

Chapter 1 Introduction

This chapter includes a brief review of systematic methodology, species concepts for practical application and systematic study of Schoeneae (Cyperaceae), and a detailed taxonomic history of *Carpha*. The review of systematic methodology and species concepts for practical application aims to identify limitations of systematic methods and species concepts, and consequently to provide a theoretical basis for the methods applied in this study. The review of systematic studies in Schoeneae (Cyperaceae) and *Carpha* aims to identify existing problems and knowledge gaps within Schoeneae, especially relating to *Carpha*.

1.1 Systematics: Definition and Methodology

Use of the term systematics in Botany can be traced at least as far back as Linnaeus (1751, 1754; also see Stuessy 1990). Before the publication of the theory of the origin of species by Darwin (1859), systematics was regarded as synonymous with taxonomy (Stuessy 1990). Since Darwin's time, systematists have not only continued their interest in taxonomy, but have also attempted to understand evolutionary relationships and processes. Consequently, systematics was modified and defined as:

‘the study of the nature and origin of the natural populations of living organisms, both present and past’ (Myers 1952, p. 106);

‘the scientific study of the kinds and diversity of organisms and of any and all relationships among them’ (Simpson 1961, p.7); and

‘the study of the diversity of organisms’ (Mayr 1969b, p. 2).

Stuessy (1990, Fig. 1.2) further illustrated clearly the concept and scope of systematics. It consists of three areas: taxonomy, and theoretical and practical aspects of evolution and phylogeny.

Methodology and the procedures used for modern systematics were outlined by Stuessy (1990), who included two main steps. The first is to collect comparative data from the

organism and the organism-environment interactions. The second is to use comparative data to answer specific questions of classification, evolution and phylogeny. Four principal approaches, i.e. artificial, phyletic (= evolutionary), phenetic and cladistic, have been employed for addressing these issues.

The artificial approach involved selection of one or, at most, a few characters for use in making comparisons among objects. Early classifications of plants were artificial, for example, the classification by Linnaeus (1735, 1753) which represents the most complete artificial system developed for all plants (Stuessy 1990).

After Darwin (1859) published his theory of the origin of species, evolutionary relationships of organisms started to be emphasised. As a result, some clearly phyletic systems of classification of plants were produced, e.g. the systems of Hutchinson (1926, 1934), Takhtajan (1969), Thorne (1976), Dahlgren (1980) and Cronquist (1981). However, because the phyletic approach involves a subjective selection of characters and subjective comparison and evaluation of character states, legitimate differences have arisen among these phyletic systems of classification even when the same sets of organisms were examined (Stuessy 1990). Thus, the phyletic approach has been criticised, e.g. Bremer and Wanntorp (1978, p. 322) comment that 'such a system is not falsifiable, not truly part of science according to Popper, and in fact more a work of art, and as such highly personal and not repeatable'.

Attempts to avoid (or at least reduce) the subjectivity of the phyletic approach have led to development of the phenetic approach. The origin of the phenetic approach can be traced back to the French botanist Michel Adanson in the 18th Century (Sneath and Sokal 1973; Stuessy 1990). Although a few minor developments in phenetics occurred in the two centuries after Adanson, there was no significant development until Michener and Sokal (1957) and Sneath (1957) independently published their papers (see Sneath and Sokal 1973 for a review). At present, the phenetic approach is based on a measure of overall similarity and defined as 'similarity (resemblance) based on a set of phenotypic characteristics of the objects or organisms under study' (Sneath and Sokal 1973, p 29). This approach relies heavily on computer assistance for data analysis, has been enormously stimulating to taxonomy in many aspects (see Stuessy 1990 for details) and has played several important roles in systematic work, particularly in identification and determining whether organisms

comprise one or more distinct entities (Quicke 1993). However, this approach is not based on evolutionary thinking, and should not be used to study evolutionary relationships (Stuessy 1990; Quicke 1993). This approach has been recommended to study patterns of variation at low taxonomic levels, i.e. species and infraspecific taxa (Stuessy 1990; Stevens 2000) where the relationship of the organisms of study are usually not hierarchical (Davis and Nixon 1992; Doyle 1995; Olmstead 1995; Brower et al. 1996; Brower 1999).

To reflect evolutionary relationships, cladistics (or phylogenetics, a term not recommended; see Stuessy 1990 pp. 93–94 for reason) has developed. ‘Cladistics is a method of classification that groups taxa hierarchically into discrete sets and subsets. Cladistics can be used to organise any comparative data (e.g. linguistics) but its greatest application has been in the field of biological systematics’ (Kitching et al. 1998, p. 1). It ‘can be defined as the concepts and methods for the determination of branching patterns of evolution’ (Stuessy 1990, p. 93). Its algorithms can be grouped into three rather different methods: parsimony analysis, compatibility analysis and maximum likelihood analysis (Stuessy 1990; Quicke 1993). At present, cladistics has attracted much attention and cladistic analysis has become widely accepted as the most rigorous way to study phylogenetic relationships. However, cladistic analysis yields nested hierarchical patterns of relationships among organisms, regardless of whether such patterns actually exist, i.e. it is inappropriate for assessing relationships among organisms that are related by tokogeny (or reticulate relationship) which exist among individuals of a sexually reproducing population (Davis and Nixon 1992; Doyle 1995; Olmstead 1995; Brower et al. 1996; Brower 1999; Goldstein and DeSalle 2000; Stevens 2000).

In practice, most systematists are interested in using cladistics to study phylogenetic relationships between species or at higher levels (Stevens 2000). At low taxonomic levels, i.e. species and infraspecific taxa where the relationship of the organisms of study are usually not hierarchical, cladistics is inappropriate for assessing relationships among organisms that are not hierarchical. It is recommended that ‘the identification of species should be fundamentally decoupled from the elucidation of relationships’ (Goldstein and DeSalle 2000, p. 378). As indicated previously, phenetic methods are appropriate to study patterns of variation at low taxonomic levels (species and infraspecific taxa), i.e. to identify and test definitions and limits of species.

1.2 Species Concept and its Practical Application

The species is the fundamental category of the taxonomic hierarchy. Over the past century or so, numerous papers and books have been written on it and many species concepts have been proposed (Quicke 1993). Of these, the following four have had most effect on theory and practice: morphological species concept, biological species concept, evolutionary species concept and phylogenetic species concept. The morphological species concept, also called morphospecies concept, classical phenetic species concept (Sokal 1973) and Linnaean or classical species concept (Burger 1975), is the most frequently employed one (Stuessy 1990). Its exact definition has varied. This concept recognizes species on morphological bases. 'In practice we usually do not have sufficient information on reproductive behaviour to allow the biological species concept to be applied successfully. As a result, workers have stressed the importance of recognising species on morphological bases alone' (Stuessy 1990, p. 171). 'The Linnaean or classical species concept of readily recognized and morphologically defined species has served as a practical and efficient system for information retrieval in most flowering plants. There are very few groups where morphological correlations as a basis for taxonomy have failed to identify meaningful taxa. Even in those cases where intermediates and hybridisation are known, the classical concepts have often continued to be useful and meaningful' (Burger 1975, p. 45). This concept has been employed in general systematic practice — herbarium taxonomy, floristic and monographic work — over the last fifty years, or even over the last century (Stevens 2000).

'The biological species concept is the one held conceptually by most systematists' (Stuessy 1990, p. 172). According to this concept, species are groups of interbreeding populations that are genetically isolated from other groups by reproductive isolating mechanisms (Mayr 1969a). Although this concept is useful in many ways, it does not by definition refer to evolution directly and could be misleading in the study of evolutionary processes. It has been the target of much criticism (Wiley 1978; Cracraft 1983; Donoghue 1985; de Queiroz and Donoghue 1988).

