Chapter 3 Species Limits of Carpha Based on Phenetic Analyses

3.1 Introduction

Carpha was first described by Brown (1810) based on five Australian species (C. alpina, C. deusta, C. avenacea, C. diandra and C. clandestina). After Brown, the definition and composition of Carpha was modified (see Chapter 1 for detailed discussion). Four of Brown's five species were transferred to Cyathochaeta or Mesomelaena (Nees 1846; Bentham 1878). The African genera Asterochaete, Oreograstis and Ecklonea (Trianoptiles) were sunk into Carpha by Boeckeler (1874), Clarke (1902) and Pfeiffer (1931) respectively. Many new species of Carpha were published (Nees 1835; Hooker 1847; Mueller 1855; Philippi 1857–58; Boeckeler 1874, 1879; Clarke 1894, 1904, 1905; Gandoger 1919; Chermezon 1922; 1935; Curtis 1984; Reid and Arnold 1984; Table 1.3). Some species were transferred to Carpha from Schoenus, Elynanthus and Chaetospora (Nees 1832; Boeckeler 1874; Clarke 1894, 1901; Pfeiffer 1927, 1931), while some species of Carpha were moved to Schoenus and Eriospora (or Coleochloa) (Clarke 1894; Pfeiffer 1927; Kükenthal 1938; Fig. 1.2).

In the only worldwide revision of the genus since Brown (1810), Kükenthal (1939c, 1939d) recognized two subgenera, 11 species and four varieties in *Carpha* and transferred nine species and one variety to *Ptilanthelium*, *Costularia*, *Schoenus*, *Cladium* and *Tetraria*. One of his subgenera was upgraded to the genus, *Trianoptiles*, by Levyns (1943). His synonymising of *C. nivicola* with *C. alpina*, as had already been done by Mueller (1875), Bentham (1878) and Pfeiffer (1931), was not accepted by some later authors (Blake 1940; Costin et al. 1979; Thompson 1981; Thompson and Gray 1981; Wilson 1993, 1994a, 1994b). *Carpha alpina* R.Br. var. *subacaulis*, one of his four varieties, was included in *C. nivicola* by Wilson (1994b), and the other three (*C. alpina* var. *schoenoides*, *C. capitellata* var. *bracteosa* and *C. eminii* var. *angustissima*) were not universally accepted by later authors (Gunckel 1971; Haines and Lye 1983; Reid and Arnold 1984; for details see chapter 1).

Since Kükenthal (1939c, 1939d), estimates of the number of species in *Carpha* have varied from 4 (or possibly 5) (Wilson 1986, 1993, 1994a) to 11–15 (Kern 1974; Dyer 1976;

Haines and Lye 1983; Bruhl et al. 1992; Goetghebeur 1998) due to the different narrow or broad definitions of the genus (see Chapter 1 for details).

In view of the above problems, it is necessary to make a complete and systematic study of *Carpha*, especially of generic and species limits. In this chapter, I aim to test and set species limits in *Carpha* using phenetic analyses of morphological data.

3.2 Materials and Methods

3.2.1 Specimens Sampled

Herbarium specimens of *Carpha* from B, BM, BOL, CANB, EA, HO, K, MEL, MO, NE, NSW, NU, NY, P, PRE and Z and fresh specimens of *Carpha* collected for this study (lodged at NE and NSW) were examined. These specimens (c. 650) included most material of *Carpha sensu lato* studied by Kükenthal as well as many more recent collections. Of these, 163 specimens (see Appendix 1) were selected to serve as operational taxonomic units (OTUs) in phenetic analyses. Within the limits of available material, the OTUs were selected to capture the full range of morphological variation and geographic range of each species. Within these criteria, complete, ample specimens were chosen to minimise missing values, and type specimens (where available) were included to check on the application of names. Where sheets were composed of more than one plant, only one was measured.

Identification of each of these OTUs was carefully examined, checked or corrected according to the literature. For three taxa whose status is controversial, *C. angustissimal C. eminii* var. *angustissima* (Chermezon 1935; Kükenthal 1939d; Haines and Lye 1983), *C. bracteosal C. capitellata* var. *bracteosa* (Clarke 1894, 1897–1898; Pfeiffer 1931; Kükenthal 1939c; Reid and Arnold 1984) and *C. schoenoides/C. alpina* var. *schoenoides* (Hooker 1847; Steudel 1855; Philippi 1881; Kükenthal 1939c; Barros 1969), the shorter names *C. angustissima*, *C. bracteosa* and *C. schoenoides* respectively were used to represent them in the analyses. *Carpha discolor* and *C. ulugurensis* are manuscript names written on specimens by T. H. Arnold and E. Nelmes respectively.

3.2.2 Characters

The annotated characters listed in DELTA format (Dallwitz et al. 1999) are presented in Appendix 2. The characters represent aspects of growth habit, and vegetative and reproductive morphology. These characters can reflect the differences among various taxa, i.e. reveal the patterns of discontinuity among the taxa.

3.2.3 Dissection, Measurement and Scanning Electron Microscopy

General morphological observations were made using Stemi 2000 Zeiss or Leica MZ75 dissecting microscopes. Glumes were removed carefully from base to apex of a spikelet to reveal details of 'rachilla' and flowers. Herbarium material was softened by boiling in water with a drop of domestic detergent where necessary.

