

## Chapter 6 Synthesis

This chapter reports a cladistic analysis of combined morphological and molecular data, summarises the major systematic findings from previous chapters, and revises *Carpha* taxonomically in the light of some of these findings.

### 6.1 Phylogenetic Relationships of *Carpha* and its Relatives (Schoeneae, Cyperaceae) Inferred from Combined Morphological and Molecular Data

#### 6.1.1 Introduction

There has been much debate as to whether or not different data sets should be combined. An argument for combining data sets is that they can use the 'total evidence' available, and enhance detection of real phylogenetic groups (Kluge 1989; Barrett et al. 1991; Vane-Wright et al. 1992; de Queiroz 1993; Eernisse and Kluge 1993; Jones et al. 1993; Kluge and Wolf 1993; de Queiroz et al. 1995; Pennington 1996; Myllys et al. 1998; Smith 2000). An argument against combining data sets is that different data sets could track different phylogenetic histories, so that combining these data sets could give misleading results (Bull et al. 1993; de Queiroz 1993; de Queiroz et al. 1995; Hillis and Huelsenbeck 1995; Miyamoto and Fitch 1995).

A solution to this problem is to test whether data sets are significantly heterogeneous or not. Analysis of combined data sets is only applicable when datasets are not significantly heterogenous (Bull et al. 1993; de Queiroz 1993; Huelsenbeck et al. 1994; de Queiroz et al. 1995; Huelsenbeck and Bull 1996).

A suite of tests has been proposed to investigate whether heterogeneity is statistically significant, or possibly an artefact of stochastic variation (e.g. Bull et al. 1993; Farris et al. 1994; Miyamoto and Fitch 1995; Huelsenbeck and Bull 1996). Among these tests, the incongruence length difference test (ILD, also called the partition homogeneity test; Farris et al. 1994) is the most useful (Cunningham 1997).

However, it has been argued that even if statistically significant heterogeneity exists between data sets, analysis of combined data sets generally results in cladograms that are more fully resolved than those of individual data sets (Myllys et al. 1998; Smith 2000).

In this study, a cladistic analysis of combined morphological and molecular data of *Carpha* and its relatives was undertaken after the ILD test to get the most information possible to reveal phylogenetic relationships.

## **6.1.2 Methods**

### **6.1.2a Sampling**

Because of the limitations of time, funding and availability of materials, the species sampled for the molecular data (Chapter 5) were basically a subset of those sampled for the morphological data (Chapter 4). Only the species sampled for both data sets were included in this combined analysis; they were *Carpha alpina*, *C. capitellata*, *C. curvata*, *C. filifolia*, *C. glomerata*, *C. nitens*, *C. nivicola*, *C. rodwayi*, *Cyathochaeta diandra*, *Gahnia sieberiana*, *Gymnoschoenus sphaerocephalus*, *Oreobolus distichus*, *Oreobolus pumilio*, *Ptilothrix deusta*, *Schoenoides oligocephalus*, *Schoenus paludosus*, *Schoenus turbinatus*, *Trianoptiles solitaria*, *Tricostularia pauciflora* and outgroups *Rhynchospora brownii* and *Rhynchospora corymbosa*.

### **6.1.2b Characters**

The same 94 morphological characters (37 quantitative and 57 qualitative) used in Chapter 4 and the same alignment sequences used in Chapter 5 were combined in this cladistic analysis.

### **6.1.2c Character Coding and Weighting**

The 37 quantitative characters were coded using the same gap weighting (Thiele 1993) method described in Chapter 4. Likewise, qualitative characters were weighted using the same procedure as in Chapter 4. A weight of 24 was applied to each molecular character to maintain the same weights as assigned to 94 morphological characters, i.e. each molecular character was treated as a four-state character and weighted by 8.

### 6.1.2d Combinability Test

Combinability of the morphological and molecular data sets of *Carpha* and its relatives was assessed using the cladistic permutation tail probability (PTP) test (Faith and Cranston 1991) and the ILD test (Farris et al. 1994). The PTP test for the presence or absence of phylogenetic signal of two data sets was performed using TBR branch-swapping with 1000 replicates. The ILD test to examine potential conflicts in the phylogenetic signals between the two data sets was carried out with invariant characters excluded (Cunningham 1997) using TBR branch-swapping with 1000 replicates. These analyses were undertaken using PAUP\* 4.0b8 (Swofford 2000).

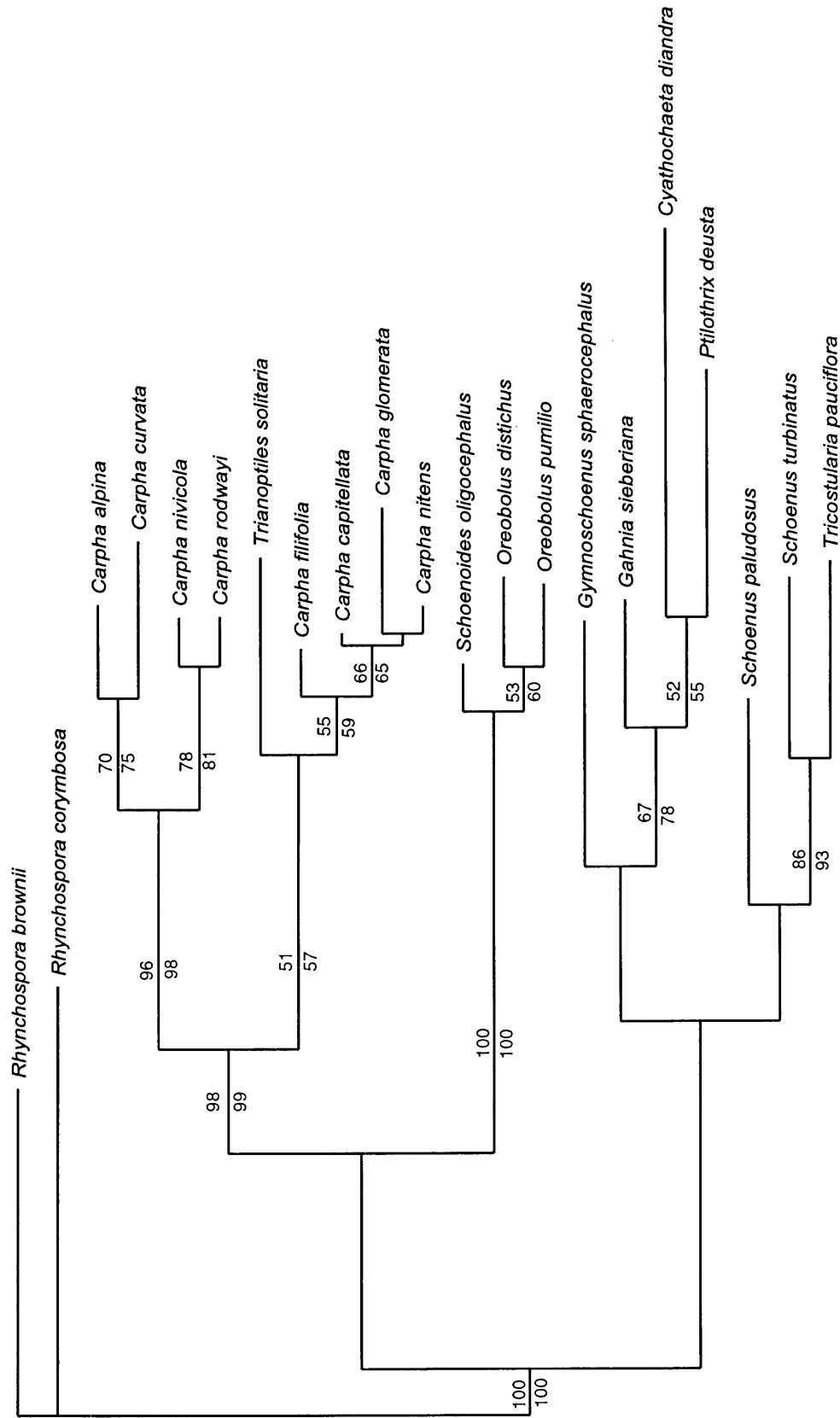
### 6.1.2e Analyses

Maximum parsimony analysis, bootstrap analysis and jackknife analysis of the combined data were carried out as described in Chapter 4.

### 6.1.3 Results and Discussion

The PTP test indicated that each data set had significant cladistic covariation ( $p = 0.001$  for both data sets). The ILD test indicated that the two data partitions were significantly heterogenous ( $p = 0.001$ ), i.e. statistically significant incongruence existed between the two data sets. Despite this, a combined analysis was conducted to get the most information possible to elucidate phylogenetic relationships as suggested by Myllys et al. (1998), Yoder et al. (2001) and Smith (2000). The caveat of the ILD test result should be kept in mind.

Maximum parsimony analysis of the combined morphological and molecular data resulted in one most parsimonious tree, 11528 steps long, with a retention index of 0.6374 and consistency indices of 0.6626 (0.5512 excluding autapomorphies) (Fig. 6.1). The bootstrap and jackknife support for the clades, especially for the two clades of *Carpha*, generally increased in the cladogram resulting from the combined data set compared with the molecular and morphological data sets analysed separately (Figs 4.1, 5.1, 6.1), although the ILD test showed significant incongruence between the two data sets.



100

**Fig. 6.1.** The most parsimonious tree from cladistic analysis of combined morphological and molecular data of *Carpha* and its relatives, using *Rhynchospora* as outgroup. Bootstrap values (> 50%), for 2000 replicate analyses, are presented above the branches. Jackknife values (> 50%), for 2000 replicate analyses, are presented below the branches.

Comparing the results from the analysis of the combined data sets with that derived from morphological data alone (Figs 6.1, 4.1, 4.2), it was found that both analyses were consistent in many aspects. Both analyses grouped species of *Carpha* into two paraphyletic clades, revealed the close relationships of *Cyathochaeta*, *Gahnia*, *Gymnoschoenus* and *Ptilothrix*, indicated that *Oreobolus* and *Schoenoides* formed a well-supported clade and that *Schoenus* was not a monophyletic genus. The differences between the two analyses was the relationships among some major clades, for example, the relationship of the clade composed of *Oreobolus* and *Schoenoides* to the clades composed of species of *Carpha* was different in the two analyses. These inconsistencies occurred at those nodes that were without support in both analyses.

Comparing the results from the analysis of the combined data set with that derived from molecular analyses alone, the two analyses revealed similar patterns in grouping genera and species with exceptions such as the monophyletic or paraphyletic status of *Carpha*, the relationship of *Trianoptiles* to species of *Carpha*, and the relationship of *Gymnoschoenus* to *Cyathochaeta*, *Gahnia*, and *Ptilothrix* (Figs 5.1, 6.1).

These findings are synthesised in the next section with those from the previous chapters to determine the generic limits of *Carpha* and estimate phylogenetic relationships in and around *Carpha*.

## **6.2 Major Systematic Findings**

### **6.2.1 Sympodial Structure of Spikelets in Tribe Schoeneae**

In the study of spikelet morphology (Chapter 2), spikelets of 250 specimens of 47 species from 15 of 27 genera of Schoeneae (Cyperaceae) were dissected and examined using light microscopy and/or SEM. The study found the spikelet structure in Schoeneae to be cymose (a rhipidium) with a sympodial 'rachilla'. Monopodial spikelets of Schoeneae described by most of the current literature including Floras were not found in the study.

The study has improved our understanding of spikelet structure and has led to clarified interpretations and concepts in Schoeneae.