To improve perceived weaknesses of the biological species concept, additional species concepts, including the evolutionary species concept and phylogenetic species concept, have been developed. The evolutionary species concept was first proposed by Simpson

(1961). It has undergone a series of revisions and improvements. It was defined by Wiley (1978, p. 18) as 'a species is a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate'. This definition incorporates the historical perspective that the biological species concept lacks (Harris and Rogers 1999). However, this definition has a practical disadvantage because it is not possible at any one time to know the historical fate or evolutionary tendencies for groups of organisms (Quicke 1993).

The phylogenetic species concept was developed by Cracraft (1983). This concept also has subsequently undergone many modifications. According to this concept a 'species is the smallest possible group of a sexually reproducing organism that possesses at least one diagnostic character which is present in all group members but is absent from all close relatives of the group' (Quicke 1993, p. 49). This definition is a useful and dramatic improvement over biological species concepts, and is a pattern-based concept that requires no assumptions about mechanisms and maintains the idea of lineages of the evolutionary species concept (Olmstead 1995; Harris and Rogers 1999). However, 'this approach neglects much historical evolutionary information (specifically that concerning relationships among populations within species and between progenitor and derivative species) and divorces the study of what constitutes species from the study of evolutionary processes and the processes that maintain species identity' (Olmstead 1995, p. 623). In addition to that, an overly strict application of the phylogenetic species concept would almost certainly give far larger estimates of the total number of species than the more traditional biological species concept (Quicke 1993). 'Published discussions of the phylogenetic species concept (PSC) have been hampered by persistent misconceptions surrounding its ontology and applicability, and by confusion of various incompatible versions of species concepts claiming to follow from Hennig's ... work. Especially problematic are topology- or tree-based versions of species diagnosis, which render diagnoses dependent on relationships depicted as hierarchically structured regardless of any lack of underlying hierarchy. Because the applicability of concepts such as monophyly, paraphyly, and polyphyly rests ultimately on the underlying hierarchical distribution of characters, representations of tokogenetic or reticulating systems as nested hierarchies are necessarily inaccurate' (Goldstein and DeSalle 2000, p. 364).

A number of different species concepts are still employed currently because there is not yet universal acceptance of a single species concept (Luckow 1995). There are large gaps between theoretical and practical work at the species level (McDade 1995). 'It is notable that discussions about species concepts have generally had little effect on those actually describing species' (Stevens 2000, p. 648).

As reviewed in Section 1.1 of this Chapter, the phenetic approach has become an integral part of the methodology of systematists attempting to understand details of patterns of variation at species or infraspecies levels. Although phenetic clusters could result from the study of genetics, cytology, chemistry, anatomy, etc., in practice, they tend to be based on morphology. Using phenetic methods and morphological data to define the limits of species is an extension of the morphological species concept (Stuessy 1990) that is adopted in this study.

1.3 Taxonomic Status of Schoeneae (Cyperaceae)

Cyperaceae (sedges) are a cosmopolitan family of monocotyledons with 104 genera and over 5000 species, very diverse in tropical regions but also common in temperate and cold temperate regions of the world (Goetghebeur 1998). They differ from other monocotyledonous families by their pistil with only one basal ovule, their indehiscent fruit, and their pollen in pseudomonads (i.e. tetrads in which three microspores degenerate and only one develops) (Haines and Lye 1983; Dahlgren et al. 1985; Kubitzki 1998). Their reduced flowers and highly condensed inflorescences have led to different interpretations and uncertain assessment of homology (Muasya et al. 1998). This in turn has led to different classification systems of the family, and even the circumscription and classification of subfamilies is still controversial (Bentham 1883; Pax 1887; Clarke 1908; Koyama 1961, 1969; Schultze-Motel 1964; Hooper 1973; Goetghebeur 1986, 1998; Bruhl 1995).

Among the classification systems of Cyperaceae, the tribe Schoeneae has been recognized by Clarke (1908), Kükenthal (1940b, 1944, 1952), Goetghebeur (1986, 1998) and Bruhl (1995), while the classifications of Bentham (1883), Koyama (1961), Schultze-Motel (1964), Hooper (1973), Kern (1974) and Haines and Lye (1983) placed all the genera that are now included in the Schoeneae in the tribe Rhynchosporae (Fig. 1.1).

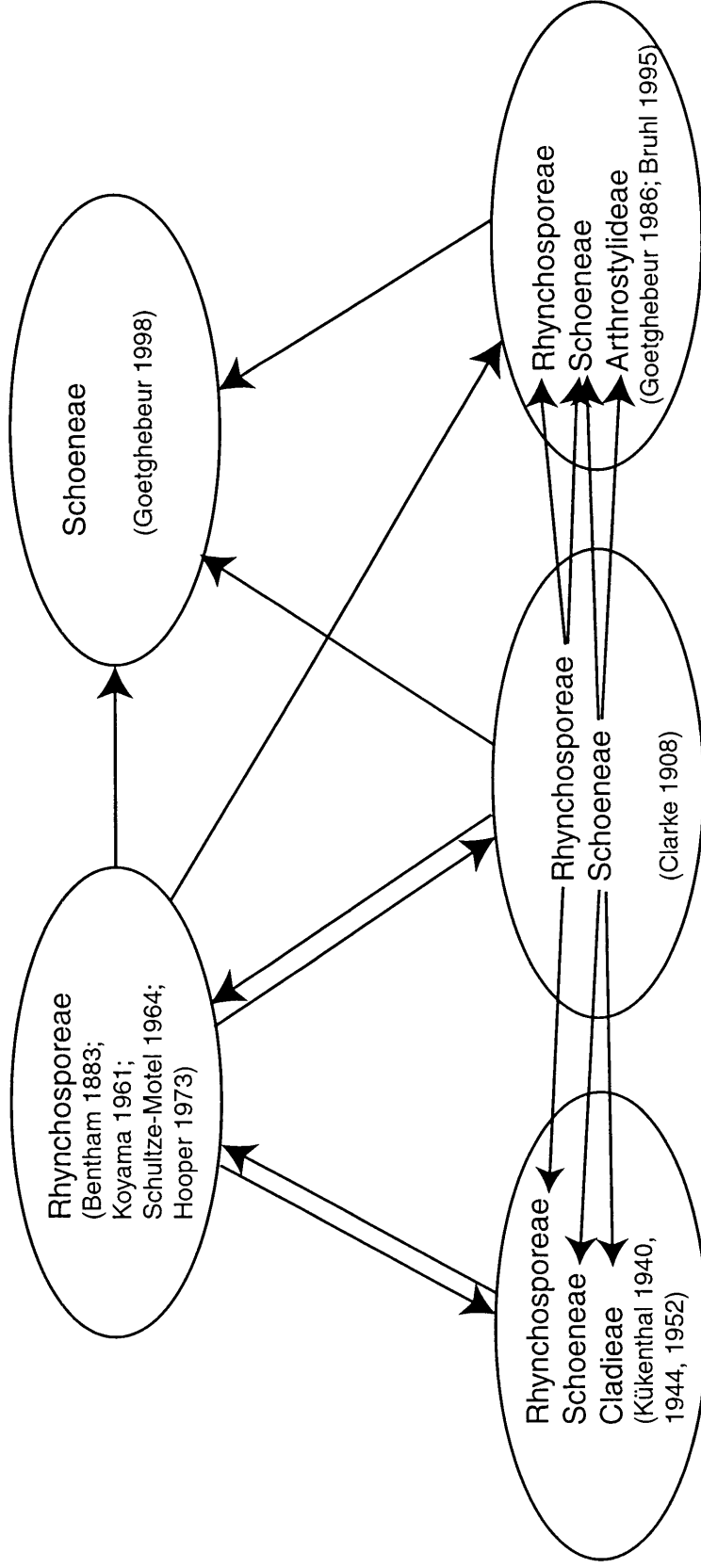


Fig. 1.1.1. Different definitions of Schoeneae and Rhynchosporae. See text for discussion.