Characters related to spikelet, flower and nut morphology, and those involving measurements of less than 1 cm were measured with an ocular micrometer in dissecting microscopes at 10–20x. Otherwise, measurements were made using a ruler.

Nuts from herbarium specimens, after removal of selected perianth parts where necessary, were mounted on stubs using double-sided tape, sputter-coated with gold using a SEM coating unit E5100, and viewed under a JEOL JSM-5800LV scanning electron microscope at 15 kV.

The full data matrix used in phenetic analyses is presented in Appendix 3.

3.2.4 Phenetic Analyses

3.2.4a Character Weight

The morphological data were analysed phenetically using PATN (Belbin 1993a). Characters were given an equal weight, i.e. each character was assigned a weight of one. If a character took one column in the data set, the column was assigned a weight of 1; two columns, 0.5; three columns, 0.33; four columns, 0.25 and five columns 0.2.

3.2.4b Association Measure

The data displayed short gradient lengths (2.2 standard deviation) calculated using Detrended Correspondence Analyses (ter Braak and Prentice 1988; ter Braak and Smilauer 1998; Li 2001), indicating a linear nature of the data. Therefore, the Gower metric, a range-standardized Manhattan distance, was chosen as the association measure as it is robust for data displaying a linear response (Belbin 1993b).

3.2.4c Multivariate Analyses

Ordination and clustering are two commonly used approaches to implement phenetic analysis (Sneath and Sokal 1973; Stuessy 1990). The results of ordination and clustering differ greatly in appearance (ordination diagrams vs phenograms) and may lead to different taxonomic results (Sneath and Sokal 1973).

It has been argued that ordination has the advantage of making few assumptions about the nature of relationships in the data and to have the power to identify multiple, overlapping patterns (Faith and Norria 1989; Crisp 1991). However, ordination may not disclose sharp discontinuities if these patterns cannot be displayed in the first few dimensions (Sneath and Sokal 1973), especially with many OTUs and clusters (Williams and Lance 1968). These patterns overlapped in 2- or 3-dimensional space may be quite distinct in hyperspace (Sneath and Sokal 1973). Therefore, ordination is often impracticable for very large numbers of characters and OTUs (Sneath and Sokal 1973). Moreover, ordination diagrams are examined and their limits are decided visually, which is counter to the aims of objectivity and explicitness (Sneath and Sokal 1973).

Clustering can produce sharp and tidy classes, even if the OTUs have been forced together to produce them, but the inadvertent chopping of continuous variation into somewhat arbitrary clusters does not usually damage the analysis irretrievably, because the continuity is generally fairly evident (Sneath and Sokal 1973). Clusterings and ordinations usually reveal similar major structure, but the finer divisions are less evident in ordinations than in clusterings (Webb et al. 1967). However, phenograms produced by clustering give poor representations of relationship between major clusters (Rohlf 1967, 1970). Therefore, in this study clustering was used to reveal formal taxonomic groupings and ordination was

used as a supplementary way of investigating the general pattern of variation as recommended by Sneath and Sokal (1973). Ordination was also used to confirm that discrete clusters produced by clustering resulted from differences among OTUs rather than from chance or other factors (D. Faith 2002, pers. comm.). Only the first two dimensions were used in this study because most information was contained by them according to the amount of variance explained by each ordination axis.

Using the distance matrix produced by the Gower metric association measure, clustering analysis was performed using Flexible WPGMA (weighted pair-group method using arithmetic averages) because it weights the groups equally and is useful when the groups of interest are of dissimilar size (Sneath and Sokal 1973; Belbin 1993b). The results produced by the clustering analyses were graphically represented in a phenogram purporting to show the degree of similarity between specimens. Flexible UPGMA (unweighted pair-group method using arithmetic averages) analysis was also performed for comparison because it weights OTUs equally throughout the fusion process, conserves the character space and shows the highest cophenetic correlation (Sneath and Sokal 1973; Belbin 1993b). Although there were differences in the exact structure of the two phenograms produced by Flexible WPGMA and Flexible UPGMA, both showed essentially the same results and supported the same conclusions. Only the results from Flexible WPGMA are presented because the sample of specimens for each species was unequal and, consequently, groups of interest were of various sizes. The dataset was also analysed using multidimensional scaling (SSH) ordination because it is a robust technique for indirect gradient analysis, and produces essentially distortion-free ordinations (del Moral 1980; Minchin 1987; Belbin 1993b). Fifty iterations were performed in the analysis to ensure the ordination with the lowest stress value. After SSH analysis, the lower dimensions gave poor representation of relationships among OTUs as expected because of the large numbers of characters and OTUs.

To investigate the detailed patterns within the main groups, efficiently use the ordination approach, and identify character contributions at lower levels, subsets of the OTUs were chosen for further analyses on the basis of the main clustering patterns revealed by the phenogram of all OTUs (see Fig. 3.1). Characters used for these subsets were the same as those in the analysis of all OTUs, but constant characters were excluded. The Gower metric association measure was used (Belbin 1993b) because the subsets were linear (gradient lengths less than 3 standard deviation). The Flexible WPGMA was used to

produce classifications of the subsets. Ordinations were performed to provide further insights on structure in the subsets using SSH. Principal components analysis (PCA) was also used to analyse the data following the Gower correction for comparison because it is appropriate for linear data containing quantitative and qualitative data (Legender and Legender 1983). Similar ordination patterns were produced using SSH (50 iterations) and PCA methods, and only SSH results are presented.