- A spikelet is usually defined as a small spike, one part of, especially in distal parts of, a compound inflorescence (Lawrence 1951; Eiten 1976; Harris and Harris 1994; Kukkonen 1994); i.e. it is a monopodial structure. This definition is not appropriate to the sympodial spikelet of Schoeneae. Therefore, a spikelet is redefined as the smallest inflorescence unit that is easily identified by the unaided eye, including both sympodial and monopodial branching structures. Spikelets with a sympodial branching pattern are called sympodial spikelets, and spikelets with a monopodial branching pattern are called monopodial spikelets.
- A rachilla is defined as ‘a diminutive or secondary axis, or rachis’ (Lawrence 1951, p. 767). This definition of rachilla is also not appropriate to the axis of the sympodial spikelets in Schoeneae. Therefore, ‘rachilla’ (in quotes) is used in Schoeneae to refer to successive axes that are composed of nodes and internodes in the sympodial spikelets.
- Spikelets of many species in the tribe Schoeneae have no prophylls although they branch sympodially, i.e. sympodial branching occurs in spikelets when a prophyll is absent. Thus, the presence or absence of prophylls cannot be used to distinguish different branching patterns in the spikelets.
- The spikelets of Schoeneae develop acropetally and the uppermost glume may or may not produce a flower. This last feature may be variable within species and within individual plants, so the presence or absence of this flower is not an indication of sympodial or monopodial structure in Schoeneae.
- The relative position of the flower, glume and axis is a reliable criterion to judge whether spikelets are sympodial or monopodial. When a fertile glume subtends an axis rather than a flower, i.e. the axis lies between the glume and the flower, the spikelet is sympodial (Fig. 1 a–c). Conversely, when a fertile glume subtends a flower rather than an axis, the spikelet is monopodial (Fig. 1 d).
- In some species of *Schoenus* and in *Ptilothrix*, the formation of an arch-shaped cavity at the base of the fertile glume is related to the shape of the inclined nodes on which the glume grows, rather than, as claimed by Browning and Gordon-Gray (1995a),

being caused by a tearing away from the portion that was adnate to the 'rachilla'. Neither is it caused by the glume being decurrent on the 'rachilla' as described by Holttum (1948) and Kern (1974).

- This study clarifies our understanding of spikelet structure in Schoeneae and highlights the need to reinvestigate other tribes of Cyperaceae, where there are similar conflicting interpretations of spikelets.

### 6.2.2 Tribal Limits of Schoeneae

The tribe Schoeneae has been defined differently by different authors (Clarke 1908; Kükenthal 1940b, 1944, 1952; Goetghebeur 1986, 1998; Bruhl 1995; also see Chapter 1). The Schoeneae of Bruhl (1995) was found to be paraphyletic by Muasya et al. (1998). The cladistic analysis in this study based on morphological data (Chapter 4) indicated that *Rhynchospora*, which was included in the tribe Rhynchosporeae by Clarke (1908), Bruhl (1995) and Goetghebeur (1986), nested in Schoeneae with 100% bootstrap and jackknife support (Fig 4.1). This indicated some problems with the limits of Schoeneae. The cladistic analysis in this study based on molecular data (Chapter 5) grouped all the sampled species of Schoeneae into a monophyletic group using two species of *Rhynchospora* as outgroup members (Figs 5.1, 5.2), but these more limited molecular analyses did not include species of *Scleria*, *Capeobolus*, *Cyathocoma* or *Tetraria*. Thus, the molecular analyses did not provide a good test of corroboration and the conclusion must rely on the cladistic analyses of morphological data. On this basis, *Rhynchospora* should be included in Schoeneae, i.e. the finding is consistent with Goetghebeur's (1998) combination of Rhynchosporeae with Schoeneae.

Contradicting his definition of Schoeneae, Goetghebeur (1998) suggested the need for a further division of Schoeneae due to the variation in embryo types among different genera of the tribe. However, the current study did not focus on tribal limits, so the genera sampled were not enough to determine the tribal limits of Schoeneae. A further study on the Schoeneae of Goetghebeur (1998), including embryo data, should be conducted to determine the tribal limits.

### 6.2.3 Some Generic Definitions and Limits within Schoeneae

As reviewed in Chapter 1, cladistic analysis has become widely accepted as the most rigorous way to study phylogenetic relationships between species or at higher levels. Thus, discussion regarding generic definitions and limits, and phylogenetic relationships among genera and species in this section and the following two sections are based only on the results of the cladistic analyses.

#### 6.2.3a *Carpha*

Two clades of species of *Carpha* emerged in all the cladistic analyses (Chapters 4, 5, 6). One clade was composed of species that was consistent with the definition of *Carpha sensu stricto* (Hooker 1860, 1867; Bentham 1878, 1883; Wilson 1986, 1993, 1994a, 1994b; also see Chapter 1), and the other clade included the rest of the species of *Carpha sensu lato* that corresponded to the definition of *Asterochaete* (Nees 1834; Kunth 1837; Steudel 1855; Levyns 1950; also see Chapter 1). The two clades were paraphyletic in the cladistic analyses based on morphological data (Chapter 4) and on the combined data (Section 6.1 of this Chapter), and this suggested they should be separated as two different genera. They appeared as sisters based on molecular data alone (Chapter 5), which also suggested that they are two different groups but have a close relationship. Therefore, two genera, *Carpha sensu stricto* and *Asterochaete*, should be adopted rather than the currently recognized *Carpha sensu lato*. This division into two genera is consistent with the previous findings of some authors (Levyns 1947, 1950; Wilson 1986, 1993, 1994a, 1994b).

#### 6.2.3b *Costularia*

The cladistic analyses of this study found problems with the definition and limits of *Costularia*. *Costularia elongata* and *Costularia pilisepala* appeared in one clade in cladistic analyses based on morphological data (Chapter 4) but with no support. Cladistic analyses based on molecular data (Chapter 5) revealed further problems with the limits of *Costularia* because the three species from New Caledonia studied here dispersed into two different clades (Figs 5.1, 5.2). Moreover, the supposed discriminating characters of *Costularia*, such as the large loosely paniculate inflorescences, spikelets with lowest flower male and plumose perianth (Kern 1974; Dyer 1976; Goetghebeur 1998), are not unique to the genus and are not shared by all members of the genus. For example, loosely



paniculate inflorescences also occur in other genera such as *Schoenus*, and the paniculate inflorescences of *Costularia pilisepala* can be either loose or very dense; spikelets of *C. elongata* have two bisexual flowers, do not have a male flower at all, and the perianth is not plumose, while *C. pilisepala* has the lowest flower male and a plumose perianth. The problems of the definition and limits of *Costularia* found in this study are consistent with the results of Seberg's (1986, 1988b, 1988a) analyses. Therefore, a further study that includes all species in *Costularia* (23 species) is needed to assess the definition and limits of the genus.

### 6.2.3c *Schoenus*

Even with the small sample studied (two and six species in the molecular and morphological data sets respectively), this study also found problems with the definition and limits of *Schoenus*. The non-monophyletic status of *Schoenus* was indicated by all cladistic analyses conducted in this study (Chapters 4, 5, 6). The character usually used to discriminate the genus, i.e. upper internodes of 'rachilla' elongated and prominently zig-zag (Clarke 1902; Kern 1974; Wilson 1993; Goetghebeur 1998) is homoplasious (i.e. there are parallelisms) and is not shared by all species in *Schoenus* (Chapters 4). Thus, to reliably resolve the relationships and determine the limits of *Schoenus*, more thorough sampling of the whole genus (about 100 species) and further analyses are required.

### 6.2.3d *Tricostularia*

Another genus whose problems of definition and limits were revealed by this study is *Tricostularia*. Cladistic analyses based on morphological data (Chapter 4) revealed its polyphyletic status. As with *Costularia* and *Schoenus*, its discriminating characters, i.e. non-persistent perianth of scales and lower flower functionally male (Kern 1974; Wilson 1993; Goetghebeur 1998), are not unique characters for the genus, and are not shared by all members of it (Chapter 4). Therefore, more samples and further studies are needed to define its limits and clarify its phylogenetic relationships.

### 6.2.3e *Oreobolus* and *Schoenoides*

Cladistic analyses based on morphological data (Chapter 4) and on combined data (Section 6.1 of this Chapter) placed *Schoenoides* as sister to *Oreobolus*. These reconstructions of

phylogeny were, therefore, consistent with both possible classificatory outcomes: recognition of *Schoenoides* as a distinct genus or its inclusion in *Oreobolus*. By contrast, the estimate of phylogeny based only on molecular data (Chapter 5) had *Schoenoides* nested in *Oreobolus*. Thus, in light of the cladistic analyses in this study, the better treatment is to place *Schoenoides* back in *Oreobolus* as done by Goetghebeur (1998).

### **6.2.3f *Capeobolus***

Cladistic analyses of morphological data in this study (Chapter 4) indicated that *Capeobolus* did not group with either *Costularia* or *Tetraria* directly (Figs 4.1, 4.2). This result is consistent with Bruhl's (1995) findings and supports separating *Capeobolus* from *Costularia* or *Tetraria* as done by Browning and Gordon-Gray (1999).

### **6.2.4 Phylogenetic Relationships of *Carpha* and its Relatives**

Both phylogeny reconstructions for *Carpha* and its relatives, inferred from 94 morphological characters (Chapter 4) and estimated using molecular data (Chapter 5), failed to provide strong support for the relationships of *Carpha* with its relatives with one exception. The exception is *Trianoptiles*, which was sister to *Carpha* with 100% bootstrap and jackknife support in the molecular data analysis (Figs 5.1). The combined data and morphological data also confirmed that *Trianoptiles* has a close relationship with *Carpha* but in these *Trianoptiles* was sister to (Fig.6.2) or closer to (Figs 4.1, 4.2) *Asterochaete*.

*Gymnoschoenus* was grouped with *Cyathochaeta*, *Gahnia* and *Ptilothrix* in the cladistic analyses based on both the morphological data and the combined data. Although this is consistent with some previous studies (Bentham 1878; Kükenthal 1940a; Goetghebeur 1986; also see Chapter 4), there was no support (Figs 4.1, 4.2, 6.1). In contrast to the morphological and the combined analyses, the molecular analyses separated *Gymnoschoenus* from the well-supported clade formed by *Cyathochaeta*, *Gahnia* and *Ptilothrix* (93% bootstrap and 98% jackknife support), indicating *Gymnoschoenus* to be distant from the three genera. The latter result is supported by embryological data (Wilson 1981).

The weak support or no support for the clades of *Carpha* and its relatives in cladistic analyses based on both morphological and molecular data require study of other sources of data, such as other genes and embryo morphology, to re-evaluate and test these relationships.

### 6.2.5 Phylogenetic Relationships of species within *Carpha*

*Carpha* was separated into two clades, *Carpha sensu stricto* and *Asterochaete*, in the cladistic analyses of this study (Chapters 4, 5, 6). Within the *Carpha sensu stricto* clade, the sister relationship of *C. nivicola* and *C. rodwayi* was identified by all analyses (Chapters 4, 5, 6). The sister relationship of *C. alpina* and *C. curvata* was also identified by both cladistic analyses based on molecular data and on combined data, although analyses based on morphological data indicated that *C. curvata* is sister to the clade formed by *C. alpina*, *C. nivicola* and *C. rodwayi*. Cladistic analyses based on morphological data revealed the relationship of *C. schoenoides* as sister to the other four species in this clade.

The two data sets consistently failed to provide strong support for relationships within the *Asterochaete* clade. This lack of support for relationships within this clade requires the use of further sources of data, such as other genes and embryo ontogeny and form, to re-evaluate and test these relationships.