Clarke (1908) divided the tribe Rhynchosporeae, as delimited in the classification of Bentham (1883), into two tribes, Rhynchosporeae and Schoeneae (Fig. 1.1). Clarke (1908) included 21 genera in the tribe Schoeneae (Table 1.1). Clarke (1902, p. 267) considered the main characters of the tribe Schoeneae to be ‘empty glumes at the base of the spikelet 3 or more; fertile flowers usually 1 or few (sometimes many); inflorescence paniced or capitate, not umbelled’.

Kükenthal (1940b, 1944, 1952) kept eight genera that have a distichous arrangement of the glumes as his Schoeneae (Table 1.1) and put all the other genera of Schoeneae of Clarke (1908) in the tribe Cladieae (Fig. 1.1).

Goetghebeur (1986) and Bruhl (1995) divided the tribe Rhynchosporeae of Bentham (1883), Koyama (1961), Schultze-Motel (1964) and Hooper (1973) into three tribes: Arthrostylideae, Rhynchosporeae and Schoeneae (Fig. 1.1). Goetghebeur (1986) included 24 genera in the Schoeneae (Table 1.1). Bruhl (1995) added three more segregate genera (*Lophoschoenus*, *Schoenoides*, *Tetrariopsis*) to the Schoeneae (Table 1.1).

Goetghebeur (1998) combined two tribes Arthrostylideae and Rhynchosporeae of Goetghebeur (1986) and Bruhl (1995) in the Schoeneae and included 29 genera in the tribe (Fig. 1.1; Table 1.1). Goetghebeur (1998, p. 152) described Schoeneae as ‘with a (mostly) restricted number of bisexual flowers per spikelet, often provided with a \pm well-developed perianth. The spikelets are remarkable for the inclusion of the flower(s) by the wings of the next glume’. He commented on the need for further division of his Schoeneae (Goetghebeur 1998) due to variation in embryo types among different genera of the tribe.

The classifications of Goetghebeur (1986) and Bruhl (1995) are the most convincing because they were based on cladistic analysis of a wide range of morphological, anatomical, embryological, phytochemical and physiological data. In this study, the more recent one defined by Bruhl (1995) is used.

Table 1.1. The genera included in Schoeneae by different authors. “*” indicates inclusion in the tribe; “(*)” indicates treatment as a synonym of another name.

Genera	Clarke (1908)	Kükenthal (1940, 1944)	Goetghebeur (1986)	Bruhl (1995)	Goetghebeur (1998)
<i>Actinoschoenus</i>					*
<i>Arthrostylis</i>	*				*
<i>Baumea</i>			*	*	(*)
<i>Carpha</i>	*	*	*	*	*
<i>Caustis</i>	*		*	*	*
<i>Cladium</i>	*		*	*	*
<i>Costularia</i>	*	*	*	*	*
<i>Cyathochaeta</i>			*	*	*
<i>Cyathocoma</i> (<i>Macrochaetium</i>)	*		*	*	*
<i>Epischoenus</i>	*		*	*	*
<i>Evandra</i>	*		*	*	*
<i>Gahnia</i>	*		*	*	*
<i>Gymnoschoenus</i>	*	*	*	*	*
<i>Lepidosperma</i>	*		*	*	*
<i>Lophoschoenus</i>			(*)	*	(*)
<i>Machaerina</i>			*	*	*
<i>Mesomelaena</i>	*	*	*	*	*
<i>Microschoenus</i>	*		(*)	(*)	
<i>Morelotia</i>			*	*	*
<i>Neesenbeckia</i>			*	*	*
<i>Oreobolus</i>	*	*	*	*	*
<i>Phylloscirpus</i>	*				
<i>Pleurostachys</i>					*
<i>Ptilothrix</i> (<i>Ptilanthelium</i> auct.)	*	*	*	*	*
<i>Reedia</i>	*		*	*	*
<i>Rhynchocladium</i>			*	*	*
<i>Rhynchospora</i>					*
<i>Schoenoides</i>				*	(*)
<i>Schoenus</i>	*	*	*	*	*
<i>Tetaria</i>	*	*	*	*	*
<i>Trachystylis</i>					*
<i>Trianoptiles</i> (<i>Ecklonea</i>)	*		*	*	*
<i>Tetariopsis</i>			(*)	*	(*)
<i>Trichoschoenus</i>					*
<i>Tricostularia</i>	*		*	*	*

1.4 Spikelet Morphology in Schoeneae

One of the most important characteristics to be considered in the systematic study of Cyperaceae is the branching pattern in the spikelet. This character has received considerable attention from taxonomists, especially in Schoeneae (or Rhynchosporeae) (Pax 1886, 1887; Celakovský 1887; Holttum 1948; Hamlin 1956; Koyama 1961; Kern 1962, 1974; Schultze-Motel 1964; Haines 1967; Raynal 1971; Eiten 1976; Haines and Lye 1977, 1983; Kukkonen 1986; Browning and Guthrie 1994). However, extremely contracted spikelets have resulted in conflicting interpretations of spikelet morphology in Schoeneae (or Rhynchosporeae). Some authors have interpreted the spikelet of Schoeneae (or Rhynchosporeae) as developing sympodially, i.e. the spikelet is a cymose structure (Pax 1886, 1887; Celakovský 1887; Hamlin 1956; Kern 1962; Schultze-Motel 1964). Others have preferred the interpretation that the spikelet develops monopodially, i.e. the spikelet is a racemose structure (Holttum 1948; Koyama 1961; Haines 1967; Raynal 1971; Eiten 1976; Haines and Lye 1977; Kukkonen 1986). Currently, spikelets of Schoeneae are generally treated as monopodial structures (e.g. Haines and Lye 1983; Kukkonen 1986; Wilson 1993; but see Kern 1974).

1.5 Relatives of *Carpha*

Within Schoeneae, generic limits have not been always clearly defined nor stable, and phylogenetic relationships are not fully understood. Close relatives of *Carpha*, based on intuitive assessment, have been thought to be *Schoenus* (Clarke 1902; Kükenthal 1939c), *Trianoptiles* (*Ecklonea*) (Clarke 1897-1898; Kükenthal 1939c), *Costularia* (Kükenthal 1939c) and *Ptilothrix* (*Ptilanthelium* auct.) (Kükenthal 1939c). The results of recent phylogenetic studies of Cyperaceae based on morphology were not in agreement on this issue (Goetghebeur 1986; Bruhl 1995). Goetghebeur's (1986) results indicated that *Carpha*, *Costularia*, *Oreobolus* and *Trianoptiles* formed a monophyletic clade, in which *Trianoptiles* was sister to *Carpha*, while Bruhl's (1995) analyses revealed *Oreobolus*, *Schoenoides* (a segregate of *Oreobolus*), *Ptilothrix*, *Trianoptiles* and *Carpha* to be a robust group and *Trianoptiles* was sister to *Ptilothrix*.

1.6 Taxonomic History of *Carpha*

Carpha Banks et Sol. ex R.Br. was first described by Brown (1810, p. 230) as having: ‘Spicula uniflora, squamis subdistichis, inferioribus vacuis. Setae hypogynae 3–6 squamas floriferas aequantes, plumosae v. capillares. Stylus subulatus, cum ovario inarticulatus. Stigmata 3 v. 2. Nux prismatica, stylo persistenti cuspidata.’ (Spikelets 1-flowered, glumes sub-distichous, lower glumes empty. Hypogynous bristles 3–6, as long as the glume that subtends the flower, plumose or capillary. Style subulate, continuous with the ovary at the base. Stigmas 3 or 2. Nut ellipsoid, trigonous, style base persistent.) Five Australian species (*Carpha alpina*, *C. deusta*, *C. avenacea*, *C. diandra* and *C. clandestina*) were included in the genus by Brown, who took the generic name from a manuscript name of Banks and Solander.

After Brown, *Carpha* was studied by many systematists, who held different views not only about species limits within the genus, but also about definitions of the genus (Table 1.2). The taxonomic and nomenclatural changes made to the genus (summarised in Figs 1.2, 1.3 and Table 1.3) and important works on *Carpha* are detailed below.

