radiation in the mountains of the western Cape (1); this region has many endemics and low affinities with other regions. The central southern coast is depauperate, and contains species with centres of distribution to both east and west, while, except for some restricted endemics in the Drakensberg, the floras of the northeast (4-5) are impoverished versions of those in 3,

declining northwards. These patterns are clearly reflected in the distribution of species groups.

One species found and sampled in the study is as yet undescribed, *Berkheya* sp. (Clark 1988); it is a restricted western Cape species.

For the species recorded in the study, the following features were noted:

1. Region (as defined above) in which the sample was made. No samples were made in region 2, and those of 4 and 5 have been combined, as many were close to the arbitrary border, and were not numerous.
2. Geographical extent, the size of area over which the species could be found. This has been expressed as ranks (1 small–4 large) obtained from average rankings of

maximum distance between known occurrences, number of 1° squares in which known and total number of localities recorded by Roessler (1959). All 3 estimates were highly intercorrelated.

3. Head size, ranked (1 low–5 high) on mean area of head *within* the bracts, using measurements made on our own samples.

Maximum height of plant, median achene size and whether heads are single or in inflorescences, data obtained from Roessler (1959), and modified where necessary on the basis of field experience. All are highly variable characteristics. Roessler describes nearly all *Berkheya* as short-lived perennials; some may be biennial, but there are no data to support categorisation.

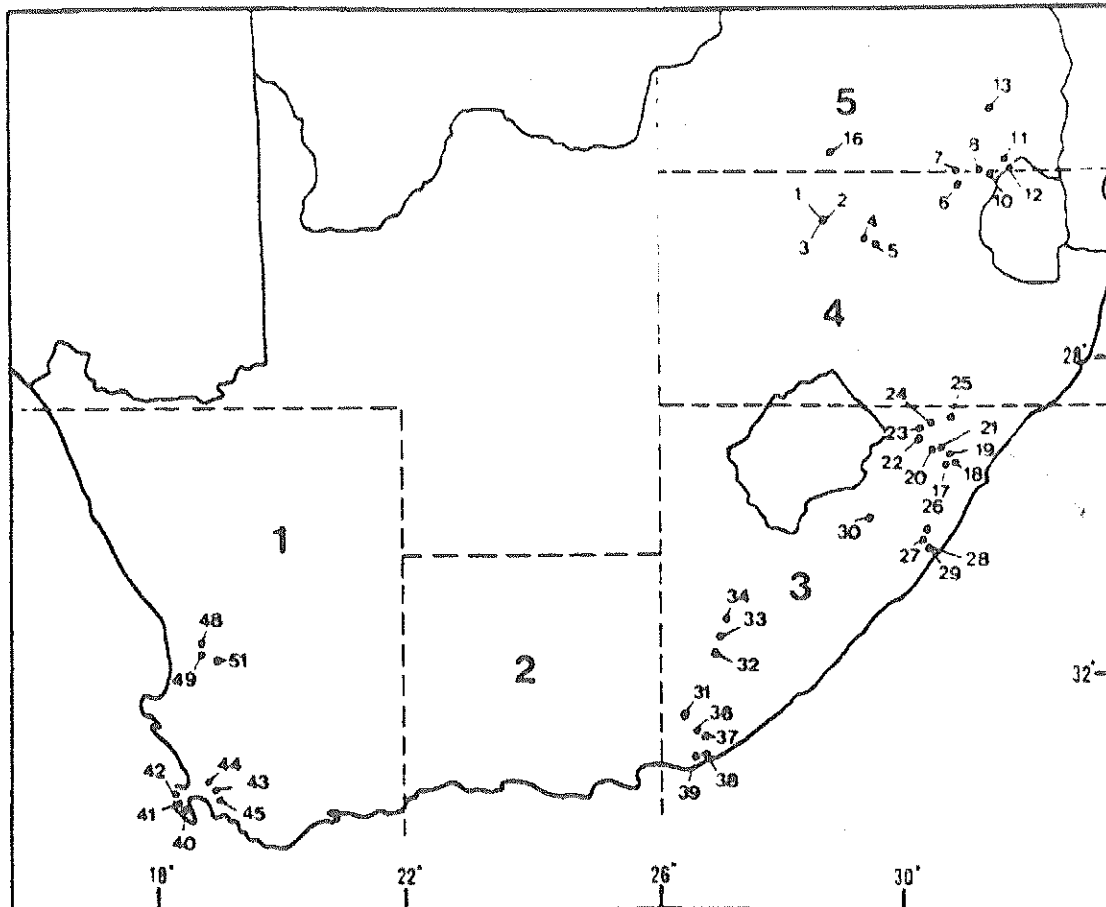


Figure 1. A map of southern Africa, showing approximate positions of sample sites (small numbers) and regions (large numbers) referred to in the text. National boundaries shown as thin continuous lines.