### 6.2.6 Some Species Limits within *Carpha*

As reviewed in Chapter 1, phenetic analysis has been recommended to study patterns of variation at lower taxonomic levels, i.e. species and below (Stevens 2000) where the relationships of the organisms of study may not be hierarchical (Davis and Nixon 1992; Doyle 1995; Olmstead 1995; Brower et al. 1996; Brower 1999).

Phenetic analyses (Chapter 3) in this study identified 16 species of *Carpha*. They are *C. alpina*, *C. curvata*, *C. nivicola*, *C. rodwayi*, *C. schoenoides*, *C. angustissima*, *C. borbonica*, *C. capitellata* (var. *capitellata* and var. *bracteosa*), *C. eminii*, *C. filifolia*, *C. glomerata*, *C. nitens*, *C. schlechteri*, and three new species (*C. cf. bracteosa*, *C. discolor* ms and *C. ulugurensis* ms) (also see Table 3.5). These species were placed in two clades by cladistic analyses (Chapters 4, 5, 6). As indicated before, the first five species formed

one clade, which is consistent with the definition of *Carpha sensu stricto* by Hooker (1860, 1867), Bentham (1878, 1883) and Wilson (1986, 1993, 1994a, 1994b), and will be kept in *Carpha*. All other species of *Carpha sensu lato* formed the other clade, which corresponds to *Asterochaete* Nees (Nees 1834; Kunth 1837; Steudel 1855; Levyns 1950), and will be transferred back to *Asterochaete*.

### 6.3 Review of *Carpha sensu lato*

*Carpha sensu lato* is separated into two genera, *Carpha sensu stricto* and *Asterochaete*, on the basis of the analyses presented in the previous chapters.

#### Key to *Carpha* and *Asterochaete*

- 1 Glumes all persistent; hypogynous bristles plumose; nut with obvious stalk ...1. *Carpha*  
 1\* Only lower sterile glumes persistent, upper fertile glumes deciduous; hypogynous  
 bristles antrorsely scabrous or lower-half plumose; nut sessile .....2. *Asterochaete*

#### 6.3.1 *Carpha* Banks et Sol. ex R.Br.

Perennial herbs with short rhizome. Culms erect, obtusangular-circular. Leaves basal and cauline. Inflorescence a panical with slender branches, spikelets forming 1–3 loosely obovoid or obconical to oblong clusters. Spikelets compressed; flowers in each spikelet 1–2, bisexual. Glumes 5–6(–7), distichous, the lower ones empty, about half the size of the upper glumes, the uppermost glume usually linear, empty; all glumes persistent. Hypogynous perianth consisting of 6 plumose bristles, which are more or less equal in length and fall with the nut. Stamens 3, rarely 2; anthers linear, yellow-green, with a conical apical appendage. Style slender, continuous with the ovary, persistent; stigmas 3. Nut trigonous, with stalk, reticulate or minutely punctulate on surface.

A genus of five species, found in Australia, New Guinea, New Zealand and South America. The lectotype species is *Carpha alpina* R.Br. (Koyama 1961).

### Key to species in *Carpha*

- 1 Spikelets 1-flowered; nut epidermis punctulate.
  - 2 Upper third of leaves conspicuously curled on drying; terminal flowering head loosely oblong to obconical; nut surface finely reticulate and punctulate .....2. *C. curvata*
  - 2\* Leaves straight throughout their length, tips only tending to curl on drying for some specimens of *C. alpina*; terminal flowering head loosely obconical; nut surface punctulate.
    - 3 Plants forming extensive mats; leaf-blades rigid; spikelets 2–6 in 1–3 clusters .....4. *C. rodwayi*
    - 3\* Plants tufted; leaf-blades not rigid, spikelets 8–30 in 3–5 clusters.
      - 4 Spikelets 13–18 mm long; nut 3.5–4.5 mm long, c. 1.2 mm diam.; hypogynous bristles 12–15 mm long; leaves 1.5–3 mm wide .....3. *C. nivicola*
      - 4\* Spikelets 8–12 mm long; nut 2.5–3.5 mm long, 0.8–1.0 mm diam.; hypogynous bristles 7–12 mm long; leaves 0.5–1.5 mm wide..... 1. *C. alpina*
- 1\* Spikelets 2-flowered; nut epidermis reticulate, not punctulate ..... 5. *C. schoenoides*

1. *Carpha alpina* R.Br., Prodr. Fl. Nov. Holl. 230 (1810); Kunth, Enum. Pl. 2: 322 (1837); Hooker f., Fl. Nov. Zeland. 1: 273 (1853), Fl. Tasm. 2: 84 (1860), Handb. N. Zeal. Fl. 299 (1867); Steudel, Synops. Cyper. 159 (1855); Boeckeler, Linnaea 38: 269 (1874); Bentham, Fl. Austral. 7: 381 (1878), *p.p.*; Clarke, Illustr. Cyp. t. LXXVI, figs 1–4 (1909); Pfeiffer, Feddes Repert. 29: 178 (1931), *p.p.*; Kükenthal, Feddes Repert. 47: 112 (1939), *p.p.*; Blake, J. Arnold Arboretum 29: 94 (1948); Hamlin, Tuatara 6: 36 (1956); Edgar, Fl. New Zealand 2: 199–200 (1970); Kern, Fl. Malesiana 7: 666 (1974); Costin et al., Kosciusko Alpine Fl. 141 (1979); Thompson, Telopea 2: 245 (1981); Thompson and Gray, Telopea 2: 310 (1981); Wilson, Fl. New South Wales 4: 307 (1993), Fl. Victoria 2: 259 (1994); Curtis and Morris, Student's Flora of Tasmania 4B: 87 (1994). — *Chaetospora alpina* (R.Br.) F.Muell., Fragm. 9: 39 (1875), *p.p.*

Type citation: 'D'.

Type: Australia: Tasmania: on the summit of Table Mt [now called Mt Wellington], near the Derwent River, *R. Brown* (*Bennett 6020*), Mar.–Apr. 1804. The syntypes of this species are currently housed in BM (three sheets), K and MEL; also sheets in G

(n.v.), FI–Webb (n.v.), and P (n.v.) (seen by K. Wilson 2002, pers. comm.). Because BM houses Brown's main collection, the best specimen there, BM 000092170, with collecting tag of R. Brown and Bennett's label, is chosen as lectotype here. Isolectotypes: BM, K, MEL 49294, G (n.v.), FI–Webb (n.v.), and P (n.v.).

*C. tasmanica* Gand., Bull. Soc. Bot. France 66: 297 (1919).

Type citation: 'Tasmania, in m. Wellington (*Lucas!*)'.

Type: Australia: Tasmania: Mt Wellington, *Lucas s.n.*, Jan. 1901; holotype: ?LY, n.v.; isotype: NSW 120927 (McGillivray 1973).

*C. novae-zelandiae* Gand., Bull. Soc. Bot. France 66: 297 (1919).

Type citation: 'Nova Zelandia, in Maungatua (*Thomson!*)'.

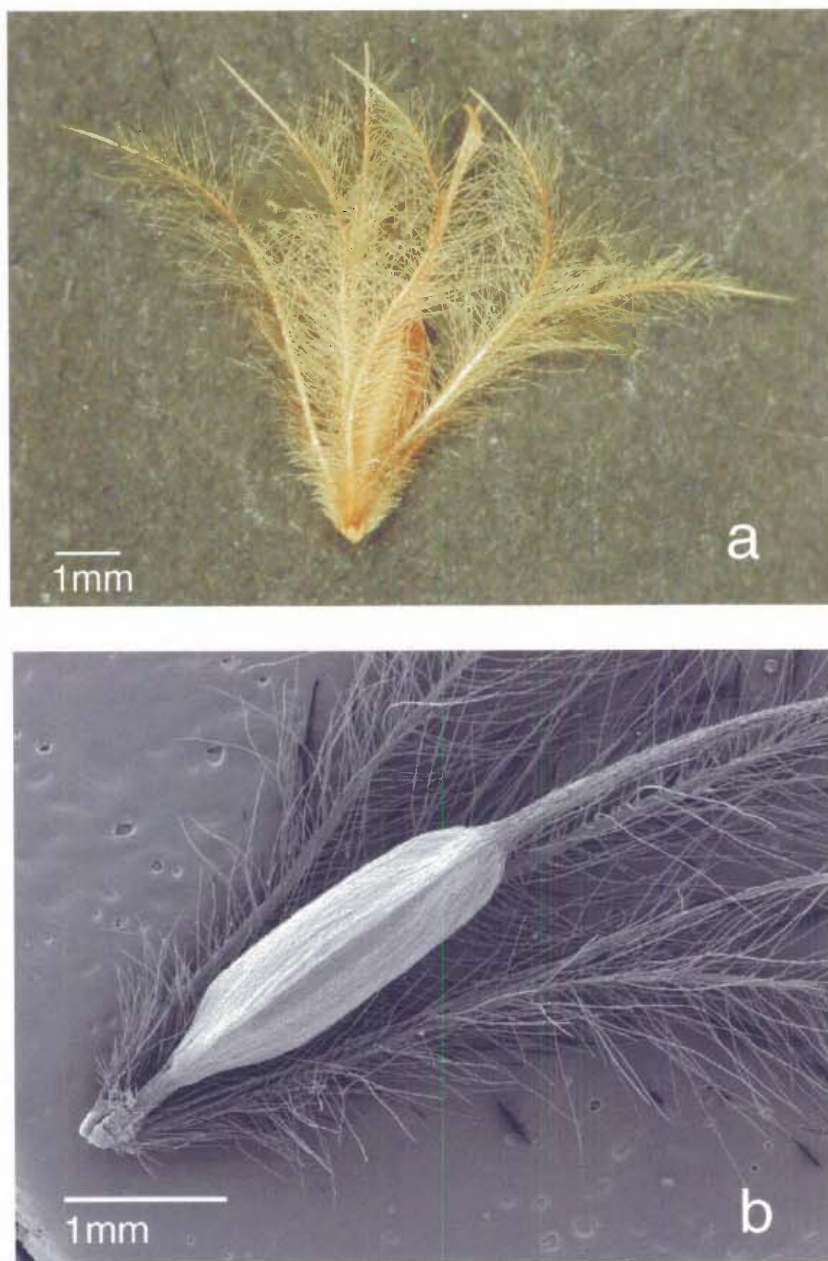
Type: New Zealand: Maungatua, *Thomson s.n.*; holotype: ?LY, n.v.

See Edgar (1970), Kern (1974) and Wilson (1993, 1994a) for descriptions of this species. (Figs 6.2, 6.3 a; also Fig 2.2 b (rarely f) for spikelet structure).