Nees (1832) moved the African *Schoenus glomeratus* Thunb. to *Carpha*. Two years later, he (1834) described a new genus *Asterochaete* for *Carpha glomerata* (Thunb.) Nees and two new African species *Asterochaete angustifolia* Nees and *A. capitellata* Nees. However, the latter two new species were not validly published as he provided names without any descriptions. Next year, Nees (1835) validly published *A. capitellata* Nees. ‘*A. angustifolia* Nees’ was later treated as a synonym of *Carpha capitellata* (Nees) Boeck. by Boeckeler (1874). Nees (1834) also listed three new species in *Carpha*: *Carpha aubertii* Nees from Réunion, *C. urvilleana* Gaudich. ex Nees from Borneo and the Moluccas and *C. hexandra* Nees from Africa. However, these three new species were not validly published either as he provided names without any description. The following year, Nees (1835) validly published *C. hexandra* Nees. ‘*Carpha aubertii* Nees’ and ‘*C. urvilleana* Gaudich. ex Nees’ were later published validly, with morphological descriptions, by Boeckeler (1874). Nees (1846) transferred *Carpha diandra* to the genus *Cyathochaeta* as *C. diandra* (R.Br.) Nees.

Table 1.2. Different definitions of *Carpha*. See text for discussion. “—” indicates the absence of information.

Author	Glume arrangement within spikelet	Glume no. per spikelet	Uppermost glume	Flower no. per spikelet	Shape of perianth parts	No. of perianth parts per flower	No. of stigma per flower	No. of fruit per spikelet
Brown (1810)	subdistichous	—	—	1	plumose or capillary	3-6	2-3	—
Kunth (1837)	distichous	—	—	1-2	plumose or capillary	3-6	2-3	—
Hooker (1853)	distichous	—	—	1-2	plumose	3-6	3	—
Hooker (1860, 1867)	distichous	—	sterile	1	plumose	3-6	3	—
Boeckeler (1874)	subdistichous	4-5-8	—	1-2	plumose or hair-like	6	3	1
Bentham (1878, 1883)	distichous	4-5	—	1	plumose	6	3	—
Clarke (1902)	subdistichous	5-7	sterile	—	bristle	3-6	3	1-3
Kükenthal (1939)	distichous	3-6	sterile or fertile	1-2(-3)	bristles with short antrorse hairs or plumose	3-6	—	2-3
Kern (1974)	distichous	3-6	—	1-2(-3)	plumose	6	3	1-2(-3)
Haines and Lye (1983)	distichous	—	sterile or fertile	1-several	bristles with short or long hairs or teeth directed towards the tip.	—	3	—
Bruhl et al. (1992)	distichous	3-7	sterile	1-2	barbate or plumose	6	3	—
Wilson (1993, 1994a, 1994b)	distichous	4-5	sterile	1	plumose	6	3	1
Goetghebeur (1998)	distichous	3-6	—	1-2(-3)	bristle ciliate to fimbriate or plumose	6	3	—

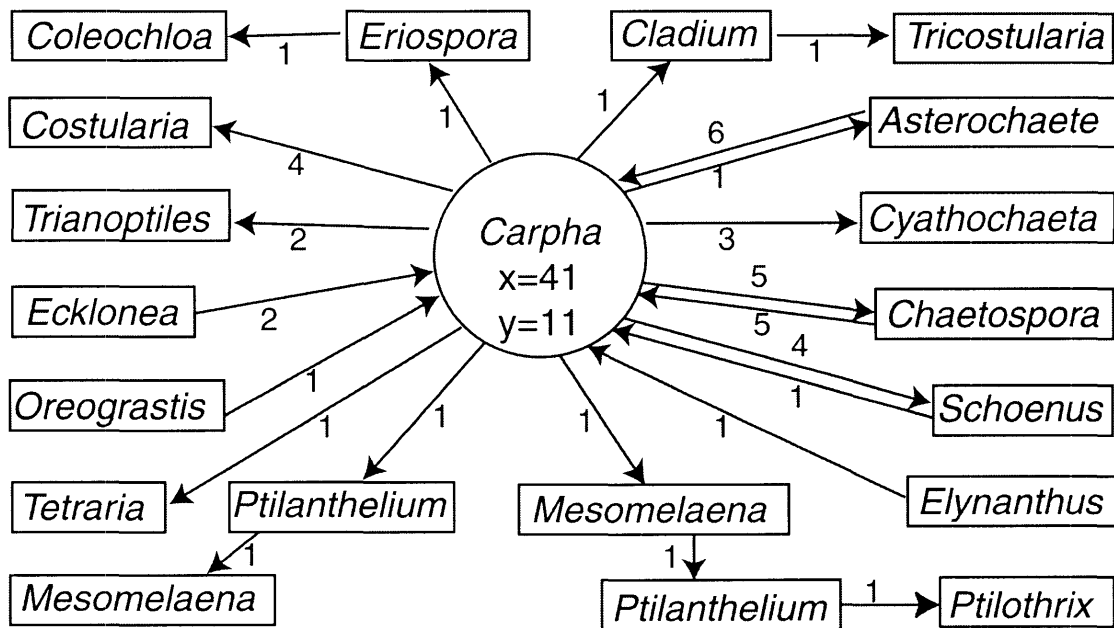


Fig. 1.2. Taxonomic changes related to *Carpha*. Numbers refer to species transferred from one genus to the other genus by various authors. See text for discussion and sources. x = maximum number of species names described in *Carpha*; y = number of species in *Carpha* recognized by Kükenthal (1939c, 1939d).

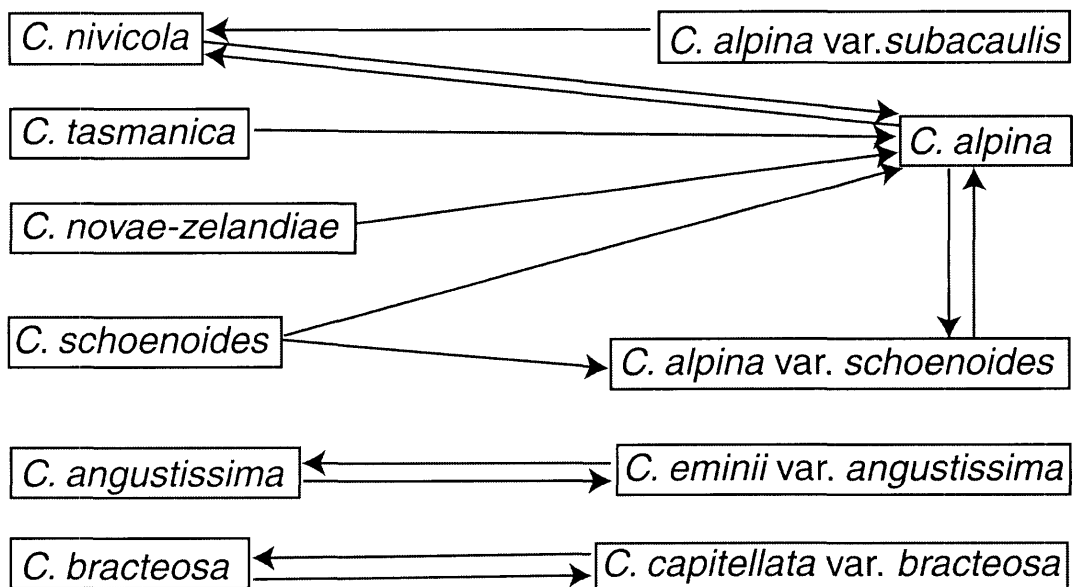


Fig. 1.3. Taxonomic changes within *Carpha*. See text for discussion and sources. The species or varieties on the right hand side were recognized by Kükenthal (1939c, 1939d).

Table 1.3. Summary of nomenclatural history of species included in *Carpha* at various time.