For each classification, the GSTA program was used to produce Kruskai-Wallis statistics for recognized groups and to determine a set of significant characters discriminating these groups.

3.3 Results

3.3.1 Analyses of All Specimens of Carpha

A phenogram of all specimens (OTUs) of *Carpha* was produced using the Gower metric and Flexible WPGMA agglomerative strategy (Fig. 3.1). *Carpha* was separated into three main groups according to similarity, which are labelled as A–C in Fig. 3.1. Group A included what had been previously considered to be five species, *C. alpina*, *C. curvata*, *C. nivicola*, *C. rodwayi*, and *C. schoenoides*. One specimen named as *C. discolor* formed group B. Group C included all other species which are from South Africa, Madagascar and Réunion.

All characters contributed significantly (p-value < 0.001) to distinguishing the three main groups with the exception of character (character state) 28(2) (head of spikelets oblong or ellipsoid) and character 43 (proximal fertile glume maximum width)—see Appendix 2. The most significant characters and character states contributing to group discrimination include features of the glumes, perianth bristles and leaf shape (summarized in Table 3.1).

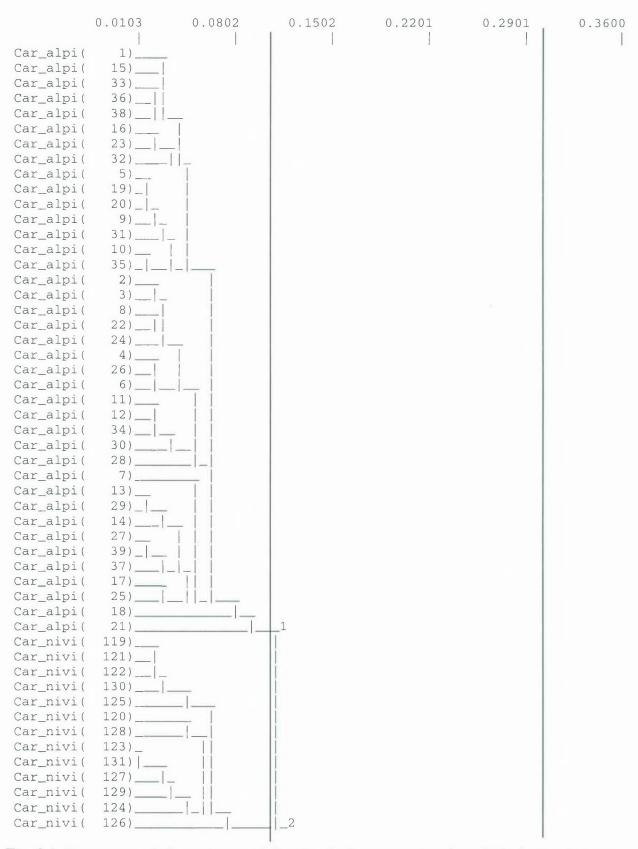


Fig. 3.1. Phenogram of all specimens of *Carpha*. Scale represents value of Manhattan distance (Gower metric). One solid line (threshold value of 0.3050) truncates three main groups labelled as A–C, the other solid line (threshold value of 0.1100) truncates 16 subgroups labelled as 1–16. For full name of each species see Appendix 1.

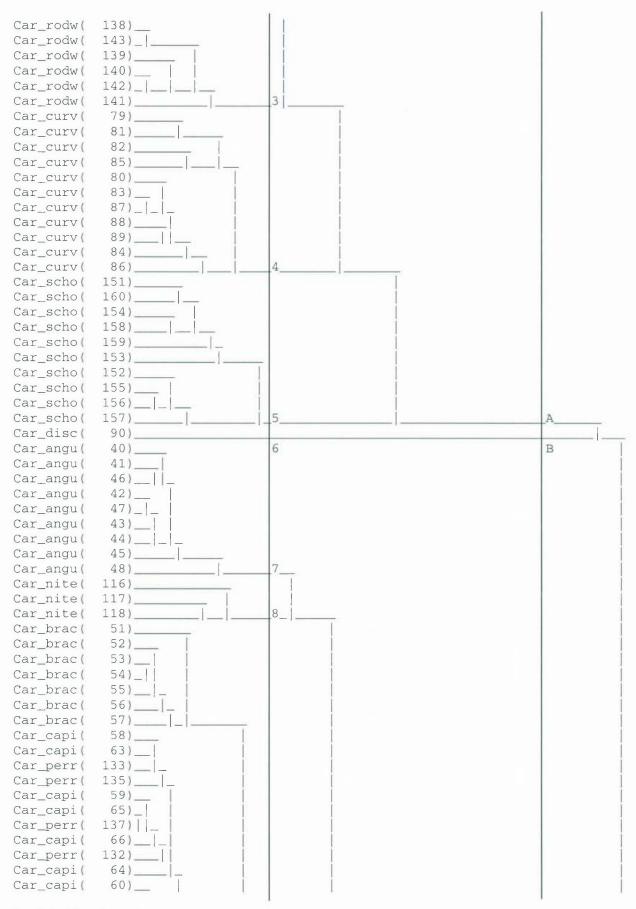


Fig. 3.1. (Continued)