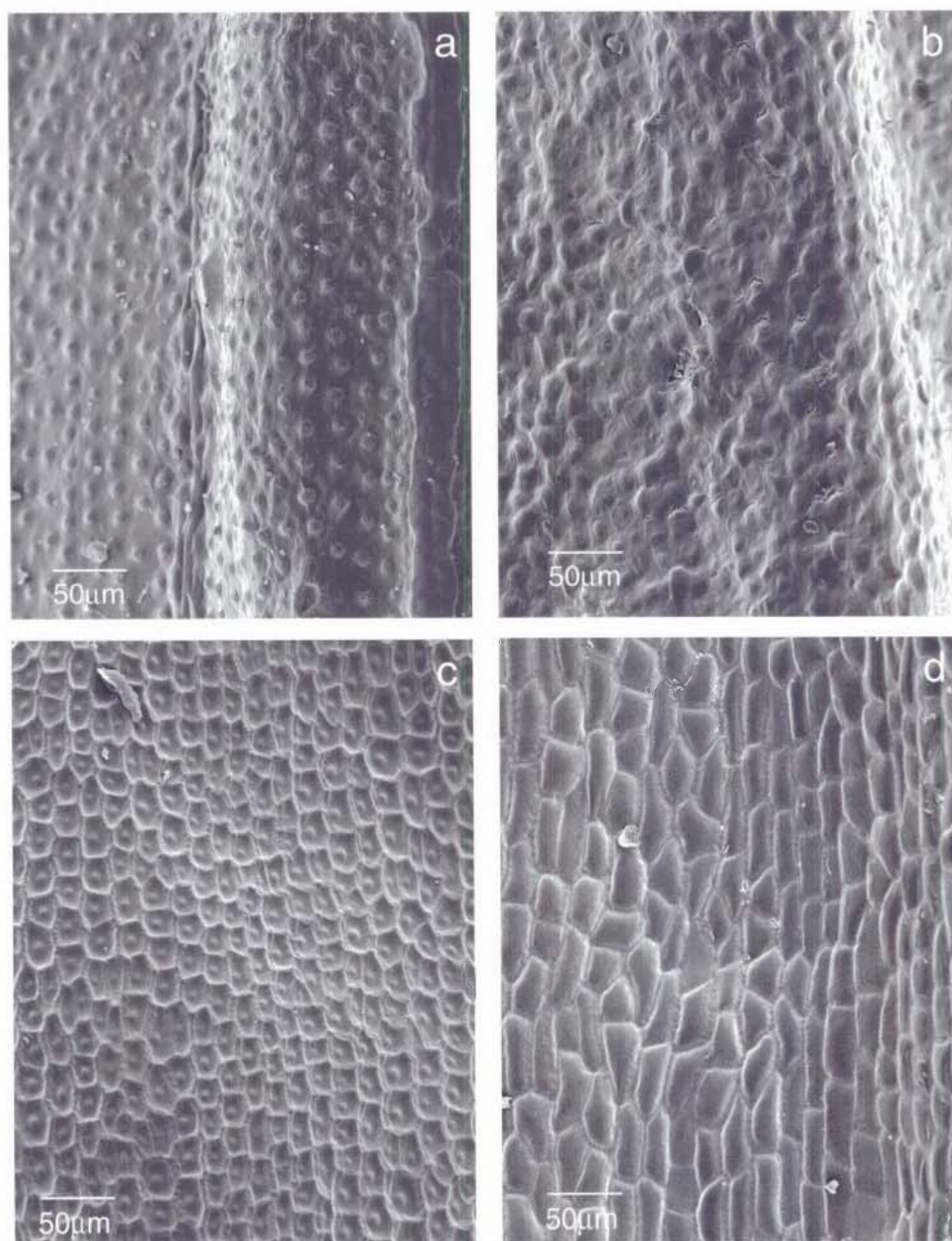
In bogs, fens and other wet alpine and subalpine areas. In Australia (NSW, Vic. and Tas.), New Zealand, and New Guinea.

2. *Carpha curvata* W.M.Curtis, Brunonia 7(2): 303 (1984); Curtis and Morris, Student's Flora of Tasmania 4B: 88 (1994).

Type citation: 'Holotypus: *J. & M. Davies s.n.*, Eliza plateau, South-west National Park, east of Lake Pedder, 25. i. 1982, HO 49444: isotype: NSW.'



**Fig. 6.2.** *Carpha alpina* (MEL 49294). **a**, Micrograph of fruit with perianth, showing six plumose bristles more or less equal in length. **b**, SEM micrograph of a fruit similar to that in Fig. 6.2 a with three bristles removed to show fruit with stalk.



**Fig. 6.3.** SEM micrographs of fruit epidermis. **a**, *Carpha alpina* (MEL 49294). Epidermis punctulate. **b**, *C. nivicola* (MEL 649163). Epidermis punctulate. **c**, *Carpha curvata* (HO 53801). Epidermis reticulate and punctulate. **d**, *C. schoenoides* (W. J. Eyerdam 10586A, NY). Epidermis reticulate.



Type: Australia: Tasmania: Eliza Plateau, South-west National Park, east of Lake Pedder, J. & M. Davies s.n., 25 Jan. 1982; holotype: HO 49444, n.v.; isotype: NSW.

See Curtis (1984) for a description of this species. (Fig. 6.3 c; also see Figs 2.2 b, 2.3 a for spikelet structure).

On mountain slopes, and mudstone streamsides in shrubby heathland. Only in Tasmania, Australia.

3. *Carpha nivicola* F.Muell., Defin. Austral. Pl. 34 (1855), Trans. Phil. Soc. Victoria 1: 111 (1855); Blake, Proc. Roy. Soc. Queensland 51: 48 (1940); Costin et al., Kosciusko Alpine Fl. 140 (1979); Thompson, Telopea 2: 245 (1981); Thompson and Gray, Telopea 2: 311 (1981); Wilson, Fl. New South Wales 4: 307 (1993), Fl. Victoria 2: 259 (1994), Telopea 5 (4): 592 (1994). — *Chaetospora alpina* (R.Br.) F.Muell., Fragm. 9: 39 (1875), p.p. — *Carpha alpina*, Bentham, Fl. Austral. 7: 381 (1878), p.p.; Pfeiffer, Feddes Repert. 29: 178 (1931), p.p.; Kükenthal, Feddes Repert. 47: 112 (1939), p.p.

Type citation: ‘On the highest summits of the Australian Alps, near swamps.’

Type: Australia: New South Wales: Southern Tablelands: Australian Alps, F. Mueller, 1853; holotype: MEL, n.v., seen and labelled by K. Wilson (2002, pers. comm.); isotype: MEL, n.v., seen by K. Wilson (2002, pers. comm.).

*C. alpina* var. *subacaulis* Kük., Feddes Repert. 47: 113 (1939).

Type citation: ‘Neu-Süd-Wales: Mt Kosciusko, Baumgrenze bis 7000’, I. 1899 (J. H. Maiden!).’

Type: Australia: New South Wales: Southern Tablelands: Mt Kosciuszko, Baumgrenze [tree-line] bis 7000 ft, J. H. Maiden 4, Jan. 1899; holotype: B, n.v., seen by K. Wilson (2002, pers. comm.); isotype: NSW.

See Wilson (1993, 1994a) for a description of this species. (Fig 6.3 b; also see Figs 2.2 b for spikelet structure).

In bogs, fens and other wet subalpine areas. Only in NSW and Victoria, Australia.

Notes: Mueller (1875) included his new species *Carpha nivicola* in *C. alpina* twenty years after he published *C. nivicola*. This was accepted by some subsequent authors (Bentham 1878; Pfeiffer 1931; Kükenthal 1939c). However, some other authors (Blake 1940; Costin et al. 1979; Thompson 1981; Thompson and Gray 1981; Wilson 1993, 1994a, 1994b) regarded *Carpha nivicola* as being separate from *C. alpina*. This study (see Chapter 3) indicates that *Carpha nivicola* should be treated as a species. *Carpha nivicola* differs from *C. alpina* in having larger spikelets, flowers and nuts, and wider leaves.

4. *Carpha rodwayi* W.M. Curtis, *Brunonia* 7(2): 302 (1984); Curtis and Morris, *Student's Flora of Tasmania* 4B: 88 (1994).

Type citation: 'Holotypus: *J. Davies s.n.*, Eliza plateau, south-west Tasmania, 4. ii. 1982, HO 53808.'

Type: Australia: South-west Tasmania: Eliza Plateau, *J. Davies s.n.*, 4 Feb. 1982; holotype: HO 53808, n.v.; isotype: NSW.

See Curtis (1984) for a description of this species. (See Figs 2.2 b for spikelet structure).

On mountains, at the margins of alpine and subalpine pools and in permanently wet areas. Only in Tasmania, Australia.

5. *Carpha schoenoides* Banks et Sol. ex Hook.f., *Fl. Antarct.* 362. t. 148 (1847); Steudel, *Synops. Cyper.* 160 (1855). — *Carpha alpina*, Phillipi, *Catal. Pl. Chilens.* 306 (1881); Clarke, *Bot. Jahrb.* 30: 40 (1901); Pfeiffer, *Feddes Repert.* 29: 178 (1931), *p.p.*; Gunckel, *Annales del Museo de Historia Natural Valparaiso* 4, 28 (1971); Moore, *Fl. Tierra del Fuego* 329 (1983). — *Carpha alpina* R.Br. var. *schoenoides* (Banks et Sol. ex Hook.f.) Kük., *Feddes Repert.* 47: 113 (1939); Barros, *Fl. Patagonica* 2: 56 (1969).

Type citation: 'Southern parts of Tierra del Fuego; Good Success Bay, *Banks & Solander*; Hermite Island, Cape Horn, *J. D. H.*'

Type: *Banks & Solander*, Tierra del Fuego, Jan. 1769 (BM 000092178), is chosen as lectotype here. This was chosen as lectotype because it is the only extant specimen collected by Banks and Solander, who proposed the name for the species.

The other syntype, *J. D. Hooker*, Hermite Island, Cape Horn, 1839–1843 (BM 000092175) is on a sheet with two other plants collected from a different locality (Cord Pelade Valdivia).

See Hooker (1847) for a description of this species. (Fig 6.3 d; also see Figs 2.2 m or p, f or i for spikelet structure).

On stream edges, open ground, or along forest roads. Only occurring in South America (Chile and Argentina).

Notes: After *Carpha schoenoides* was described by Hooker (1847, p. 362, t. 148), it was synonymised with *C. alpina* by Philippi (1881), who was followed in this by Clarke (1901), Pfeiffer (1931), Gunckel (1971) and Moore (1983). Later, Kükenthal (1939c) treated it as a variety of *C. alpina* and was followed in this by Barros (1969). This study (Chapter 3) shows that *C. schoenoides* should be treated as a species. This species is different from *C. alpina* in having two flowers in each spikelet, both developing nuts which have an epidermis that is not punctulate (Table 3.3; Fig. 6.3 d). This species is disjunct from other species of *Carpha*.

### 6.3.2 *Asterochaete* Nees

Perennial herbs with short rhizome. Culms erect, obtusangular-circular to triangular. Leaves basal and cauline. Inflorescence a narrow panicle with slender branches, spikelets loosely arranged to densely clustered. Spikelets compressed, flowers in each spikelet 1–2, bisexual, lower flower male in *A. schlechteri*. Glumes 4–6(–7), distichous, the lower ones empty, about half the length of the upper glumes, the uppermost glume sometimes linear, empty; lower sterile glumes persistent. Hypogynous perianth consisting of 6 bristles, which are antrorsely scabrous or plumose in the lower half, and usually with the inner whorl much longer than the outer whorl, usually falling with the nut. Stamens 3; anthers yellow-

green, with a pyramidal to conical apical appendage. Style slender, continuous with the ovary, persistent; stigmas 3. Nut trigonous, sessile, reticulate sometimes punctulate.

A genus of eleven species, found in Africa, Madagascar and Réunion. The type species is *Asterochaete glomerata* (Thunb.) Nees.