Name published under <i>Carpha</i>	Original name, and subsequent name changes, ending with name current at start of project
<i>Carpha alpina</i> R.Br.	<i>Carpha alpina</i> R.Br. → <i>Chaetospora alpina</i> (R.Br.) F.Muell. → <i>Carpha alpina</i> R.Br.
<i>C. alpina</i> R.Br. var. <i>schoenoides</i> (Banks et Sol. ex Hook.f.) Kük.	<i>Carpha schoenoides</i> Banks et Sol. ex Hook.f. → <i>Carpha alpina</i> R.Br. → <i>Carpha alpina</i> R.Br. var. <i>schoenoides</i> (Banks et Sol. ex Hook.f.) Kük. → <i>Carpha schoenoides</i> Banks et Sol. ex Hook.f./ <i>Carpha alpina</i> R.Br. var. <i>schoenoides</i> (Banks et Sol. ex Hook.f.) Kük.
<i>C. alpina</i> R.Br. var. <i>subacaulis</i> Kük.	<i>C. alpina</i> R.Br. var. <i>subacaulis</i> Kük. → <i>Carpha nivicola</i> F.Muell.
<i>C. andina</i> Phil.	<i>Carpha andina</i> Phil. → <i>Schoenus andinus</i> (Phil.) H.Pfeiff.
<i>C. angustissima</i> Cherm.	<i>Carpha angustissima</i> Cherm. → <i>Carpha eminii</i> (K.Schum.) C.B.Clarke var. <i>angustissima</i> (Cherm.) Kük. → <i>Carpha angustissima</i> Cherm./ <i>Carpha eminii</i> (K.Schum.) C.B.Clarke var. <i>angustissima</i> (Cherm.) Kük.
<i>C. antarctica</i> (Hook.f.) C.B.Clarke	<i>Chaetospora antarctica</i> Hook.f. → <i>Carpha antarctica</i> (Hook.f.) C.B.Clarke → <i>Schoenus antarcticus</i> (Hook.f.) Dusén
<i>C. aristata</i> Kük.	<i>Carpha aristata</i> Kük.
<i>C. arundinacea</i> Brongn.	<i>Carpha arundinacea</i> Brongn. → <i>Asterochaete arundinacea</i> Kunth → <i>Carpha urvilleana</i> Gaudich. ex Boeck. → <i>Costularia urvilleana</i> (Gaudich.) Kük. → <i>Tetraria urvilleana</i> (Gaudich.) T.Koyama → <i>Costularia pilisepala</i> (Steud.) J.Kern
<i>C. arundinacea</i> (Sol. ex Vahl) Boeck.	<i>Schoenus arundinaceus</i> Sol. ex Vahl → <i>Asterochaete arundinacea</i> Kunth → <i>Carpha arundinacea</i> (Sol. ex Vahl) Boeck. → <i>Costularia arundinacea</i> (Sol. ex Vahl) Kük. → <i>Tetraria arundinacea</i> (Sol. ex Vahl) T.Koyama → <i>Costularia arundinacea</i> (Sol. ex Vahl) Kük.
' <i>C. aubertii</i> Nees', nom. nud.	' <i>Carpha aubertii</i> Nees' → <i>Carpha aubertii</i> Nees ex Boeck. → <i>Carpha nitens</i> (Kunth) Kük.
<i>C. aubertii</i> Nees ex Boeck.	<i>Carpha aubertii</i> Nees ex Boeck. → <i>Carpha nitens</i> (Kunth) Kük.
<i>C. aubertii</i> Nees ex Boeck. var. <i>explicatior</i> C.B.Clarke	<i>Carpha aubertii</i> Nees ex Boeck. var. <i>explicatior</i> C.B.Clarke → <i>Carpha costularioides</i> C.B.Clarke → <i>Costularia elongata</i> (Kunth) Kük. → <i>Tetraria elongata</i> (Kunth) T.Koyama → <i>Costularia elongata</i> (Kunth) Kük.
<i>C. avenacea</i> R.Br.	<i>Carpha avenacea</i> R.Br. → <i>Chaetospora avenacea</i> (R.Br.) F.Muell. → <i>Cyathochaeta avenacea</i> (R.Br.) Benth.
<i>C. borbonica</i> (Steud.) C.B.Clarke	<i>Elynanthus borbonicus</i> Steud. → <i>Carpha borbonica</i> (Steud.) C.B.Clarke
<i>C. bracteosa</i> C.B.Clarke	<i>Carpha bracteosa</i> C.B.Clarke → <i>Carpha capitellata</i> (Nees) Boeck. var. <i>bracteosa</i> (C.B.Clarke) Kük. → <i>Carpha capitellata</i> (Nees) Boeck. → <i>Carpha bracteosa</i> C.B.Clarke/ <i>Carpha capitellata</i> (Nees) Boeck. var. <i>bracteosa</i> (C.B.Clarke) Kük.

Table 1.3. (Continued)

Name published under <i>Carpha</i>	Original name, and subsequent name changes, ending with name current at start of project
<i>Carpha capensis</i> (Steud.) H.Pfeiff.	<i>Ecklonea capensis</i> Steud. → <i>Trianoptiles capensis</i> (Steud.) Harv. → <i>Carpha capensis</i> (Steud.) H.Pfeiff. → <i>Trianoptiles capensis</i> (Steud.) Harv.
<i>C. capitellata</i> (Nees) Boeck.	<i>Asterochaete capitellata</i> Nees → <i>Carpha capitellata</i> (Nees) Boeck.
<i>C. capitellata</i> (Nees) Boeck. var. <i>bracteosa</i> (C.B.Clarke) Kük.	<i>Carpha bracteosa</i> C.B.Clarke → <i>Carpha capitellata</i> (Nees) Boeck. var. <i>bracteosa</i> (C.B.Clarke) Kük. → <i>Carpha capitellata</i> (Nees) Boeck. → <i>Carpha bracteosa</i> C.B.Clarke/ <i>Carpha capitellata</i> (Nees) Boeck. var. <i>bracteosa</i> (C.B.Clarke) Kük.
<i>C. clandestina</i> R.Br.	<i>Carpha clandestina</i> R.Br. → <i>Chaetospora clandestina</i> (R.Br.) F.Muell. → <i>Cyathochaeta clandestina</i> (R.Br.) Benth.
<i>C. costularioides</i> C.B.Clarke	<i>Carpha aubertii</i> Nees var. <i>explicatior</i> C.B.Clarke → <i>Carpha costularioides</i> C.B.Clarke → <i>Costularia elongata</i> (Kunth) Kük. → <i>Tetraria elongata</i> (Kunth) T.Koyama → <i>Costularia elongata</i> (Kunth) Kük.
<i>C. curvata</i> W.M.Curtis	<i>Carpha curvata</i> W.M.Curtis
<i>C. deusta</i> R.Br.	<i>Carpha deusta</i> R.Br. → <i>Chaetospora deusta</i> (R.Br.) F.Muell. → <i>Mesomolaena deusta</i> (R.Br.) Benth. → <i>Ptilanthelium deustum</i> (R.Br.) Kük. → <i>Ptilothrix deusta</i> (R.Br.) K.L.Wilson
<i>C. diandra</i> R. Br	<i>Carpha diandra</i> R.Br. → <i>Cyathochaeta diandra</i> (R.Br.) Nees → <i>Chaetospora diandra</i> (R.Br.) F.Muell. → <i>Cyathochaeta diandra</i> (R.Br.) Nees
<i>C. elongata</i> (Kunth) Boeck.	<i>Asterochaeta elongata</i> Kunth → <i>Carpha elongata</i> (Kunth) Boeck. → <i>Costularia elongata</i> (Kunth) Kük. → <i>Tetraria elongata</i> (Kunth) T.Koyama → <i>Costularia elongata</i> (Kunth) Kük.
<i>C. eminii</i> (K.Schum.) C.B.Clarke	<i>Oreograstis eminii</i> K.Schum. → <i>Carpha eminii</i> (K.Schum.) C.B.Clarke
<i>C. eminii</i> (K.Schum.) C.B.Clarke var. <i>angustissima</i> (Cherm.) Kük.	<i>Carpha angustissima</i> Cherm. → <i>Carpha eminii</i> (K.Schum.) C.B.Clarke var. <i>angustissima</i> (Cherm.) Kük. → <i>Carpha angustissima</i> Cherm./ <i>Carpha eminii</i> (K.Schum.) C.B.Clarke var. <i>angustissima</i> (Cherm.) Kük.
<i>C. filifolia</i> Reid & T.H.Arnold	<i>Carpha filifolia</i> Reid & T.H.Arnold
<i>C. glomerata</i> (Thunb.) Nees	<i>Schoenus glomeratus</i> Thunb. → <i>Carpha glomerata</i> (Thunb.) Nees → <i>Asterochaete glomerata</i> (Thunb.) Nees → <i>Carpha glomerata</i> (Thunb.) Nees
<i>C. graciliceps</i> C.B.Clarke	<i>Carpha graciliceps</i> C.B.Clarke → <i>Ptilanthelium graciliceps</i> (C.B.Clarke) Kük. → <i>Mesomelaena graciliceps</i> (C.B.Clarke) K.L.Wilson
<i>C. hexandra</i> Nees	<i>Carpha hexandra</i> Nees → <i>Tetraria hexandra</i> (Nees) Kük. → <i>Cyathocoma hexandra</i> (Nees) J.Browning