**Methods**

At each site, samples of at least 100 flower heads were collected, except where only a few individual plants were available. In most heads, the florets were dead and achenes well developed. Heads were kept in muslin bags and transported to England where they were dissected, receptacle width inside the bracts measured and insect inhabitants counted.

**Results**

Fifty-one samples were made in January and February 1991, examining about 9,800 heads in 26 species of *Berkheya* (Table 2). One-hundred-ten mutually exclusive taxa were recognised in the herbivorous insects found, about half of them identified to species level. The range of taxa found in individual samples was 3-23.

*Species Packing*

Samples varied in numbers of heads examined and the size of flower head varied in each species. Additional variation in *S* (number of taxa) and *n* (number of individuals) will be caused by the particular circumstances of individual sites. Zwölfer (1987) was able to compensate for these variables in his much larger study of *Cardueae* by using only species for which at least 10 samples were available.

We have attempted to remove as much of these errors as possible by scaling. There is a significant regression of *S* on  $\log n$  ( $r=0.645$ ,  $p<0.001$ ) which accounts for 42% of the variation in *S*. Numbers, however, are a function of sample size (area of plant tissue searched, estimated as mean basal area/head x number of heads) and of density (numbers/unit area of plant tissue).

*S* is highly correlated with area sampled (Fig. 2), but just fails to achieve significance on density ( $r=0.274$ ,  $p>0.05$ ). Since area sampled has no biological meaning, we have used the regression to scale *S*, using the residuals as indicators of the values of *S* had sample sizes been constant throughout.

While the range of these residuals is considerable (-5.8 to +8.1 species) relative to the mean, their significance might be doubted given that most plant species are represented by single samples. Two pieces of evidence suggest that they are meaningful:

1. In 8 of 9 possible comparisons of species sampled at the same site, most of which were also sampled elsewhere, the values of *S* corrected for sample size are in the direction predicted ( $p<0.05$ , exact test).

2. Five species sampled were also sampled by Clark (1988), who provides estimates of *S* for each based on 11-16 samples/species. There is a high correlation between values of *S* in each study ( $r=0.94$ ,  $p<0.02$ , using residuals for this study).

**Table 1. (a) Distribution of South African species of *Berkheya* by region (see text) and species group (Roessler 1959). Restricted= confined to 1 area; \*= includes 1 undescribed *Berkheya* of unknown affinity (Clark 1988). (b) Jaccard Indices of Similarity between the *Berkheya* floras of each region.**

Species Groups	(a) Regions				
	1	2	3	4	5
Fruticosae	6	5	1	0	0
Angustae	1	0	0	0	0
Cruciatae	0	1	0	0	0
Armatae	3	0	2	1	0
Speciosae	0	1	8	6	5
Rigidae	8	6	7	3	2
Subulatae	0	0	2	5	5
Decurrentes	0	4	14	10	5
Total	19*	17	34	25	17
Total restricted	12*	2	9	3	2

	(b) Regions			
	2	3	4	5
1	0.39	0.11	0.09	0.06
2		0.39	0.19	0.18
3			0.54	0.43
4				0.71

Despite this evidence that variation in *S* is meaningful, there are no significant associations

with plant characteristics, nor with features of geographical range. In particular, there is no sign of any trend related to head size.

Three non-significant trends may merit further investigation: 4 of 5 *Berkheya* species with solitary flower heads have below-average  $S$ ; all 6 *Berkheya* species with very restricted geographical ranges have below average  $S$ , and samples from the extreme east of Cape Province have the highest mean  $S$ .

Against this notable lack of association, corrected  $S$  does correlate significantly with density ( $r=0.410$ ,  $p<0.01$ ). We cannot estimate resource utilization by percentage of heads infested (Zwölfer 1985) but density seems an adequate alternative. High values for species packing are associated with high resource utilization.

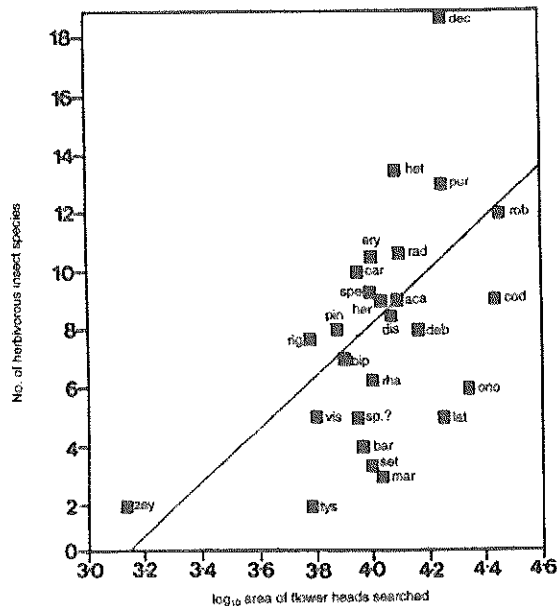


Figure 2. Scatter of mean  $S$  (herbivore species/sample) on mean  $\log_{10}$  area of plant sampled for each species of *Berkheya* (Table 2). Species are indicated by the first 3 letters of their names, and the regression line based on all samples shown ( $r=0.512$ ,  $S=9.04 \log_{10}$  area [ $\text{mm}^2$ ]-27.83).