### Key to species in *Asterochaete*

- 1 Glumes green to yellow-green; hypogynous bristles antrorsely scabrous or sometimes the bristles in the inner whorl compressed in the lower half with short hairs along the margins and the upper half antrorsely scabrous; leaves not trigonous in cross-section and not curling.
  - 2 Spikelets in dense ovoid heads.
    - 3 Plants large, 80–300 cm high; heads of spikelets numerous in a large oblong panicle; leaves 5–28 mm wide; culm trigonous in cross-section.
      - 4 Spikelets with two bisexual flowers; ‘rachilla’ elongated above proximal fertile node..... 8. *A. glomerata*
      - 4\* Spikelets with two flowers, one male flower below the bisexual flower; ‘rachilla’ not elongated above proximal fertile node..... 10. *A. schlechteri*
    - 3\* Plants small, less than 70 cm high; heads of spikelets few; leaves 2–4 (–5) mm wide; culm obtusangular-circular in cross-section .....4. *A. capitellata*
    - 5 Bracts at the base of heads of spikelets not conspicuous, lanceolate, narrow at base .....4a. *A. capitellata* var. *capitellata*
    - 5\* Bracts at the base of heads of spikelets conspicuous, ovate or subcordate at the base, sheathing heads of spikelets..... 4b. *A. capitellata* var. *bracteosa*
  - 2\* Spikelets in dense oblong to obconical heads, or loosely arranged.
    - 6 Spikelets in densely clustered oblong or obconical heads.
      - 7 Leaf blade thickly crescentiform or circular in cross-section.
        - 8 Involucral bracts (including bracts to the heads of spikelets) leaf-like; spikelets in one very dense obconical head (rarely two heads); leaves filiform, 0.5–0.8 mm diam.; nuts 3.5–4.3 mm long ..... 7. *A. filifolia*

- 8\* Involucral bracts (including bracts to the heads of spikelets) with enlarged bases sheathing the heads of spikelets; spikelets in one or few oblong heads; leaves 1.5–2.5 mm wide; nuts 2.8–3.5 mm long .....1. *A. acuminata*
- 7\* Leaf blade V-shaped or thinly crescentiform or flat in cross-section.
9. Leaf blade V-shaped in cross-section, keeled, 1.7–5.5 mm wide  
.....11. *A. ulugurensis*
- 9\* Leaf blade thinly crescentiform or flat in cross-section, not keeled, 0.9–1.1 mm wide.....3. *A. borbonica*
- 6\* Spikelets loosely arranged.
- 10 Nut surface irregularly reticulate; lower part of bristles in inner whorl compressed and with short hairs along the margins, and upper half antrorsely scabrous, bristles in outer whorl antrorsely scabrous.
- 11 Spikelets 1-flowered; ‘rachilla’ not elongated above fertile glumes and not adnate to the fertile glume base; leaf blade V-shaped in cross-section, 1.6–4.8 mm wide.....6. *A. eminii*
- 11\* Spikelets 2-flowered or sometimes both 1-flowered and 2-flowered spikelets can be found in same plant; ‘rachilla’ elongated above fertile glumes and adnate to the fertile glume base; leaf blade usually thinly crescentiform in cross-section, 0.7–1.6 mm wide .....2. *A. angustissima*
- 10\* Nut surface regularly reticulate; all bristles antrorsely scabrous.....9. *A. nitens*
- 1\* Glumes mainly red to dark red, but white at base and on margins; the lower half of hypogynous bristles plumose, the upper half of hypogynous bristles antrorsely scabrous; leaves trigonous in cross-section and older leaves curling .....5. *A. discolor*

1. *Asterochaete acuminata* X.F.Zhang, **sp. nov.**

Planta forma *A. capitellata* Nees var. *capitellata* et *A. capitellata* Nees var. *bracteosa* (C.B.Clarke) X.F.Zhang simulans sed in characteribus foliorum, bracteolarum et inflorescentiarum differt. Folia crassa canaliculata ecarinata. Bracteolae basi dilatatae ovatae, inflorescentia vel capitula superantes 2–10 cm. Spiculae in oblongas dispositae, non in capitula ovata dense congestae.

Type: South Africa: Eastern Cape: Hogsback, alt. 1700 m, B. Sonnenberg 301, 24 Nov. 1994; holotype: NU; isotype: NE 66170. (Fig 6.4).

Erect perennial, 35–70 cm high. Rhizome short. Culms erect, striate, single-noded, the node bearing a single leaf, rarely nodeless. Leaves crowded at the base of the culms; blades straight, 32–58 cm long, 1.5–2.5 mm wide; proximal half thickly concave, thickly crescentiform in cross-section; distal half nearly terete or with adaxial surface shallowly, thickly crescentiform or subcircular-circular in cross-section. Inflorescence with several short internodes; spikelets in one or few oblong heads. Bracts several, enlarged at the base, with a long acuminate apex, overtopping the heads of the spikelets by 2–10 cm. Spikelets 6–8 mm long, composed of 5–6 distichously arranged glumes; lowest 3–4 glumes empty, persistent, shorter than the upper two; the upper two fertile, deciduous; ‘rachilla’ elongated above proximal fertile glume and adnate to the base of the proximal fertile glume. Flowers 2, bisexual. Bristles 6, scabrous, usually not or slightly overtopping nut, in two whorls, outer 3 bristles shorter than inner 3. Stamens 3; anthers 2.0–2.7 mm long, yellow-green, with apical appendage 0.1–0.3 mm long, 0.1 mm wide. Style branches 3; style base 0.9–1.9 mm long, 0.15–0.2 mm wide. Nuts 2, ellipsoid, trigonous in cross-section, 2.8–3.5 mm long, 0.9–1.1 mm diam., brown at maturity, surface reticulate and punctulate. (Also see Figs 3.11, 3.12, 2.2 k).

In mountain grassland, in marshes or on river banks, 1300–1700 m. In Eastern Cape Province, South Africa.

Etymology: the specific epithet reflects the shape of bracts, which are ovate at the base and tapering gradually to the apex, one of the key distinguishing features of this species.

Notes: As indicated in Chapter 3, two specimens of this species, *MacOwan 1616, 2187* (Figs 3.11, 3.12), were cited as *Carpha bracteosa* by Clarke (1894, 1897–1898). More recent specimens of this species were also identified as *C. bracteosa* by other workers. These specimens were temporarily named as *Carpha* cf. *bracteosa* previously in this thesis. *Asterochaete acuminata* resembles *A. capitellata* var. *bracteosa* and *A. capitellata* var. *capitellata*, but differs in characters of the leaves, bracts and inflorescence. Its leaves are thick, canaliculate, without a keel. Bracts are ovate at the base with a long acuminate apex, 2–10 cm longer than the inflorescence or heads of spikelets. Spikelets are in one or few oblong heads rather than in ovoid heads. The nut surface is reticulate and punctulate.



Fig. 6.4. Holotype of *Asterochaete acuminata* (B. Sonenberg 301, NU).

2. *Asterochaete angustissima* (Cherm.) X.F.Zhang, **comb. nov.**

**Basionym:** *Carpha angustissima* Cherm., Bull. Soc. Bot. France 82: 341 (1935).

Haines & Lye, Sedges and Rushes of East Africa 322 (1983). — *C. eminii* (K.Schum.) C.B.Clarke var. *angustissima* (Cherm.) Kük., Feddes Repert. 47: 210 (1939); Napper, J. E. African National Historical Society 24: 38 (1964).

Type citation: ‘Massif du Kahuzi (O. du lac Kivu), 2400 m, février 1929 (Humbert 7722); volcan Karisimbi (NE. du lac Kivu), 3300 m., juin 1929 (H. Humbert 8586).’

Type: Zaire: Massif du Kahuzi (W. du Lac Kivu), 2400m, *H. Humbert* 7722, Feb. 1929, (B 100000960; B 100000961; ?P, n.v.; ?STR, n.v.); Volcan Karisimbi (Au N.-E. du lac Kivu), 3300m, *H. Humbert* 8586, June 1929 (B 100000959; NSW; ?P, n.v.; ?STR, n.v.).

Because Chermeson’s herbarium is either in STR or P, choosing a lectotype for this species should wait until all specimens of this species in STR or P are examined.

For description, see the descriptions of *Carpha angustissima* by Chermeson (1935) and Haines and Lye (1983). (Also see Fig 2.2 k (rarely e) for spikelet structure).

In alpine bogs. On Mt Mgahinga-Muhavura, Kigezi, Uganda and also in adjacent parts of Rwanda and Zaire.

Notes: *Asterochaete angustissima* was previously treated either as a species of *Carpha* (Chermeson 1935; Haines and Lye 1983) or as a variety of *C. eminii* (= *Asterochaete eminii*) (Kükenthal 1939d; Napper 1964). This study indicates (Chapter 3) that it should be a species rather than a variety of *A. eminii*. This species differs from *A. eminii* by usually having two flowers in each spikelet with the ‘rachilla’ elongated above the proximal fertile glume and adnate to the fertile glume base, and with the leaf blade narrow and usually thinly crescentiform in cross-section (Table 3.4).



3. *Asterochaete borbonica* (Steud.) X.F.Zhang, **comb. nov.**

**Basionym:** *Elynanthus borbonicus* Steud., Synops. Cyper. 155 (1855) (as *E.? borbonicus*).

*Carpha borbonica* (Steud.) C.B.Clarke in Durand & Schinz, Consp. Fl. Afr. 5: 655 (1894); Pfeiffer, Feddes Repert. 29: 179 (1931); Kükenthal, Feddes Repert. 47: 119 (1939).

Type citation: ‘Ins. Borbonia’.

Type: Réunion: ?P, n.v.; Insel Bourbon, *Boivin 999* (B 100000966, only glumes and fruits. These fragments were apparently removed by Kükenthal from the main type collection for examination during his work on this group. Its label is in Kükenthal’s script. It is best treated as an isotype).

For description, see the description of *Carpha borbonica* by Kükenthal (1939c). (Also see Fig 2.2 e, k for spikelet structure).

Only in Réunion.

4. *Asterochaete capitellata* Nees, [Linnaea 9: 300 (1834) (nomen nudum)], Linnaea 10: 194 (1835); Kunth, Enum. Pl. 2: 312 (1837); Steudel, Synops. Cyper. 155 (1855); Levyns, Fl. Cape Peninsula 119 (1950). — *Carpha capitellata* (Nees) Boeck., Linnaea 38: 266 (1874); Clarke in Durand and Schinz, Consp. Fl. Afr. 5: 656 (1894), in Dyer, Fl. Capens. 7: 270 (1898), Illustr. Cyp. t. LXXVI, fig. 2 (1909); Pfeiffer, Feddes Repert. 29: 179 (1931); Kükenthal, Feddes Repert. 47: 116 (1939); Reid & Arnold, Bothalia 15: 141–142 (1984).

Type citation: ‘In Cap. b. Sp. Forbes in Herb. Lindleyii; e districtu Zwellendam Herb. Eckl.’

Type: South Africa: Cape of Good Hope, Forbes in herb. Lindley (syntype: ?CGE, n.v.); Zwellendam district, herb. Ecklon (syntype: ?B, ?CGE, ?LE, ?M; n.v.).

*A. tenuis* Kunth, Enum. Pl. 2: 312 (1837); Steudel, Synops. Cyper. 155 (1855).

Type citation: ‘Cap. b. Spei.’ [= Caput Bonae Spei].

Type: South Africa: Cape of Good Hope: Zuurberg Range, Alexandria Div., 2000–3000, *Drège 1840* (K, two sheets).

*Carpha perrieri* Cherm. **synon. nov.**, Bull. Soc. Bot. France 69: 721 (1922), Catal. Pl. Madag. 39 (1931), Mem. Acad. Malgache 10: 39 (1931), Arch. Bot. 7(2): 76 (1936), in Humbert, Fl. Madag. 29: 231 (1937); Pfeiffer, Feddes Repert. 29: 179 (1931); Kükenthal, Feddes Repert. 47: 117 (1939).

Type citation: ‘Massif d'Andringitra (*Perrier de la Bâthie, 14555*).’