Table 1.3. (Continued)

Name published under <i>Carpha</i>	Original name, and subsequent name changes, ending with name current at start of project
<i>Carpha junciformis</i> Boeck.	<i>Carpha junciformis</i> Boeck. → <i>Cladium undulatum</i> Thwaites → <i>Tricostularia undulata</i> (Thwaites) J.Kern
<i>C. laxa</i> (Hook.f.) H.Pfeiff.	<i>Chaetospora laxa</i> Hook.f. → <i>Carpha laxa</i> (Hook.f.) H.Pfeiff. → <i>Schoenus rhynchosporoides</i> (Steud.) Kük.
<i>C. nitens</i> (Kunth) Kük.	<i>Asterochaete nitens</i> Kunth → <i>Carpha nitens</i> (Kunth) Kük.
<i>C. nivicola</i> F.Muell.	<i>Carpha nivicola</i> F.Muell. → <i>Carpha alpina</i> R.Br. → <i>Carpha nivicola</i> F.Muell.
<i>C. novae-zelandiae</i> Gand.	<i>Carpha novae-zelandiae</i> Gand. → <i>Carpha alpina</i> R.Br.
<i>C. paniculata</i> Phil.	<i>Carpha paniculata</i> Phil. → <i>Carpha laxa</i> (Hook.f.) H.Pfeiff. → <i>Schoenus rhynchosporoides</i> (Steud.) Kük.
<i>C. perrieri</i> Cherm.	<i>Carpha perrieri</i> Cherm.
<i>C. rodwayi</i> W.M.Curtis	<i>Carpha rodwayi</i> W.M.Curtis
<i>C. schlechteri</i> C.B.Clarke	<i>Carpha schlechteri</i> C.B.Clarke
<i>C. schoenoides</i> Banks et Sol. ex Hook.f.	<i>Carpha schoenoides</i> Banks et Sol. ex Hook.f. → <i>Carpha alpina</i> R.Br. → <i>Carpha alpina</i> R.Br. var <i>schoenoides</i> (Banks et Sol. ex Hook.f.) Kük. → <i>Carpha schoenoides</i> Banks et Sol. ex Hook.f./ <i>Carpha alpina</i> R.Br. var <i>schoenoides</i> (Banks et Sol. ex Hook.f.) Kük.
<i>C. schweinfurthiana</i> Boeck.	<i>Carpha schweinfurthiana</i> Boeck. → <i>Eriospora schweinfurthiana</i> (Boeck.) Benth. ex C.B.Clarke → <i>Coleochloa schweinfurthiana</i> (Boeck.) Nelmes
<i>C. solitaria</i> (C.B.Clarke) H.Pfeiff.	<i>Ecklonea solitaria</i> C.B.Clarke → <i>Carpha solitaria</i> (C.B.Clarke) H. Pfeiff. → <i>Trianoptiles solitaria</i> (C.B.Clarke) Levyns
<i>C. tasmanica</i> Gand.	<i>Carpha tasmanica</i> Gand. → <i>Carpha alpina</i> R.Br.
<i>C. urvilleana</i> Gaudich. ex Boeck.	<i>Carpha arundinacea</i> Brongn. → <i>Asterochaete arundinacea</i> Kunth → <i>Carpha urvilleana</i> Gaudich. ex Boeck. → <i>Costularia urvilleana</i> (Gaudich.) Kük. → <i>Tetraria urvilleana</i> (Gaudich.) T.Koyama → <i>Costularia pilisepala</i> (Steud.) J.Kern
' <i>C. urvilleana</i> Gaudich. ex Nees', nom. nud.	' <i>Carpha urvilleana</i> Gaudich. ex Nees' → <i>Carpha urvilleana</i> Gaudich. ex Boeck. → <i>Costularia urvilleana</i> (Gaudich.) Kük. → <i>Tetraria urvilleana</i> (Gaudich.) T.Koyama → <i>Costularia pilisepala</i> (Steud.) J.Kern
' <i>C. viridis</i> Phil.' nom. nud.	' <i>Carpha viridis</i> Phil.' → <i>Carpha alpina</i> R.Br. var. <i>schoenoides</i> (Banks et Sol. ex Hook.f.) Kük. → <i>Carpha schoenoides</i> Banks et Sol. ex Hook.f./ <i>Carpha alpina</i> R.Br. var <i>schoenoides</i> (Banks et Sol. ex Hook.f.) Kük.

Kunth (1837) described *Carpha* as having the spikelet 1–2-flowered and glumes distichous (Table 1.2). This was different from Brown (1810) although Kunth included the same five species in the genus *Carpha*. Kunth (1837) also described four new species in *Asterochaete* Nees. They were *A. tenuis* from Cape Province South Africa, *A. arundinacea* from Malesia and New Caledonia, and *A. elongata* and *A. nitens* from Mauritius.

Carpha schoenoides from South America was described by Hooker (1847) based on a manuscript name of Banks and Solander. It was treated as a synonym of *C. alpina* by Philippi (1881) and this was followed by Clarke (1901), Pfeiffer (1931), Gunckel (1971) and Moore (1983). Later, Kükenthal (1939c) reduced *C. schoenoides* to a variety of *C. alpina*.

Hooker's (1853) description of hypogynous bristle shape and stigma number of *Carpha* was different to that of all the former authors (Table 1.2). He considered *Carpha* as possessing: spikelets 1–2-flowered; glumes distichous; hypogynous bristles 3–6, plumose; style 3-fid. A few years later, he (1860, 1867) changed his description of flower number per spikelet and was the first to point out that spikelets of *Carpha* have an empty uppermost glume (Table 1.2). He (1867, p. 299) wrote '[*Carpha* is a] small genus, native in Australia, Tasmania, New Zealand and Fuegia'.

The description of *Carpha* by Steudel (1855) was the same as that of Kunth (1837), but he included a different five species in *Carpha*: *C. alpina*, *C. deusta*, *C. schoenoides*, *C. avenacea* and *C. clandestina* (*C. diandra* had been transferred to *Cyathochaeta* by Nees in 1846).

In the same year, Mueller (1855) published a new Australian species, *Carpha nivicola* F.Muell., which he (1875) subsequently included in *C. alpina*, as did later authors (e.g. Bentham 1878; Pfeiffer 1931; Kükenthal 1939c). But more recently Blake (1940), Costin et al. (1979), Thompson (1981), Thompson and Gray (1981) and Wilson (1993, 1994a, 1994b) all regarded this as a separate species. Mueller (1875) also transferred Brown's five species (*Carpha alpina*, *C. deusta*, *C. avenacea*, *C. diandra* and *C. clandestina*) to the genus *Chaetospora*, but no later author has accepted this transfer. *Chaetospora* was described by Brown (1810). He included 15 species in this genus, most of which (11 species) are now regarded as species of *Schoenus*, and two others are now regarded as

belonging to the genus *Gymnoschoenus* and two to *Mesomelaena*. None of these 15 species is very similar to *Carpha* in morphology.