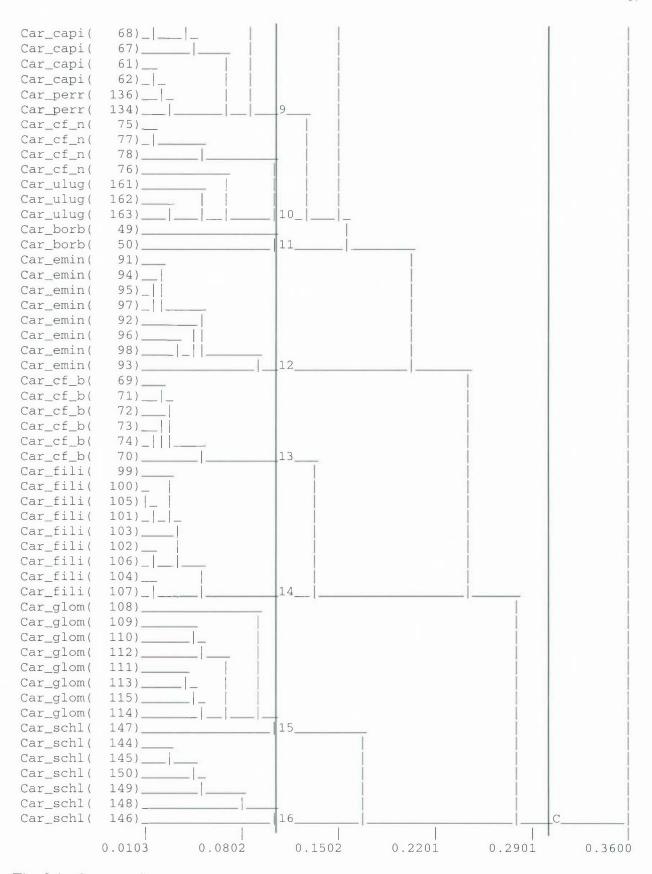


Fig. 3.1. (Continued)

Table 3.1. The most significant characters and character states (Kruskal-Wallis values > 2500, df = 2) contributing to discrimination of the three main groups (A, B and C) in the first analysis. Character numbers refer to Appendix 2. Number in brackets beside a character number indicates the state number of a multistate character. Values in square brackets indicate the range of values of each character. See Fig. 3.1 for phenogram.

	Character (character states)	Kruskal- Wallis	A	В	С
39(2)	Only proximal glumes persistent [0/1]	3340.50	0	1	1
62(1)	Perianth bristle plumose [0/1]	3340.50	1	1	0
62(2)	Perianth bristle scabrous [0/1]	3340.50	0	0	1
39(1)	All glumes persistent [0/1]	3338.50	1	0	0
57	Perianth members more or less equal in length between inner whorl and outer whorl [0/1]	2805.80	0	1	0/1
16(2)	Leaf blade thinly crescentiform or flat in cross-section [0/1]	2522.80	1	0	0/1

These specimens were further divided into subgroups. To classify these specimens at species level, an appropriate threshold had to be selected to truncate the phenogram. An ideal threshold should be that at which most specimens can be clearly grouped into species. Above that threshold, specimens from different species could be grouped together, while, below it, specimens from the same species may be separated. A value of dissimilarity of 0.1100 was selected as a threshold for this study to group specimens into species by examining the phenogram. As a result, 16 subgroups of specimens were recognized and labelled as 1 to 16 in Fig. 3.1. Most of these subgroups recovered previously recognized species. Each of the subgroups 1-8 and 11-14 consisted of specimens of what had previously been considered to be individual species. They are Carpha alpina, C. nivicola, C. rodwayi, C. curvata, C. schoenoides, C. discolor, C. angustissima, C. nitens, C. borbonica, C. eminii, C. cf. bracteosa and C. filifolia respectively. Subgroup 9 was a mixture of specimens of Carpha bracteosa, C. capitellata and C. perrieri. Within this subgroup all specimens of C. bracteosa formed a secondary subgroup. Subgroup 10 included specimens of C. cf. nitens, and C. ulugurensis. One specimen of C. schlechteri (B. Sonnenberg 458, NU) and specimens of C. glomerata clustered in subgroup 15, while all other specimens of *C. schlechteri* formed subgroup 16. All 54 characters (see Appendix 2) contributed significantly (p-value < 0.001) to distinguishing these 16 subgroups.

Ordination analysis of all specimens of Carpha revealed the general patterns (Fig. 3.2, stress = 0.132), but gave poor representation of relationships among specimens because of the large numbers of characters and specimens.

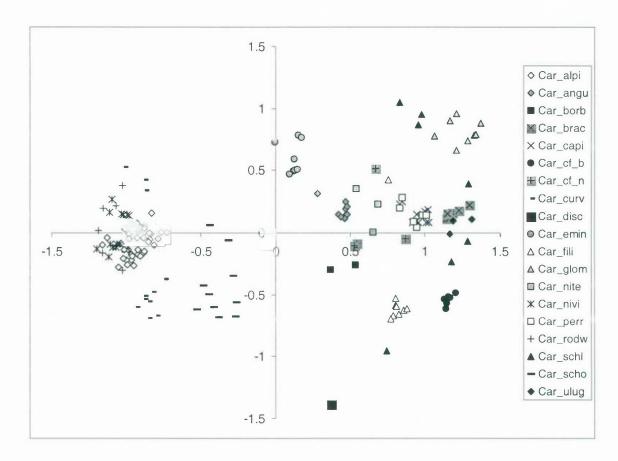


Fig. 3.2. SSH axis 1 and 2 of all specimens of Carpha (stress = 0.132). For full name of each species see Appendix 1.