#### Faunal Associations

Of the 110 insect taxa recorded, 55 were each found only once, and are excluded from further analysis. Seventeen of the remaining 55 have so far been recognised only to family. All 17

were found in samples from the central area of Natal and the eastern Cape; samples from the Transvaal (12 taxa) and western Cape (9) are poorer. Many are probably casual visitors.

Thirty-eight taxa are believed to represent species, although not all have been determined. Table 3 shows their distribution between regions, and the Jaccard *Indices of Similarity* (Southwood 1966) between regions, expressed as a proportion of the maximum similarity possible given the number of species found in each. In each case, figures are given separately for the whole array, for the endophagous tephritids (Diptera: Tephritidae), *Larinus* weevils (Coleoptera: Curculionidae) and lepidopteran larvae, and for the mainly externally feeding remainder.

The fauna of the central Natal/eastern Cape region is the richest and shows strong overall similarity with those of both other regions, which differ rather more between themselves. It is apparent, however, that there are differing patterns of distribution between the endophagous (and potentially specialist) species and the rest. All species recorded uniquely in the western Cape belong to the endophagous group, and this group differentiates the region from its central neighbor, which the others do not.

Full lists of species as identified are available from the authors.

#### Guild Structure

Although no receptacle galls were found, 2 tephritids and 3 *Larinus* spp. were sometimes recorded at  $>10$  individuals in a single head. These would appear to occupy the "early aggregated attack" niche defined by Zwölfer (1986). One other tephritid, "*Urophora*" *agromyzella* (Freidberg, in preparation; *Urophora* from southern Africa is not congeneric with European *Urophora*), develops inside individual achenes and was occasionally recorded in large numbers. Other *Larinus* and tephritids occurred singly or in small multiples only.

Many heads were badly damaged and full of frass, probably originating from chrysomelid beetles as well as from the lepidopteran larvae.

**Table 2. Species of *Berkheya*, location, flower head number and widths, number of herbivore species (*S*) and individuals (*n*) found in the survey. Undescribed species after (Clark 1988). Nomenclature after Roessler (1959).**

<i>Berkheya</i> Species	Site	Mean Head Width (mm)	No. of Heads	<i>S</i>	<i>n</i>
<i>acanthopoda</i> (DC.) Roessler	21	10.1	153	9	49
<i> barbata</i> (L.F.) Hutch.	41	13.5	110	6	110
	45	9.8	41	2	14
<i>bipinnatifida</i> (Harv.) Roessler	21	5.1	582	12	115
	28	5.1	345	5	41
	36	4.0	391	4	5
<i>carduoides</i> (Less.) Hutch.	31	7.7	167	9	47
	32	8.6	173	11	38
<i>coddii</i> Roessler	10	14.2	174	9	130
<i>debilis</i> MacOwan	26	8.7	244	8	69
<i>decurrens</i> (Thunb.) Willd.	31	14.5	113	19	234
	36	16.0	107	23	161
	38	16.5	63	14	339
<i>discolor</i> (DC.) O. Hoffm. & Muschler	30	12.5	147	9	26
	33	12.2	42	8	21
<i>erysithales</i> (DC.) Roessler	19	9.6	186	11	138
	29	8.8	152	10	110
<i>herbacea</i> (L.F.) Druce	41	13.9	122	11	141
	43	10.4	73	4	30
	45	9.5	101	12	87
<i>heterophylla</i> (Thunb.) O. Hoffm.	37	7.4	200	12	136
	39	7.9	322	15	109
<i>latifolia</i> Wood & Evans	12	12.7	127	5	9
<i>maritima</i> Wood & Evans	22	10.0	137	3	17
<i>onopordifolia</i> (DC.) O. Hoffm. ex Burt Davy	24	14.0	143	6	224
<i>pinnatifida</i> (Thunb.) Thell.	4	7.4	178	8	19
<i>purpurea</i> (DC.) Masters	34	12.7	136	13	351
<i>radula</i> (Harv.) De Wild.	2	15.4	43	10	24
	4	16.4	109	13	183
	16	12.8	151	9	150
<i>rhapontica</i> (DC.) Hutch. & Burt Davy	8	8.0	201	5	14
	17	5.8	448	11	98
	20	6.5	414	6	18
	25	7.2	138	3	3
<i>rigida</i> (Thunb.) Bolus & Wolley Dod ex Adams. & Salt.	40	5.4	298	8	56
	42	5.3	365	4	268

Table 2. Continued.