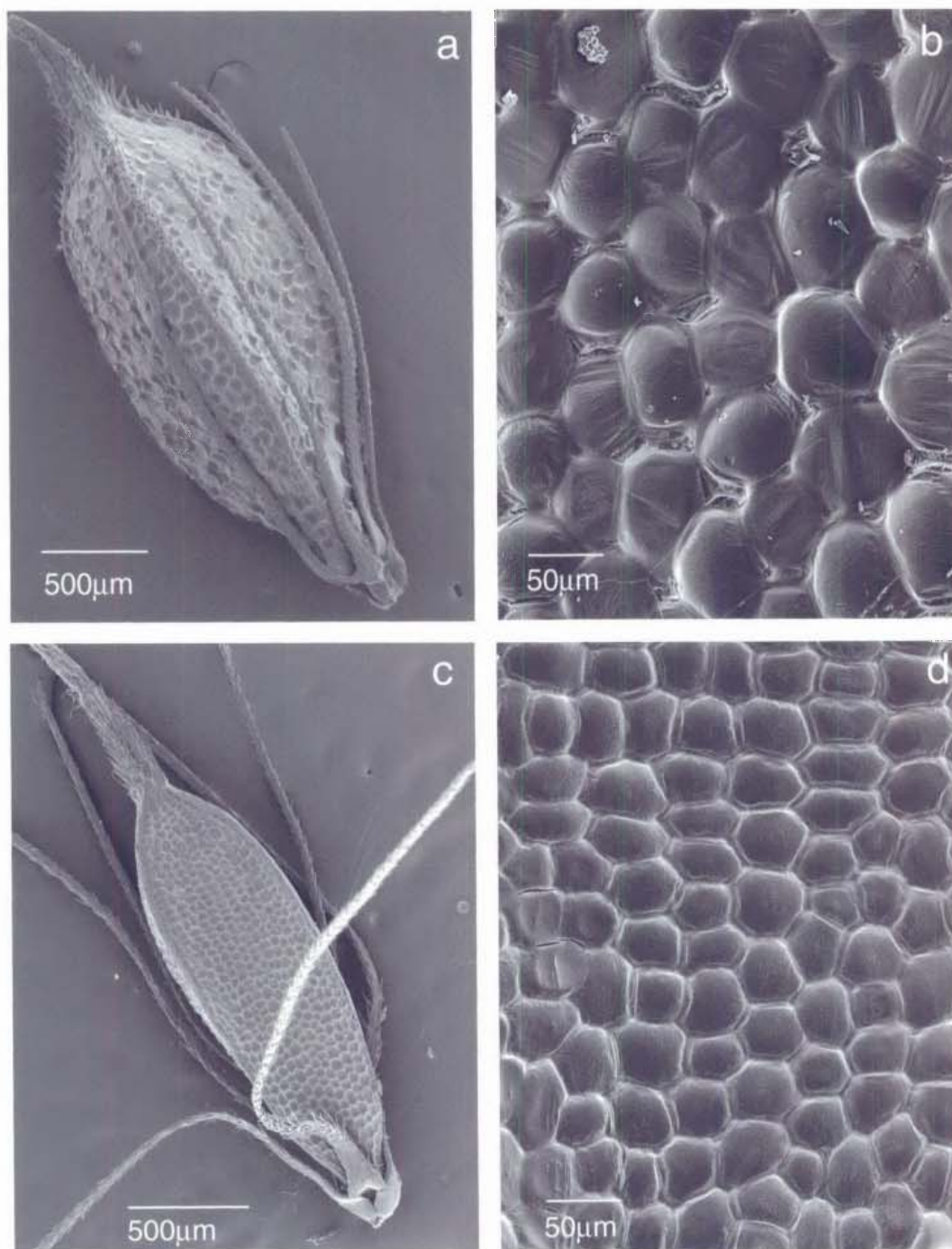
Type: Madagascar: Massif d'Andringitra, *Perrier de la Bâthie 14555*, Feb. 1922; holotype: P 00199383; isotypes: B 100000969, K, NSW, P 00199384.

Erect perennial, 31–70 cm high. Rhizome short. Culms erect, striate, 1–2 nodes, each node bearing a single leaf, rarely nodeless. Leaves crowded at the base of the culms; blades straight, 16–36 cm long, 1.5–7 mm wide, V-shaped in cross-section. Inflorescence with several short internodes; spikelets in a few (2–8) ovoid heads. Bracts several, leaf-like or ovate, the same length as or slightly longer than the heads of spikelets. Spikelets 5–7.5 mm long, composed of 5 (rarely 4) distichously arranged glumes; lowest 3 (rarely 2) glumes empty, persistent, shorter than the upper two; the upper two usually fertile (but the uppermost one sometimes sterile), deciduous; ‘rachilla’ elongated above proximal fertile glume and adnate to the base of the proximal fertile glume. Flower(s) 1–2, bisexual. Bristles 6, scabrous, usually not or slightly overtopping nut, in two whorls, outer 3 bristles shorter than inner 3. Stamens 3; anthers 2.0–2.9 mm long, yellow-green, with apical appendage 0.1–0.3 mm long, c. 0.1 mm wide. Style branches 3; style base 0.3–1.0 mm long, 0.15–0.3 mm wide. Nut(s) 1–2, ellipsoid, trigonous in cross-section, 2.0–2.7 mm long, 0.8–1.4 mm diam., brown at maturity, surface reticulate. (Figs 6.5, 6.6 a, b; also see Fig 2.2 e, k, 2.5 d, e, 2.6 a for spikelet structure).

In marshy places, flats and lower slopes, 0–1960 m. In South Africa, Zimbabwe and Madagascar.



**Fig. 6.5.** A specimen of *Asterochaete capitellata* (Drège [1840], K). A syntype of *Asterochaete tenuis*.



**Fig. 6.6.** SEM micrographs of fruit and fruit epidermis. **a** and **b**, *Asterochaete capitellata* (Levyns 8391, K). **a**, Fruit with six scabrous bristles, showing bristles not overtopping nut and bristles in outside whorl shorter than those in inside whorl. **b**, Reticulate fruit epidermis. **c** and **d**, *Asterochaete ulugurensis* (C. Barclay 1251, K). **c**, Fruit with six scabrous bristles, showing bristles much longer than nut. **d**, Reticulate fruit epidermis.

Notes: *Carpha perrieri* was described by Chermезon (1922) from Madagascar. He regarded it as close to *C. capitellata* but differing from *C. capitellata* by its slightly bigger glumes, its longer hypogynous bristles, its larger style base, and its narrower nut. This study found that glume, hypogynous bristle and style base length and nut diameter of *C. perrieri* overlap with those of *C. capitellata* (Table 3.5). Specimens of the two species grouped together in the analyses, and *C. perrieri* does not have any unique characters to differentiate it from *C. capitellata*; i.e. *C. perrieri* should be included in *C. capitellata*.

4a. *Asterochaete capitellata* Nees var. *capitellata*

In Cape Province of South Africa and Madagascar.

4b. *Asterochaete capitellata* Nees var. *bracteosa* (C.B.Clarke) X.F.Zhang, **comb. nov.**

**Basionym:** *Carpha bracteosa* C.B.Clarke in Durand and Schinz, Consp. Fl. Afr. 5: 656 (1894).

Clarke in Dyer, Fl. Capens. 7: 270 (1898), in Wildem., Pl. Nov. Hort. Thenensis 39, t. 10 (1904); Pfeiffer, Feddes Repert. 29: 179 (1931); Reid & Arnold, Bothalia 15: 141–142 (1984). — *Carpha capitellata* (Nees) Boeck. var. *bracteosa* (C.B.Clarke) Kük., Feddes Repert. 47: 117 (1939).

Type citation: ‘Afr. Austr.: colonie du Cap, Bolus 2867, MacOwan 1616, 2187.’

Type: South Africa: Cape Province: Worcester Div., *Bolus 2867*, 1873; lectotype, selected here, K.

*MacOwan 1616, 2187* are now regarded as belonging to the new species *Asterochaete acuminata*.

In Cape Province of South Africa.

Notes: When Clarke (1894) published his new species *C. bracteosa*, he cited three specimens (*Bolus 2867*, *MacOwan 1616*, *2187*). The syntype *Bolus 2867* (see Figs 3.10) is selected as lectotype here. The other two syntypes *MacOwan 1616*, *2187* (see Figs 3.11, 3.12) are considered to belong to the new species *Asterochaete acuminata*. *Asterochaete capitellata* var. *bracteosa* differs from *A. acuminata* in having leaves with a keel, V-shaped in cross-section, ovate bracts more or less equal in length to the head of spikelets, spikelets in ovoid heads, and the nut surface reticulate.

*Carpha bracteosa* was treated as a variety of *C. capitellata* by Kükenthal (1939c) or as conspecific with *C. capitellata* by Levyns (1950), while other authors (Clarke 1894, 1897–1898, 1904; Pfeiffer 1931; Reid and Arnold 1984; Browning and Guthrie 1994) recognized it as a species. In the phenetic analyses in this study, the specimens of *C. bracteosa* and *C. capitellata* always formed a group, but the specimens of *C. bracteosa* formed a subgroup (Chapter 3). The results suggest that *C. bracteosa* is not a separate species from *C. capitellata*, but that it is slightly different from typical *C. capitellata*. They have a similar distribution and occur in the same habitat. Therefore, *C. bracteosa* should be treated as a variety of *Asterochaete capitellata*. *Asterochaete capitellata* var. *bracteosa* differs from var. *capitellata* by having ovate bracts rather than leaf-like bracts (Figs 3.10, 6.5).

5. *Asterochaete discolor* T.H.Arnold ex X.F.Zhang, **sp. nov.**

Planta *A. capitellatae* Nees et *A. glomeratae* Nees in structura inflorescentiarum, spicularum et florum simulans, sed in characteribus foliorum, squamarum coloribus et setis hypogynis differt. Folia trigona, conspicue crispa. Squamae discoloria. Setae hypogynae in dimidio distali antrorse scabrae, in dimidio proximali plumosae.

Type: South Africa: Cape Province: Worcester Div.: damp cliff face below shale band E. side of Milner Pk., Hex River Mts, alt. 4500 ft, *E. Esterhuysen 14866*, 18 Dec. 1948; holotype: K; isotype: BOL 63171, K. (Fig. 6.7).



Fig. 6.7. Holotype of *Asterochaete discolor* (E. Esterhuysen 14866, K). The insert is a micrograph of a nearly mature nut with six bristles from this holotype.

Erect perennial c. 35 cm high. Rhizome short. Culms erect, nodeless, obtusangular-circular in cross-section. Leaves basal, curling, triangular in cross-section, up to 20 cm long, 1.6 mm wide. Inflorescence to 15 cm long, with several (usually 2) nodes; composed of a few ovoid heads of densely arranged spikelets. Bracts leaf-like, up to 8 cm long, 1 cm wide. Spikelet compressed, c. 10 mm long, composed of 6 distichously arranged glumes; glumes bicolorous, mainly red to dark red in colour, but white at base and on margins; lowest 4 glumes empty, shorter than the upper two; the upper two fertile; 'rachilla' not elongated above proximal fertile glume and not adnate to the base of the proximal fertile glume. Flowers 2, bisexual. Bristles 6, much longer than nut, lower-half plumose, upper-half antrorsely scabrous, in two whorls, outer 3 bristles shorter than inner 3. Stamens 3; anthers yellow-green, 3.7 mm long, with apical appendage linear-acuminate, c. 0.3 mm long, c. 0.1 mm wide. Style branches 3. Nut (only seen immature) trigonous in cross-section, sessile.

Etymology: the specific epithet is from the manuscript name written on the type (K, two sheets) by T. H. Arnold. It reflects the bicoloured glumes, one of the key distinguishing features of this species.