3.3.2 Subset Analyses

Of the three main groups (A, B and C) based on analysis of all specimens (Fig. 3.1), group B contains only one species, so only groups A and C were further analysed using clustering and ordination analyses.

3.3.2a Analyses of Group A

The clustering analysis of group A (Fig. 3.3) effectively separated the specimens into the same five subgroups, which correspond to species *Carpha alpina*, *C. nivicola*, *C. rodwayi*, *C. curvata* and *C. schoenoides*, as in the first analysis (Fig. 3.1). All characters contributed significantly (p-value < 0.001, but character 29 (primary spikelet pedicel length) with p-value = 0.008) to distinguishing these five subgroups/species with the exception of character 49 ('rachilla', whether adnate to fertile glume base) (see Appendix 2).

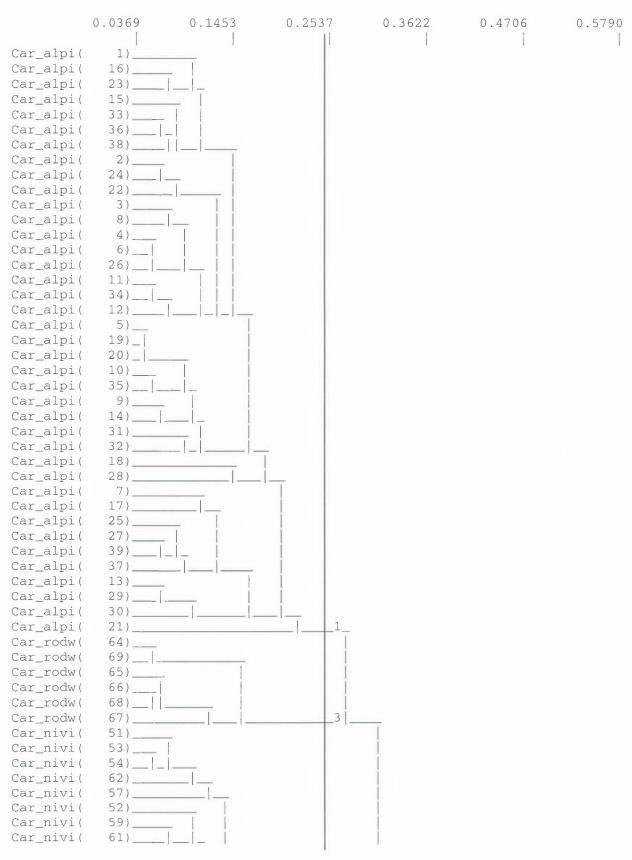


Fig. 3.3. Phenogram of specimens of group A. Scale represents value of Manhattan distance (Gower metric). Solid line truncates five subgroups labelled as 1–5, which are corresponding with the labels in Fig. 3.1. For full name of each species see Appendix 1.

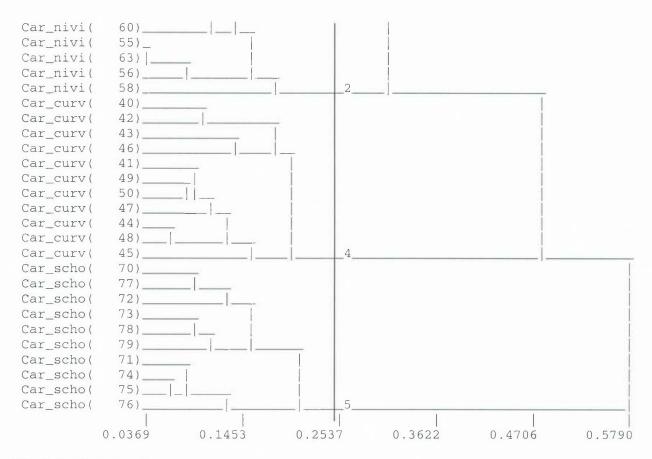


Fig. 3.3. (Continued)

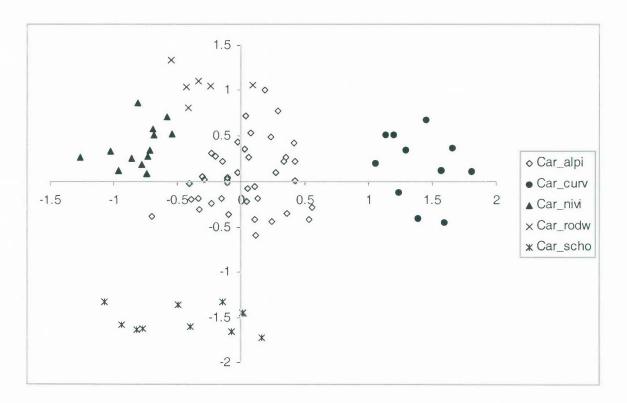


Fig. 3.4. SSH axis 1 and 2 of specimens of group A (stress = 0.229). For full name of each species see Appendix 1.