<i>Berkheya</i> Species	Site	Mean Head Width (mm)	No. of Heads	S	n
<i>robusta</i> Bohner ex Roessler	44	4.5	231	11	180
	5	22.2	77	12	43
<i>setifera</i> DC.	1	10.4	115	3	5
	3	10.7	150	2	3
	17	9.0	155	2	4
	18	7.9	103	4	8
	23	12.2	97	6	21
<i>speciosa</i> (DC.) O. Hoffm.	6	9.3	115	10	102
	7	12.9	128	9	91
	17	10.8	85	7	16
	27	11.3	79	11	84
<i>tysonii</i> Hutch.	51	9.2	94	2	165
<i>viscosa</i> (DC.) Hutch.	49	5.7	247	5	38
<i>zeyheri</i> (Sond. & Harv.) Oliv. & Hiern	11	13.6	9	2	4
<i>Berkheya</i> sp.?	48	6.5	269	5	116

Table 3. (a) Distribution of insect species level taxa by region, and separately for endophagous species and others. Restricted= confined to 1 area; (b) Jaccard Indices as a proportion of maximum between regions, separated as in (a).

	(a) Regions			(b) Jaccard Indices		
	1	3	4+5	3	4+5	
All species						
Total	22	30	18	1	0.76	0.44
Restricted	5	6	3	3		0.83
Endophagous						
Total	10	10	6	1	0.50	0.33
Restricted	5	2	1	3		0.83
Others						
Total	12	20	12	1	1.00	0.50
Restricted	0	4	2	3		0.83

### Comparison with Cardueae

In this small, exploratory survey, we cannot address questions of overall species richness, but as Zwölfer (1985, 1987, 1988) demonstrates, this variable may be of much less significance than species packing. Comparisons between genera and higher categories are likewise impossible.

Despite these limitations, the survey demonstrates that there are close resemblances between the herbivore communities of *Berkheya*

and of the Cardueae of Europe, a conclusion supported by Clark's (1988, 1990) more intensive study of a smaller number of species. In particular, species packing is not influenced by flower head size, nor, simply, by the extent of a species' geographical range. Other aspects of plant structure are similarly irrelevant. There is slight evidence that species packing is highest at the centre of *Berkheya* distribution and that resource utilization and species packing are correlated, a phenomenon applying to some but not all Cardueae (Zwölfer 1986).

Guild structure also appears similar, both in the taxa of endophagous feeders (tephritids, *Larinus* weevils, lepidopteran larvae) and in that some tephritids and *Larinus* appear to fill the "early aggregated attack" niche (Zwölfer 1985, 1988), though none form receptacle galls. We do, however, confirm frequent occurrence of Hemiptera, also noted by Clark (1988), which are not of importance in Cardueae.

There are some differences too. As with Clark (1990), we find levels of species packing on *Berkheya* to be higher than in Cardueae, but this is entirely due to large numbers of casual or infrequent generalists. It is doubtful, too, whether all workers are consistent in the inclusion of generalist taxa in the estimates. It appears that the fauna of oligophagous and closely associated insects is poorer in *Berkheya* than in Cardueae; this is expected, given the much greater number of species (ca. 2,000) in the latter than in the Arctoteae (ca. 194 species) to which *Berkheya* belongs (Nordlindh 1977, Clark 1990).

It does not appear that we have in *Berkheya* any case where 1 herbivore dominates resource utilization. This does happen in some Cardueae (Zwölfer 1988), although usually in peripheral populations or in those occupying regions colonized since the Pleistocene; our samples come mainly from or near known centres of diversity in *Berkheya*.

The feature of particular interest in the *Berkheya* system, needing further study, is the indication of parallel host and herbivore evolution in 2 centres of radiation, the southeast corner of South Africa (south from 29°S, and east from 26°E), and the extreme western Cape (west of 22°E). The dry interior of Cape province supports very few *Berkheya* populations and it is likely that, in arid (=glacial) periods of the Pleistocene, such hostile environments extended to the coast between 22-26° E (Gamble and Soffer 1990), isolating the western Cape with its characteristic climate of winter rain/summer drought. This rainfall pattern is reversed in other regions suitable for *Berkheya*. Any similar phenomenon has not been directly investigated in Cardueae but there is plenty of evidence, especially for *Larinus*, of local adaptation to different host plants, which in time could lead to speciation (Zwölfer 1988).

Overall, the similarities in the structure of these 2 herbivore communities is striking, and suggests that they are shaped by strong and similar evolutionary pressure (Zwölfer 1988).

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