Notes: This species resembles *Asterochaete capitellata* and *A. glomerata* in the structure of the inflorescence, spikelets and flowers, but differs in its leaves, the colour of its glumes, and its hypogynous bristles. Its leaves are trigonous in cross-section and old leaves curl. Glumes are bicolorous in this species. Its hypogynous bristles are plumose in the lower half, and antrorsely scabrous in the upper half.

6. *Asterochaete eminii* (K.Schum.) X.F.Zhang, **comb. nov.**

**Basionym:** *Oreograstis eminii* K.Schum. in A. Engler (ed.), Ost-Afrikas und der Nachbargebiete C, 127 (1895).

*Carpha eminii* (K.Schum.) C.B.Clarke in Thiselton-Dyer, Fl. Trop. Afr. 8: 483 (1902); Pfeiffer, Feddes Repert. 29: 179 (1931) 179; Napper, J. E. African National Historical Society 24: 38 (1964); Kükenthal, Feddes Repert. 47: 210 (1939); Haines & Lye, Sedges and Rushes of East Africa 321 (1983).



Type citation: 'R. bei 3100 m. — Stuhl. 2439'.

Type: Uganda: Ruwenzori Mountains, 3100 m, *Stuhlmann 2439*, 13 Jul. 1891 (B 10000975, only fragments of spikelets. These fragments were apparently removed by Kükenthal from the main type collection for examination during his work on this group. Its label is in Kükenthal's script. It is best treated as an isotype).

For description, see the description of *Carpha eminii* by Haines and Lye (1983). (See Fig 2.2 a, b for spikelet structure).

In mountain-bogs. In the Ruwenzori Mountains, Uganda.

7. *Asterochaete filifolia* (Reid & T.H.Arnold) X.F.Zhang, **comb. nov.**

**Basionym:** *Carpha filifolia* Reid & T.H.Arnold, *Bothalia* 15(1&2): 139 (1984).

Hilliard, *Grasses, Sedges, Restiads and Rushes of the Natal Drakensberg* 52 (1987); Hilliard & Burtt, *Botany of the southern Natal Drakensberg* 15 (1987); Gordon-Gray, *Cyperaceae in Natal* 43 (1995).

Type citation: 'Natal, 2929 (Underberg): "Storm Heights", Mpendhle District (-BC), Hilliard & Burtt 11791 (PRE, holo.; E; NU)'.

Type: South Africa: Natal 2929 (Underberg), *Hilliard & Burtt 11791*; holotype: PRE, n.v., but an image of this holotype has been seen; isotypes: E and NU, n.v.

For description, see the description of *Carpha filifolia* by Reid and Arnold (1984), but note that glumes are distichous to sub-distichous in their arrangement rather than spiral as they indicated, and spikelets have two bisexual flowers without the empty uppermost glume (the uppermost glume, described by Reid and Arnold (1984) as sometimes subtending a male flower or empty, was not found in this study) (see Fig 2.2 k for spikelet structure).

In marshes and on wet cliffs, along stream banks. In South Africa (Transvaal, Orange Free State, Natal, Lesotho and Cape).

Notes: Although the type was not examined, an image of the holotype has been seen. The protologue has a clear illustration, and other specimens cited in the protologue, such as *N. J. Devenish 1067* (K, PRE), and *1821* (K), *O. M. Hilliard 16258* (NU), *Hilliard & Burt 9788* (NU), *13462* (PRE) and *16677* (NU), *F. K. Hoener 2138* (PRE), and *Killick & Vahrmeijer 3595* (PRE) were examined.

8. *Asterochaete glomerata* (Thunb.) Nees, *Linnaea* 9: 300 (1834), 10: 194 (1835); Kunth, *Enum. Pl.* 2: 311 (1837); Steudel, *Synops. Cyper.* 155 (1855); Levyns, *Fl. Cape Peninsula* 119 (1950).

**Basionym:** *Schoenus glomeratus* Thunb., *Prodr. Fl. Capens.* 17 (1794).

*Carpha glomerata* (Thunb.) Nees, *Linnaea* 7: 529 (1832); Boeckeler, *Linnaea* 38: 265 (1874); Clarke in Durand and Schinz, *Consp. Fl. Afr.* 5: 656 (1894), in Dyer, *Flora Capensis* 7: 269 (1898), *Illustr. Cyper. t. LXXVI*, fig. 7–9 (1909); Marloth, *Fl. South Afr.* 4: t. X, fig. E and P. 39, Fig., 7, 1–4 (1915); Schönland, *Mem. Botanical Survey of South Africa* No. 3: 56 (1922); Pfeiffer, *Feddes Repert.* 29: 179 (1931); Kükenthal, *Feddes Repert.* 47: 114 (1939); Haines & Lye, *Sedges and Rushes of East Africa* 322 (1983); Reid & Arnold, *Bothalia* 15: 139–140 (1984); Gordon-Gray, *Cyperaceae in Natal* 43 (1995).

Type citation: no explicit citation; but Thunberg's herbarium is in UPS.

Type: South Africa: Kapstadt: *Thunberg*; UPS, n.v., but a photocopy of the *Thunberg 1344, 1345* specimens of *Schoenus glomeratus* from the microfiche of Thunberg's herbarium have been seen.

Erect perennial, 107–300 cm high. Rhizome short. Culms erect, striate, 1–3 nodes, each node bearing a single leaf. Leaves crowded at the base of the culms; blades straight, 40–110 cm long, 7–28 mm wide, V-shaped in cross-section. Inflorescence with several internodes; spikelets form many (10–60) ovoid heads. Bracts leaf-like. Spikelets 6–9 mm

long, composed of 6 distichously arranged glumes; lowest 3 glumes empty, persistent, shorter than the upper ones; the upper two fertile and the uppermost one empty, deciduous; 'rachilla' elongated above proximal fertile glume and adnate to the base of the proximal fertile glume. Flowers 2, bisexual. Bristles 6, scabrous, in two whorls, outer 3 bristles shorter than inner 3. Stamens 3; anthers 2.4–4.0 mm long, yellow-green with apical appendage 0.2–0.3 mm long, c. 0.1 mm wide. Style branches 3; style base 0.3–1.0 mm long, 0.1–0.3 mm wide. Nuts 2, ellipsoid, trigonous in cross-section, 2.5–3.4 mm long, 0.9–1.1 mm diam., brown at maturity, surface reticulate. (See Fig 2.2 q for spikelet structure).

In marshes or on stream sides, flats and mountain slopes, 90–2500 m. In East and South Africa.

Notes: This species resembles *A. schlechteri* but differs in having two bisexual flowers in each spikelet, both developing nuts, and the 'rachilla' elongated above the proximal fertile node. It is usually more robust and has more heads of spikelets in the inflorescence.

9. *Asterochaete nitens* Kunth, Enum. Pl. 2: 313 (1837) (as *A. ?nitens*); Steudel, Synops. Cyper. 155 (1855). — [*C. aubertii* Nees, Linnaea 9: 300 (1834) (nomen nomen as 'Aubertii')]; — *C. aubertii* Nees ex Boeck., Linnaea 38: 270 (1874); Baker, Fl. Maurit. 417 (1877); Cordemoy, Fl. Réunion 132: (1895); Clarke in Durand and Schinz, Consp. Fl. Afr. 5: 656 (1894), Illustr. Cyper. t. LXXVII, fig. 3 (1909); Pfeiffer, Feddes Repert. 29: 179 (1931); (as *Aubertii*). — *Carpha nitens* (Kunth) Kük., Feddes Repert. 47: 209 (1939).

Type citation: '*Schoenus nitens* Willd. herb. n. 1119'.

Type: Mascarenes: Mauritius, *Aubert du Petit-Thouars in herb. Willd. 1119*; B–W n.v., but an image of this specimen has been seen; B 100000965, a spikelet and some fragments of spikelets (These fragments were apparently removed by Kükenthal from the main type collection for examination during his work on this group. Its label is in Kükenthal's script. It is best treated as an isotype).

For description, see the description of *Carpha nitens* by Kükenthal (1939d). (See Fig 3.13; Fig 2.2 e, k, q for spikelet structure).

Growing by roadsides on rock face, dry ericaceous upland ridges. Only on Réunion.

10. *Asterochaete schlechteri* (C.B.Clarke) X.F.Zhang, **comb. nov.**

**Basionym:** *Carpha schlechteri* C.B.Clarke in Wildem., Pl. Nov. Hort. Thenensis 37, t. 9 (1904).

Clarke in Kew Bull. Add. Ser. 8: 43 (1908); Pfeiffer, Feddes Repert. 29: 180 (1931); Kükenthal, Feddes Repert. 47: 115 (1939); Reid & Arnold, Bothalia 15: 141–142 (1984).

Type citation: ‘Afrique australe. — Région austro-occidentale: Koude Bokkeveld, Gydow à 4,500 pieds (R. Schlechter, 17 janvier 1897).’

Type: South Africa: Koude Bokkeveld, Gydow, 4500 ft, *R. Schlechter 10010*, 17 Jan. 1897; holotype: K; isotypes: B *10000976* (fragments of inflorescence), BOL *63205*, NSW, P *00199388*, PRE (two sheets), Z.

Erect perennial, 80–130 cm high. Rhizome short. Culms erect, striate, 1–2 nodes, each node bearing a single leaf. Leaves crowded at the base of the culms; blades straight, 40–57 cm long, 4.5–8 mm wide, V-shaped in cross-section. Inflorescence with several short internodes; spikelets in 6–20 ovoid heads. Bracts leaf-like. Spikelets 4–5 mm long, composed of 5–7 distichously arranged glumes; lowest 3–4 glumes empty, persistent, shorter than the upper ones; the next upper two fertile and sometimes an empty uppermost glume present, deciduous; ‘rachilla’ not elongated above the proximal fertile glume. Flowers 2, lower one male, upper one bisexual. Bristles 6, scabrous, in two whorls, outer 3 bristles shorter than inner 3. Stamens 3; anthers 1.3–2.5 mm long, yellow-green with apical appendage 0.3–0.4 mm long, c. 0.1 mm wide. Style branches 3; style base 0.2–0.5 mm long, 0.1–0.2 mm wide. Nut 1, ellipsoid, trigonous in cross-section, 2.2–2.4 mm long, 0.7–1.0 mm diam., brown at maturity, surface reticulate. (See Fig 2.2 h, o, q for spikelet structure).

In alpine marshes, 900–1500 m. In Cape Province, South Africa.

Notes: *Carpha schlechteri* was first described by Clarke (1904, p. 37) as ‘*C. glomerata* Nees affinis; differt: foliis angustioribus (vix 5 mm. latis); inflorescentia graciliore, spiculis minoribus; nuce grosse conspicue hexagono-reticulata levi (neque, ut in *C. glomerata*, minute obscure reticulata).’ That is, he considered it to be different from *C. glomerata* by its narrower leaves, its fewer heads of spikelets in the inflorescence and larger reticulations on the nut surface. This study (Chapter 3) found that specimens of *C. schlechteri*, which have a male flower below a bisexual flower in each spikelet and the ‘rachilla’ not elongated above the proximal fertile node, were grouped together in the analyses, while one specimen of *C. schlechteri* (*B. Sonnenberg 458*, NU), which has two bisexual flowers in each spikelet and ‘rachilla’ elongated above the proximal fertile node, was grouped with *C. glomerata* (which has two bisexual flowers in each spikelet and ‘rachilla’ elongated above the proximal fertile node) despite having narrower leaves and fewer heads of spikelets in the inflorescence than specimens of *C. glomerata*. Thus, as indicated in Chapter 3, the definitions of the two species *A. glomerata* and *A. schlechteri* are revised. *Asterochaete glomerata* and *A. schlechteri* are similar morphologically, but *A. glomerata* has two bisexual flowers in each spikelet, both developing nuts, and the ‘rachilla’ elongated above the proximal fertile node, while *A. schlechteri* has the proximal flower male and only produces one nut per spikelet and the ‘rachilla’ is not elongated above the proximal fertile node.