The most significant characters and character states contributing to group discrimination are summarized in Table 3.2.

The patterns revealed by ordination analysis of group A (Fig. 3.4, stress = 0.229) were basically the same as in the clustering analysis.

Table 3.2. The most significant characters and character states (Kruskal-Wallis values > 200, df = 4) contributing to the five subgroups (1–5) distinguished in the analysis of group A. Character numbers refer to Appendix 2. Number in brackets beside a character number indicates the state number of a multistate character. Values in square brackets indicate the range of values of each character. See Fig. 3.3 for phenogram.

	Character (character states)	Kruskal- Wallis	1	3	2	4	5
88	Fruit epidermis reticulate [0/1]	616.81	0	0	0	1	1
28(2)	Head of spikelets oblong-ellipsoid [0/1]	378.79	0	0	0	1	0
12(1)	Leaf blade curled for at least one third of its length [0/1]	378.79	0	0	0	1	0
90	Fruit epidermis punctulate [0/1]	349.42	1	1	1	1	0
12(3)	Leaf blade not curled [0/1]	280.85	0/1	1	1	0/1	1
53	Flower number per female-fertile spikelet [1–2]	236.18	1/2	1	1	1	2
82	Fruit number per spikelet [1–2]	236.18	1	1	1	1	2
12(2)	Leaf blade with only tips curled [0/1]	232.24	0/1	0	0	0/1	0
14	Leaf rigid [0/1]	221.81	0	1	0	0	0
11	Pseudopetiole present [0/1]	206.20	0/1	1	0/1	0	0

3.3.2b Analyses of Group C

The phenogram produced from the clustering analysis of group C (Fig. 3.5) revealed the same ten distinct subgroups as in the first analysis (Fig. 3.1). Specimens of *Carpha angustissima*, *C. borbonica*, *C. nitens*, *C. eminii*, *C.* cf. *bracteosa* and *C. filifolia* were clearly separated into their respective species. Specimens of *Carpha bracteosa*, *C. capitellata* and *C. perrieri* were grouped together in both analyses (Figs 3.1, 3.5). Within this subgroup all specimens of *C. bracteosa* were clustered into a secondary subgroup, while specimens of *C. capitellata* and *C. perrieri* were mixed. *Carpha* cf. *nitens* and *C. ulugurensis* formed a single subgroup in both analyses (Figs 3.1, 3.5). One specimen initially identified as *C. schlechteri* (*B. Sonnenberg 458*, NU) and specimens of *C. glomerata* were grouped together, while all other specimens of *C. schlechteri* formed a separate subgroup in both analyses (Figs 3.1, 3.5).

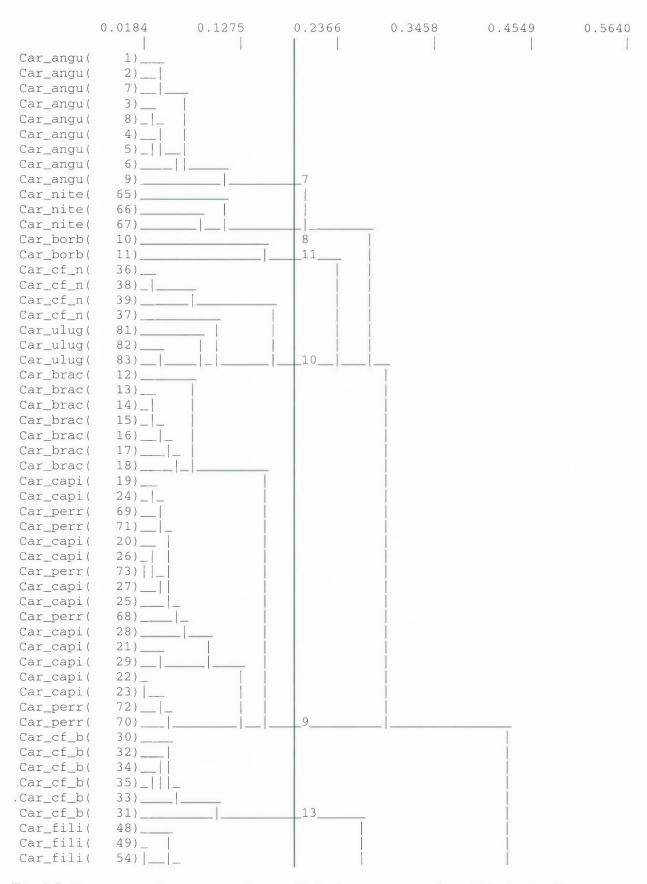


Fig. 3.5. Phenogram of specimens of group C. Scale represents value of Manhattan distance (Gower metric). Solid line truncates ten subgroups labelled as 7–16, which correspond to the labels in Fig. 3.1. For full name of each species see Appendix 1.