Philippi described two new South American species in *Carpha*: *C. paniculata* Phil. (Philippi 1857–58, p. 80) and *C. andina* Phil. (Philippi 1873, after Pfeiffer 1927 and Kükenthal 1938). *Carpha paniculata* Phil. was referred to *C. laxa* (Hook.f.) H.Pfeiff. (Pfeiffer 1927), which was in turn referred to *Schoenus rhynchosporoides* (Steud.) Kük. (Kükenthal 1938). *Carpha andina* Phil. was transferred to *Schoenus andinus* (Phil.) H.Pfeiff. (Pfeiffer 1927).

Boeckeler (1874) published *Carpha junciformis* Boeck. from Sumatra, which was put in synonymy under *Cladium undulatum* Thwaites by Kükenthal (1942). This was in turn transferred to *Tricostularia* as *T. undulata* by Kern (1959). Boeckeler (1874) also combined the southern African genus *Asterochaete* with *Carpha* by transferring *A. glomerata* (Thunb.) Nees, *A. capitellata* Nees and *A. elongata* Kunth to *Carpha*, separating *A. arundinaceus* Kunth to *Carpha arundinacea* (Sol. ex Vahl) Boeck. and *Carpha urvilleana* Gaudich. ex Boeck. and putting *A. tenuis* Kunth as a synonym of *Carpha capitellata* (Nees) Boeck. and *A. nitens* Kunth as a synonym of *Carpha aubertii* Nees ex Boeck. Boeckeler held almost the same views as Kunth (1837) about *Carpha* except about glume arrangement, bristle number and stigma number (Table 1.2). A few years later, Boeckeler (1879) recognized a new African species, *Carpha schweinfurthiana* Boeck. This was soon placed in the genus *Eriospora* as *E. schweinfurthiana* (Boeck.) Benth. ex C.B. Clarke (Clarke 1894), then in the genus *Coleochloa* (Nelmes 1953) based on its characters of compressed culms; distichous leaves, with open sheath and deciduous blade; a line of hairs in the position of the ligule; a utricle; and free membranous pericarp.

Bentham (1878) restricted *Carpha* to *Carpha alpina* and transferred Brown's other three species to *Cyathochaeta* (spelt 'Cyathochaete' by Bentham) and *Mesomelaena*. *Carpha avenacea* and *C. clandestina* were transferred to the genus *Cyathochaeta* based on the spiral arrangement of glumes and *Carpha deusta* to the genus *Mesomelaena* based on its habit, the bristles and other characters. *Mesomelaena deusta* was later moved to the genus *Ptilanthelium* (Kükenthal 1939c), and recently re-named as *Ptilothrix* (Wilson 1994b). Bentham (1878, 1883) agreed with Hooker (1860, 1867) on the description of *Carpha*,

except on bristle number (Table 1.2), and considered that *Carpha* occurred in southern Australia, New Zealand, and South America.

Clarke transferred the Réunion species *Elynanthus borbonicus* Steud. to *Carpha* (1894), and sank the monotypic African genus *Oreograstis* K.Schum. (*O. eminii* K.Schum.) in *Carpha* (1902). He (1901) also transferred the South American *Chaetospora antarctica* Hook.f. to *Carpha* as *Carpha antarctica* (Hook.f.) C.B.Clarke, which was put in synonymy under *Schoenus antarcticus* (Hook.f.) Dusén by Kükenthal (1938). Clarke published the following new species and variety in *Carpha*: the African *C. bracteosa* and the Mascarenes *C. aubertii* Nees ex Boeck. var. *explicatior* (Clarke 1894); the Western Australian *C. graciliceps* (Clarke 1905) and the African *C. schlechteri* (Clarke 1904). He (1908) raised the variety *C. aubertii* Nees ex Boeck. var. *explicatior* to specific rank as *C. costulariodes*, which was later put in synonymy under *Costularia elongata* (Kunth) Kük. (Kükenthal 1939b). *Carpha graciliceps* was transferred to *Ptilanthelium* by Kükenthal (1939d), and later to *Mesomelaena* by Wilson (1981). Clarke's view of *Carpha* was almost the same as that of Boeckeler (1874) except in describing nut number per spikelet and bristle number per flower (Table 1.2). He agreed with Hooker's (1860, 1867) view of the spikelet of *Carpha* as having an empty uppermost glume (Table 1.2). He considered that there were 13 species in the genus, native to the Southern Hemisphere: South America, Africa and Australia.

Gandoger (1919) added two new Australasian species to *Carpha*. They were *C. tasmanica* Gand. and *C. novae-zelandiae* Gand., which were put in synonymy under *C. alpina* by Pfeiffer (1931). This has been followed by all later authors.

Chermezon described two new species of *Carpha*: *C. perrieri* Cherm. (1922) from Madagascar and *C. angustissima* Cherm. (1935) from Africa. The latter was reduced to a variety by Kükenthal as *C. eminii* var. *angustissima* (Cherm.) Kük. (1939d), but this was not accepted by some authors (e.g. Haines and Lye 1983).

Pfeiffer (1927) moved the South American *Chaetospora laxa* Hook.f. to *Carpha* as *Carpha laxa* (Hook.f.) H.Pfeiff. and put *C. paniculata* Phil. in synonymy under *Carpha laxa*. Later *Carpha laxa* (Hook.f.) H.Pfeiff. was transferred to *Schoenus* as *S. rhynchosporoides* (Steud.) Kük. A few years later, Pfeiffer (1931) combined *C. tasmanica* Gand. and

C. novae-zelandiae Gand. with *C. alpina* R.Br. as indicated above. He also sank the African genus *Ecklonea* (*Trianoptiles*) in *Carpha*, moving its two species (*E. capensis* Steud. and *E. solitaria* C.B.Clarke) to *Carpha*. Later Kükenthal (1939c) described the subgenus *Trianoptiles* under *Carpha* for these two species, based on the species having three perianth parts, each with three bristles at the apex. The subgenus was raised to the level of genus by Levyns (1943) based on the perianth and on the plant possessing female 1-flowered basal spikelets.

Kükenthal (1939c, 1939d) published a treatment of *Carpha* in his series of preliminary papers towards a monograph of Rhynchosporoideae. His important work is listed below; he:

- recognized two subgenera in *Carpha*: *Trianoptiles* and *Eu-Carpha* [= *Carpha*];
- described a new Japanese species (*Carpha aristata*);
- described a new Australian variety (*C. alpina* R.Br. var. *subacaulis*, which was combined with *C. nivicola* by Wilson 1994);
- reduced *C. schoenoides* Banks et Sol. ex Hook.f. to a variety of *C. alpina*;
- reduced *C. angustissima* Cherm. to *C. eminii* var. *angustissima* (Cherm.) Kük.;
- reduced *C. bracteosa* C.B.Clarke to *C. capitellata* (Nees) Boeck. var. *bracteosa* (C.B.Clarke) Kük.;
- gave the legitimate name *C. nitens* (Kunth) Kük. to *C. aubertii* Nees ex Boeck.;
- moved *C. graciliceps* C.B.Clarke (as ‘gracilipes’) and *C. deusta* R.Br. to *Ptilanthelium* (1939d);
- moved *C. elongata* Boeck., *C. arundinacea* (Sol. ex Vahl) Boeck., *C. urvilleana* Gaudich. ex Boeck., *C. aubertii* Nees ex Boeck. var. *explicatior* C.B.Clarke and *C. costularioides* C.B.Clarke to *Costularia* (Kükenthal 1939a, 1939b);
- moved *Carpha laxa* (Hook.f.) H.Pfeiff. and *C. paniculata* Phil. to *Schoenus* (1938); and
- moved *C. hexandra* Nees to *Tetraria* (Kükenthal 1940b) as *T. hexandra* (Nees) Kük., which was later transferred to *Cyathocoma* as *C. hexandra* (Nees) J.Browning (Browning and Gordon-Gray 1996b).