11. *Asterochaete ulugurensis* Nelmes ex X.F.Zhang, **sp. nov.**

Planta *Asterochaete nitenti* Kunth simulans sed in characteribus inflorescentiarum differt. Spiculae in capitula oblonga dense congestae, non laxe dispositae. *Asterochaete borbonica* (Steud.) X.F.Zhang simulans, sed in characteribus foliorum differt. Folia plana carinata 1.7–5.5 mm lata, non perangusta canaliculata ecarinata.

Type: Tanzania: Uluguru-Mountains, Lukwangule, 2385 m, *T. Pocs 3766*, 8 Dec. 1969; holotype: K; isotype: EA. (Figs 6.6 c, d, 6.8).

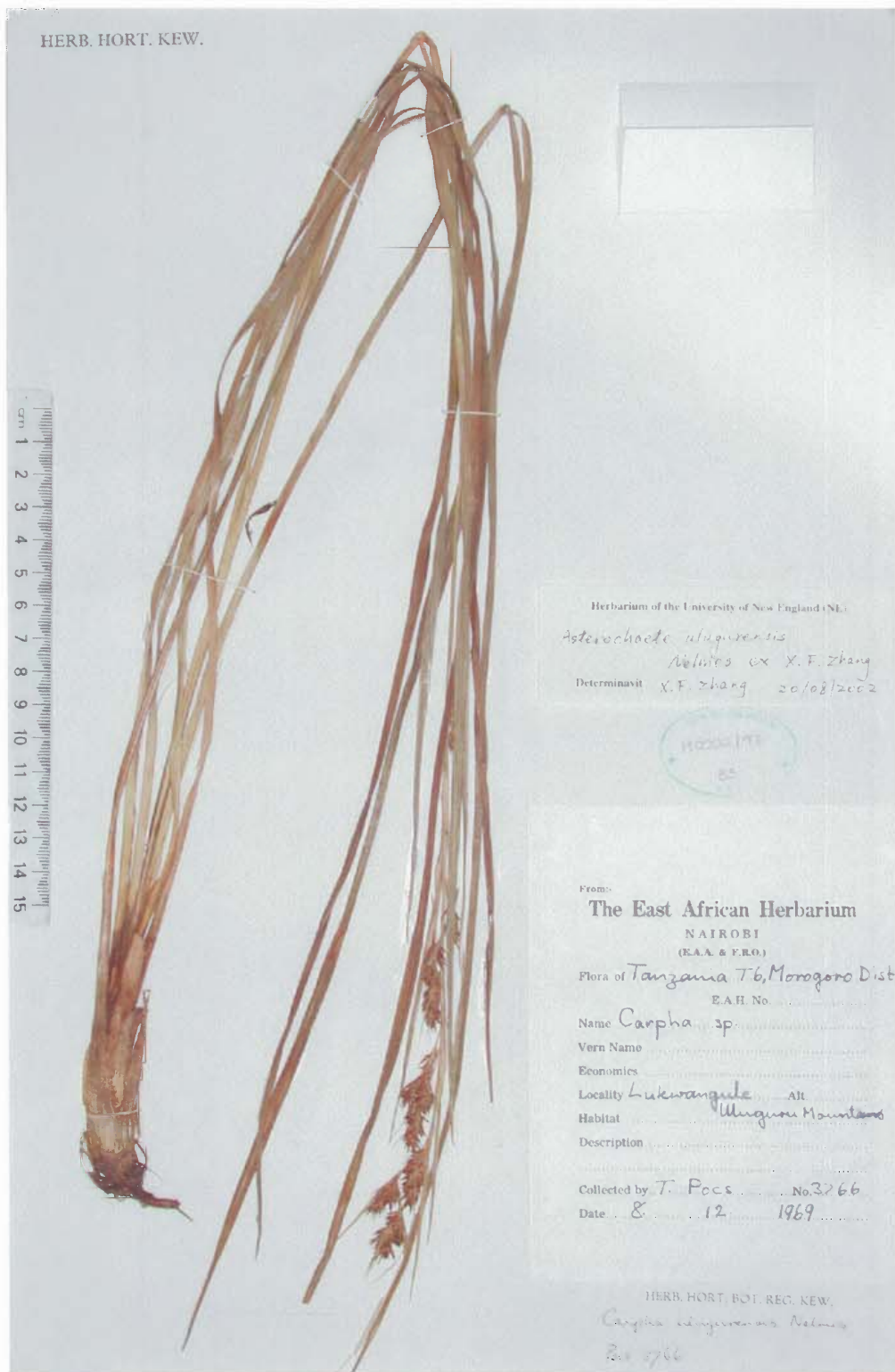


Fig. 6.8. Holotype of *Asterochaete ulugurensis* (T. Pocs 3766, K).

Erect perennial, up to 90 cm high. Rhizome short. Culms erect, striate, nodeless or single-noded, the node bearing a single leaf. Leaves crowded at the base of the culms; blades straight, 10–65 cm long, 3–7 mm wide; V-shaped in cross-section, keeled. Inflorescence with several short internodes; spikelets in a few oblong heads. Bracts leaf-like, up to 24 cm long, to 4.6 mm wide. Spikelets 5–6 mm long, composed of 5 distichously arranged glumes; lowest 3 glumes empty, persistent, shorter than the upper fertile ones, either both the upper two fertile or the uppermost one sterile, both glumes deciduous; ‘rachilla’ elongated above proximal fertile glume and adnate to the base of the proximal fertile glume. Flowers 1–2, bisexual, when the uppermost glume sterile, spikelet with 1 flower, otherwise, spikelet with 2 flowers. Bristles 6, scabrous, much longer than nut, in two whorls, outer 3 bristles shorter than inner 3. Stamens 3; anthers 1.4–2.0 mm long, yellow-green, with apical appendage 0.1–0.3 mm long, c. 0.1 mm wide. Style branches 3; style base 0.2–0.7 mm long, 0.1–0.2 mm wide. Nuts 1–2, ellipsoid, trigonous in cross-section, 1.7–2.2 mm long, 0.6–1.6 mm diam., brown at maturity, surface reticulate. (See Fig 2.2 e, k, for spikelet structure).

On Réunion: so far as known, on steep hillsides, alt. 1500–2200 m, with annual rainfall of 3000–5100 mm. Also in Uluguru Mountains of Morogoro district, Tanzania: in peat bogs or marshes among grassland.

Etymology: the specific epithet is from the manuscript name written on the type (K) and an other specimen (*G. M. Bruce 742*, K) by the late E. Nelmes, a cyperologist at RBG Kew. Another specimen there (*S. Bidgood 232*, K) was also labelled as ‘*Carpha ulugurensis* Nelmes’ by D. Simpson in 1987.

Notes: The specimens of this species were temporarily named as *Carpha ulugurensis* and *C. cf. nitens* previously in this study. This species resembles *A. nitens*, but differs in the inflorescences. Its spikelets form dense oblong heads rather than being loosely to subloosely arranged. It resembles *A. borbonica*, but differs in the leaves. Its leaves are V-shaped, keeled, and 1.7–5.5 mm wide, rather than being canaliculate without a keel.

### 6.3.3 Dubious Taxon: *Carpha aristata*

*Carpha aristata* Kük., Feddes Repert. 47: 112 (1939); Ohwi, Cyper. Japon. II 25 (1944), Flora of Japan (1965); Toyama, Flora of Nagasaki Prefecture 269 (1980).

Kükenthal (1939c) described this species based on an imperfect specimen labelled as coming from Nagasaki, Kyushu, Japan. Ohwi (1944, pp. 25–26) cited this species in “Cyperaceae Japonicae II” based on Kükenthal’s description, but he suspected this species was not native to Japan, and wrote ‘Hab. Kiushiu: Nagasaki (Schottmüller, non vid.). An planta certe in Japonia indigena?’ He (1965, p. 212) also cited this species in “Flora of Japan”, but he noted that this species was ‘reported in Kyushu (Nagasaki) by Kuekenthal’. Toyama (1980, p. 269) also listed this species in “The Flora of Nagasaki Prefecture”, but noted that information came from Ohwi. Thus, no-one has actually found this species growing in Japan.

The herbarium in Berlin (B), where the type was supposed to be, was contacted to borrow the type or any specimen of *Carpha aristata*, but no specimen of this species was obtained. K. Wilson (2002, pers. comm.) did not find any such specimen when she visited B to examine specimens of Cyperaceae.

I have also contacted some Japanese herbaria for specimens of this species. No specimen of this species has been located in Japanese herbaria, and it was suggested that *Carpha aristata* was probably an introduced plant at that time or that it may be extinct (H. Ohba 2000, pers. comm.).

K. Wilson (2000, pers. comm.) has suggested two other possibilities. One is that this species may have been re-determined as some other species (probably in Cyperaceae, and probably somewhere around *Carpha* since it was Kükenthal who named the species, and he had a good knowledge of the family). The other is that this species is probably not in Japan, because this specimen may have been mixed up with other collections from any of Schottmüller’s (the collector of the type specimen) stopping points: South America, South Africa, the Malesian region, and Asia during his long sea-voyages.



I have compared the description of *Carpha aristata* with all the specimens I observed. None are similar.

#### 6.4 Recommendations for Further Work

The sympodial structure of the spikelet in Schoeneae was identified and relevant interpretations and concepts were clarified, but further study is required to investigate spikelet development and structure in other tribes in Cyperaceae to resolve homology of the spikelet characters in Cyperaceae generally.

That *Rhynchospora* nests in Schoeneae in the cladistic analyses of the morphological data indicates some problems with the limits of Schoeneae as defined by Clarke (1908), Bruhl (1995) and Goetghebeur (1986), and implies Rhynchosporeae should probably be included in Schoeneae (Goetghebeur 1998). Contradicting his definition of Schoeneae, Goetghebeur (1998) suggested the need of a further division of Schoeneae due to variation in embryo types among different genera of the tribe. However, the current study does not focus on tribal limits, so the genera sampled are not enough to determine the tribal limits of Schoeneae. A further study on Schoeneae of Goetghebeur (1998) should be conducted to determine the tribal limits.

The non-monophyletic status of *Costularia*, *Schoenus* and *Tricostularia* has been identified, but more samples and further studies are needed to determine the definitions and limits of these genera, and to clarify their phylogenetic relationships.

The evident morphological differences of two specimens of *Tetraria capillaris* suggest the need for further study, especially phenetic analysis with more samples, to determine species limits, although they came together as expected with 75% bootstrap and 84% jackknife support in cladistic analyses (Chapter 4).

Similarly, the heterogeneities in the morphology of specimens of *Costularia pilisepala* from New Guinea and from Borneo might also suggest a further study using phenetic analysis with more samples to determine species limits, even though they formed a well-supported (92% bootstrap and 96% jackknife support) clade as expected (Chapter 4).

The weak support or no support for some clades in the cladistic analyses based on both morphological and molecular data require other sources of data, such as other genes and embryo morphology, to re-evaluate and test these relationships.

Although I have not examined type specimens of *Carpha nivicola* and *Asterochaete capitellata*, and examined only fragments of type specimens of *A. borbonica*, *A. eminii* and *A. nitens* and the images of the type specimens of *A. filifolia*, *A. glomerata* and *A. nitens*, I am confident that the protologue description and other details (such as, photographs and illustrations) in each case match the taxa to which these names are applied currently. However, further investigation is needed to make sure that the unseen types do match the current application of these names.