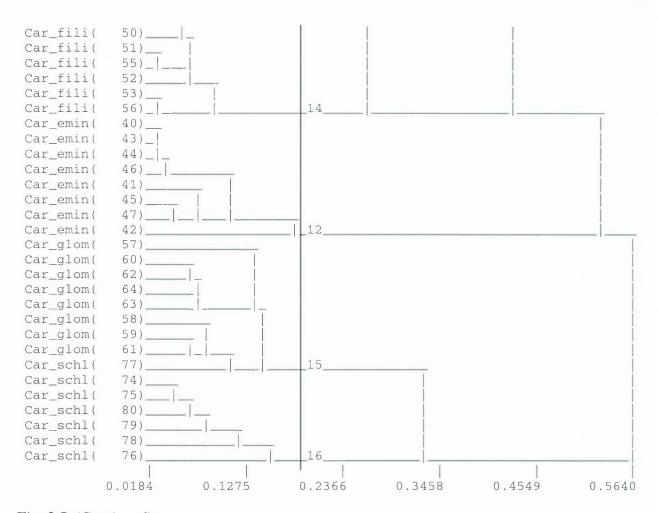


Fig. 3.5. (Continued)

All characters contributed significantly (p-value < 0.001) to distinguishing these ten subgroups/species with the exception of character 94 (fruit stalk length; see Appendix 2). The most significant characters (character states) contributing to group discrimination are summarized in Table 3.3.

The general relationship between specimens was revealed by ordination analysis of group C (Fig. 3.6, stress = 0.167), but the detailed groupings were not as clear as in the phenogram (Fig. 3.5), for example, one specimen of C. cf. bracteosa is plotted within C. filifolia, because of the large number of specimens.

To investigate the detailed patterns of these specimens using ordination approach, subgroups 7–11 and subgroups 12–16 in Fig 3.1 and Fig. 3.5 were further analysed.

subgroups (7-16) distinguished in the analysis of group C. Character numbers refer to Appendix 2. Number in brackets beside a Table 3.3. The most significant characters and character states (Kruskal-Wallis values > 280, df = 9) contributing to the ten character number indicates the state number of a multistate character. Values in square brackets indicate the range of values of each character. See Fig. 3.5 for phenogram.

	Character (character states)	Kruskal- Wallis		∞	11	10	6	13	14	12	15	16
28(1)	Head of spikelets ovoid [0/1]	834.48	0	0	0	0/1	-	0	0	0	-	
06	Fruit epidermis punctulate [0/1]	825.95	proof	0	0	0	0	-	Т	_	0	0
26(2)	Spikelets not densely clustered [0/1]	637.68	П	_	0	0	0	0	0	_	0	0
26(1)	Spikelets densely clustered [0/1]	637.67	0	0	1	1	_	I	1	0	Т	I
16(1)	Leaf blade V-shaped in cross-section [0/1]	567.84	_	_	0	_	1	0	0	1	_	1
4(1)	Culms triangular in cross-section [0/1]	520.12	0	0	0	0/1	0	0	0	0	_	-
16(4)	Leaf blade circular in cross-section [0/1]	516.22	0	0	0	0	0	T		0	0	0
16(3)	Leaf blade thickly crescentiform in cross-section [0/1]	516.22	0	0	0	0	0	1	_	0	0	0
4(3)	Culms subcircular-circular in cross-section [0/1]	506.53	П	1	-	0/1			П		0	0
48	'Rachilla' elongated above fertile node [0/1]	488.89		-	_	—	1		-	0	-	0
28(2)	Head of spikelets oblong-ellipsoid [0/1]	460.55	0	0	0	-	0	1	0	0	0	0
49	'Rachilla' adnate to fertile glume base [0/1]	425.54	_	_	-	-		1	1	0	_	0/1
16(2)	Leaf blade thinly crescentiform or flat in cross-section [0/1]	400.83	П	0	_	0	0	0	0	0	0	0
82	Fruit number per spikelet [1–2]	364.76	1/2	1/2	1/2	1/2	1/2	2	2	_	2	I
41(1)	Uppermost glume sterile [0/1]	342.05	0/1	0/1		0/1	0/1	0	0	0/1	_	0/1
1	Rhizome present [0/1]	337.06	_	1	_	_		_	0		1	
28(4)	Head of spikelets obovoid [0/1]	337.06	0	0	0	0	0	0	1	0	0	0
41(2)	Uppermost glume fertile [0/1]	335.44	-	0/1	0/1	0/1	-	_	-	0/1	0	0/1

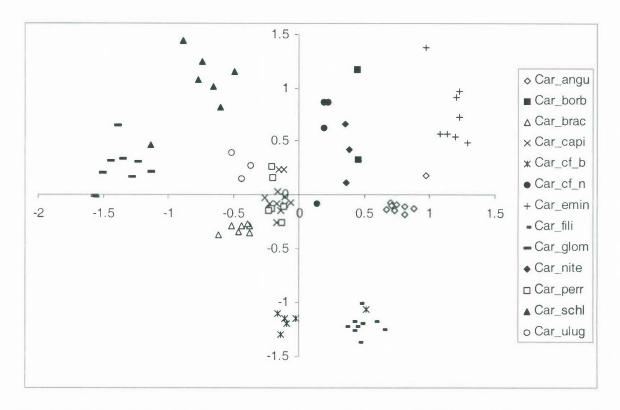


Fig. 3.6. SSH axis 1 and 2 of specimens of group C (stress = 0.167). For full name of each species see Appendix 1.