Kükenthal’s definition of *Carpha* was almost the same as that of Clarke (1902) except regarding the spikelets of all the species in *Carpha* having an empty uppermost glume (Table 1.2). He included 11 species and three varieties in the genus and considered that

Carpha occurred in southern and central Africa, Madagascar, Mascarenes, Australia, New Zealand, New Guinea, southern Japan and South America.

There has been no world-wide revision of *Carpha* since the work of Kükenthal, but only some local Floras.

Koyama (1961) in his revised classification of the family Cyperaceae designated *Carpha alpina* R.Br. as the lectotype of the genus *Carpha*.

Levyns (1947, p. 81) considered that species of *Asterochaete* that were sunk in *Carpha* by Boeckeler and followed by many authors were 'confined to southern Africa and on floral structure they merit their separation from *Carpha*'. She (1950) adopted *Asterochaete* for two species of *Carpha* in "Flora of the Cape Peninsula" and treated *C. capitellata* and *C. bracteosa* as conspecific.

Kern (1974) described *Carpha* as having a plumose perianth in "Flora Malesiana" (Table 1.2). However, while describing the distribution of *Carpha*, he included South Africa, in whose species the perianth is not plumose.

Haines and Lye (1983, p. 321) mentioned the different descriptions of *Carpha*, and wrote that 'the genus is usually defined as having plumose perianth-segments, but our species have not, perhaps because efficient wind-transport would course [cause] too great loss of fruits in a limited mountain area.' They described spikelets in *Carpha* as sometimes having 1–2 terminal empty scales. This is different from all other former authors who described spikelets in *Carpha* as either without an empty uppermost glume or with one empty uppermost glume.

Reid and Arnold (1984, p. 139) added a new African species of *Carpha* (*C. filifolia*). They described its spikelet as 'composed of 4–5 spirally arranged glumes'. This is in contrast to most authors who have accepted that glumes are distichous in *Carpha*, not spirally arranged. They (1984) treated *Carpha bracteosa* as a distinct species rather than as a variety or a synonym of *C. capitellata* (Kükenthal 1939c; Levyns 1950).

In the same year, two Australian new species, *Carpha curvata* W.M.Curtis and *C. rodwayi* W.M.Curtis, were described from Tasmania (Curtis 1984).

The descriptions by Bruhl et al. (1992) and Goetghebeur (1998) of *Carpha* are the same as those of Kükenthal (1939c) except with regard to bristle number. This is because the subgenus *Trianoptiles* with three bristles was already reinstated as a genus (Table 1.2). They estimated 13–15 species in *Carpha*, distributed in the southern and central African mountains, Madagascar, Mascarenes, New Guinea, southern Japan, southeastern Australia, New Zealand and Chile. Their studies are on the generic level and above, so there was no detailed information on species and infraspecific taxa.

Wilson (1986, 1993, 1994a, 1994b) held a different view from these other recent authors (Table 1.2). She agreed with Bentham (1878, 1883) and suggested that the genus should be regarded as having 1-flowered spikelets; 4–5 distichous glumes, the lower ones empty, about half the size of the upper glumes, the uppermost glume bristly to linear, empty; 6 plumose hypogynous bristles; and 3 stigmas. She recognized 4–5 species in the genus, found in Australia, New Guinea, New Zealand and South America.

After so many changes (Figs 1.2, 1.3; Table 1.3), the following species are included in a broadly circumscribed *Carpha*, although some of them are not clearly defined:

- 1) *C. alpina* R.Br.,
- 2) *C. angustissima* Cherm. (which is treated as a variety of *C. eminii* by some authors),
- 3) *C. aristata* Kük.,
- 4) *C. borbonica* (Steud.) C.B.Clarke,
- 5) *C. capitellata* (Nees) Boeck.,
- 6) *C. bracteosa* C.B.Clarke (which is treated as a variety or a synonym of *C. capitellata* by some authors),
- 7) *C. curvata* W.M.Curtis,
- 8) *C. eminii* (K.Schum.) C.B.Clarke,
- 9) *C. filifolia* Reid & T.H.Arnold,
- 10) *C. glomerata* (Thunb.) Nees,
- 11) *C. nitens* (Kunth) Kük.,
- 12) *C. nivicola* F.Muell. (which was sunk in *C. alpina* by some authors),

- 13) *C. perrieri* Cherm.,
- 14) *C. rodwayi* W.M.Curtis,
- 15) *C. schlechteri* C.B.Clarke, and
- 16) *C. schoenoides* Banks et Sol. ex Hook.f. (which is treated as a variety of *C. alpina* by some authors or sunk in *C. alpina* by some other authors).

What are the defining generic characteristics of *Carpha* (e.g. glume arrangement: spiral, subdistichous or distichous; flower number per spikelet: 1 or 1–2–3; uppermost glume fertile or sterile; bristle shape: plumose or capillary; bristle number: 3–6 or 6; stigma number: 2–3 or 3)? Two different definitions of the genus (Table 1.2), can be recognized. The first was/is held by various systematists (Clarke 1902, 1908; Kükenthal 1939c; Haines and Lye 1983; Bruhl et al. 1992; Goetghebeur 1998), who accepted the genus as having spikelets with 1–2 (–3) flowers, 3–6 (–8) glumes, 6 hypogynous bristles, plumose or with spine-like hairs or short spine-like teeth or antrorsely scabrous. This broad definition considers that there are about 13–15 species in *Carpha*, occurring in Africa, the Pacific, and South America. The other definition was/is held by Hooker (1860, 1867), Bentham (1878, 1883) and Wilson (1993, 1994). They have maintained that *Carpha* has 1-flowered spikelets, 4–5 glumes, 6 subequal, plumose hypogynous bristles, and its species occur in southern Australia, New Zealand, New Guinea and South America. This is a *sensu stricto* definition relative to the first one. According to this point of view, there are four or possibly five species in *Carpha*. They are *C. alpina* R.Br., *C. nivicola* F.Muell. (which was sunk in *C. alpina* by some authors), *C. curvata* W.M.Curtis, *C. rodwayi* W.M.Curtis and *C. schoenoides* Banks and Sol. ex Hook.f. (which is treated as a variety of *C. alpina* by some authors or as a synonym of *C. alpina* by others). The latter definition is supported by the view that southern African species merit separation from *Carpha* as *Asterochaete* (Levyns 1947, 1950). In this thesis, ‘*Carpha*’ refers to the former definition (i.e. *Carpha sensu lato*) until section 6.3.

1.7 Objectives of the Study

The brief review above of systematic methodology, species concept for practical application, systematic study in Schoeneae (Cyperaceae) and the taxonomic history of *Carpha* highlights that: 1) cladistics is an appropriate method to study phylogenetic relationships between species or at higher levels but should not usually be used at lower

taxonomic levels; 2) phenetics is an appropriate method to study patterns of variation at species and infraspecific levels, i.e. to identify and test definitions and limits of species; 3) there are conflicting interpretations of spikelet morphology and a detailed study of spikelet morphology is necessary to clarify our understanding of spikelet structure in Schoeneae; 4) within Schoeneae, phylogenetic relationships are not fully understood; some species and generic limits of *Carpha* are not clearly defined; 5) many species were moved out of *Carpha*, but are they closely related to *Carpha* and are these changes justified and 6) no study on phylogenetic relationships has been conducted within *Carpha*. Thus, this study aims to:

- 1) provide an improved understanding of spikelet structure of Schoeneae, test competing interpretations of spikelet morphology, and clarify some relevant interpretations and concepts;
- 2) identify and test limits of species of *Carpha* using phenetic analyses;
- 3) estimate the phylogeny of *Carpha* and its relatives using cladistic analyses of morphological and molecular data, and thereby test its monophyly and define generic limits of *Carpha*; and
- 4) taxonomically revise *Carpha* according to the results of phenetic and cladistic analyses.