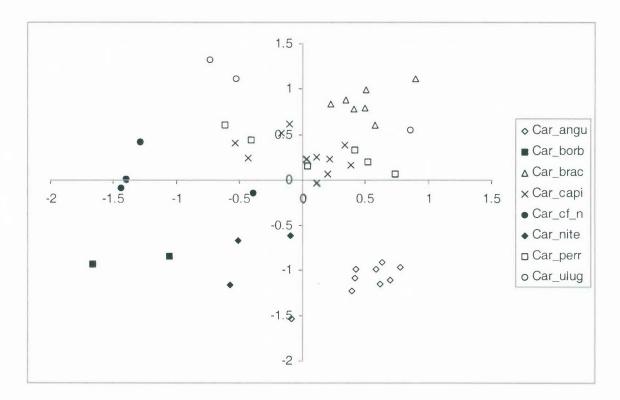


Fig. 3.7. SSH axis 1 and 2 of specimens of subgroups 7-11 (stress = 0.199). For full name of each species see Appendix 1.

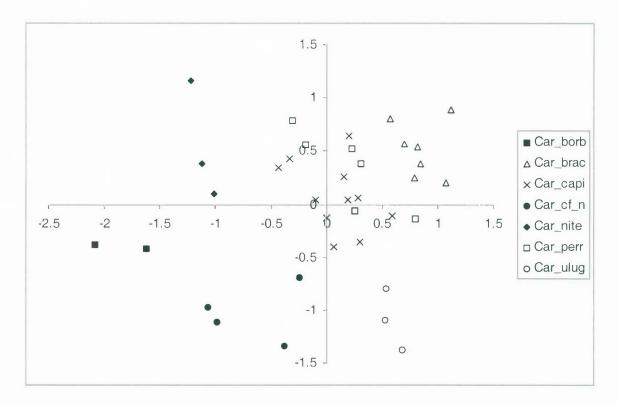


Fig. 3.8. SSH axis 1 and 2 of specimens of subgroups 7–11 but without C. angustissima (stress = 0.224; cf. Fig.3.7). For full name of each species see Appendix 1.

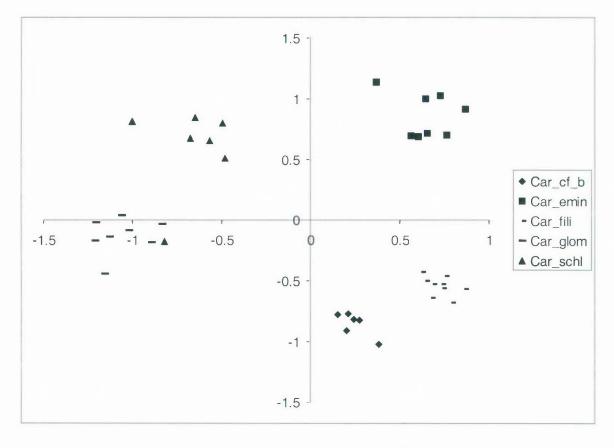


Fig. 3.9. SSH axis 1 and 2 of specimens of subgroups 12-16 (stress = 0.118). For full name of each species see Appendix 1.

The ordination diagram (Fig. 3.7, stress = 0.199) revealed the general relationship between specimens of subgroups 7–11. Specimens of *Carpha angustissima* were obviously different from specimens of any other subgroup, but the detailed groupings were not as clear as in the phenogram (Fig. 3.5). If specimens of *Carpha angustissima* were excluded, the ordination (Fig. 3.8, stress = 0.224) gave essentially the same patterns as in the clustering analysis.

The ordination diagram of subgroups 12–16 (Fig. 3.9, stress = 0.118) revealed the same patterns as in the clustering analysis (Fig. 3.5), i.e. the specimens of *C. cf. bracteosa*, *C. eminii*, *C. filifolia*, *C. glomerata* (plus one sample previously identified as *C. schlechteri*) and *C. schlechteri* were separated.

3.4 Discussion

Specimens were separated into three main groups A-C and 16 subgroups mainly corresponding to previously recognized species (Fig. 3.1). Group A, which includes five species Carpha alpina, C. nivicola, C. rodwayi, C. curvata and C. schoenoides, is consistent with the definition of Carpha sensu stricto (Hooker 1860, 1867; Bentham 1878, 1883; Wilson 1986, 1993, 1994a, 1994b; see Chapter 1). All species in this group have plumose perianth members and all glumes are persistent (Table 3.1). The group is restricted to southern Australia, New Zealand, New Guinea and South America. Group C, which consists of Carpha angustissima, C. borbonica, C. bracteosa, C. capitellata, C. cf. bracteosa, C. cf. nitens, C. eminii, C. filifolia, C. glomerata, C. nitens, C. perrieri, C. schlechteri, and C. ulugurensis, represents Asterochaete of Nees (1834), Kunth (1837), Steudel (1855) and Levyns (1950). All species in this group have scabrous perianth members and only proximal sterile glumes are persistent (Table 3.1). They are restricted to Africa, Madagascar and Réunion. Group B consists of a single new species recognized here (Carpha discolor ms; T. H. Arnold wrote this manuscript name on the specimens, but he has no intention of working on it; 2000, pers. comm.). Carpha discolor differs from species of group A by bicolorous glumes, perianth members only lower-half plumose and those in the inner whorl much longer than those of the outer whorl, spikelets forming dense ovoid heads, only lower sterile glumes persistent, nuts without a stalk, and very thick