

Phylogeny of *Carpha* and related genera (Schoeneae, Cyperaceae) inferred from morphological and molecular data

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Abstract. The limits, definitions and relationships of *Carpha* have been controversial and unclear. This study using cladistic analyses of morphological and combined morphological and molecular data indicates that: (1) *Carpha sensu lato* is paraphyletic and its species form two clades, consistent with the definitions of *Carpha sensu stricto* and *Asterochaete* respectively (i.e. the data support the division of *Carpha sensu lato* into two genera: *Carpha sensu stricto* and *Asterochaete*); (2) the morphological data show a high degree of homoplasy within Schoeneae; (3) Schoeneae is not a monophyletic tribe; (4) *Schoenus* and *Tricostularia* are polyphyletic; (5) it is better to place *Schoenoides* back in *Oreobolus*; (6) separation of *Capeobolus brevicaulis* from *Costularia* or *Tetraria* is supported; and (7) both genera *Costularia* and *Tetraria* should be maintained. The study resolves some phylogenetic relationships between *Carpha* and its relatives. Many aspects of these relationships are in agreement with previous studies, but some of these relationships have no support. The study also resolves the phylogenetic relationships of species of *Carpha*, although with lack of support for some clades, highlighting the need for other sources of data.

Introduction

The genus *Carpha* belongs to the tribe Schoeneae of the family Cyperaceae (Clarke 1908; Kükenthal 1940*b*, 1944; Goetghebeur 1986, 1998; Bruhl 1995). Schoeneae has been defined differently by different authors (see Zhang 2002 for a review of Schoeneae). Clarke (1908) divided the tribe Rhynchosporae, as delimited in the classification of Bentham (1883), into two tribes, Rhynchosporae and Schoeneae. He included 21 genera in the tribe Schoeneae. Kükenthal (1940*b*, 1944, 1952) kept eight genera that have a distichous arrangement of the glumes as his Schoeneae and put all the other genera of Schoeneae of Clarke (1908) in the tribe Cladieae. Goetghebeur (1986) and Bruhl (1995) divided the tribe Rhynchosporae of Bentham (1883), Koyama (1961), Schultze-Motel (1964) and Hooper (1973) into three tribes: 'Arthrostylideae' (informally proposed by Goetghebeur 1986), Rhynchosporae and Schoeneae. Their 'Arthrostylideae' is a small tribe of three monotypic genera (*Arthrostylis*, *Trachystylis* and *Trichoschoenus*) and one with three species (*Actinoschoenus*). Their Rhynchosporae is composed of *Micropapyrus*, *Pleurostachys*, *Rhynchospora* and *Syntrinema*. The remaining genera of the tribe Rhynchosporae of Bentham (1883), Koyama (1961), Schultze-Motel (1964) and Hooper (1973) are in Schoeneae. Goetghebeur (1986) included 24 genera in the Schoeneae. Bruhl (1995) recognised three more segregate genera (*Lophoschoenus*, *Schoenoides*, *Tetrariopsis*) in the Schoeneae. Goetghebeur (1998) combined two tribes 'Arthrostylideae' and Rhynchosporae of Goetghebeur (1986)

and Bruhl (1995) in the Schoeneae and included 29 genera in the tribe. The cladistic analysis of Muasya *et al.* (1998) recovered the Rhynchosporae of Goetghebeur (1986) and Bruhl (1995) as a monophyletic group (using a sample of only *Rhynchospora* and *Pleurostachys*) and Schoeneae as a paraphyletic group (because *Cladium* was sister to most genera in Cyperaceae). The classifications of Goetghebeur (1986) and Bruhl (1995) 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.

Within Schoeneae, generic limits have not been always clearly defined or 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 1939*b*), *Trianoptiles* (*Ecklonea*) (Clarke 1897–1898; Kükenthal 1939*b*), *Costularia* (Kükenthal 1939*b*), *Ptilothrix* (*Ptilanthelium* auct.) (Kükenthal 1939*c*), *Gymnoschoenus* (Kükenthal 1940*a*) and *Mesomelaena* (Kükenthal 1940*a*). The results of 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*, whereas Bruhl's (1995) analyses showed *Oreobolus*, *Schoenoides*, *Ptilothrix*, *Trianoptiles* and *Carpha* to be a robust group, with *Trianoptiles* sister to *Ptilothrix*. Recent cladistic

analyses based on DNA sequence data (Zhang 2002; Zhang *et al.* 2004a) identified several well-supported lineages at the generic level within the tribe Schoeneae, and found *Trianoptiles* was sister to *Carpha*, *Ptilothrix* sister to *Cyathochaeta* rather than to *Carpha*, and *Gymnoschoenus* distant from *Carpha* and its close relatives. However, the data did not provide direct means for the interpretation of relationships among these well-supported lineages.

Since *Carpha* was first described by Brown (1810), over 40 names have been applied to species in the genus (Appendix 1). The definition of *Carpha* was modified as species were moved in and out the genus (Zhang 2002; Zhang *et al.* 2006). The limits of *Carpha* have been unclear and definition of the genus controversial, with two main definitions of *Carpha* based on flower number per spikelet and whether the hypogynous bristles are plumose or not. The first was/is held by various systematists (Clarke 1902, 1908; Kükenthal 1939b; 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, and six hypogynous bristles that are plumose or with spine-like hairs or short spine-like teeth or antrorsely scabrous. This broad definition considers that there are ~13–15 species in *Carpha*, occurring in Africa, the Pacific, and South America. The other, narrower definition was/is held by Hooker (1860, 1867), Bentham (1878, 1883) and Wilson (1993, 1994a). They have maintained that *Carpha* has 1-flowered spikelets, 4 or 5 glumes, and six subequal, plumose hypogynous bristles, with its species occurring 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*. The findings of a phylogenetic study on generic limits of *Carpha* based on DNA sequence data (Zhang 2002; Zhang *et al.* 2004a) did not clarify the ambiguous treatments of *Carpha*.

The relationships among the species of *Carpha* have not all been clear, although the cladistic analysis conducted on species of this genus based on DNA sequence data (Zhang 2002; Zhang *et al.* 2004a) resolved relationships of some species of *Carpha*, such as the close relationships of *C. alpina* to *C. curvata*, *C. nivicola* to *C. rodwayi*, and *C. filifolia* to *C. glomerata*.

This study addresses the following questions by using the cladistic analyses of morphological and combined morphological and molecular data. (1) Is *Carpha* monophyletic? (2) What are the relationships of *Carpha* and its relatives? Many species were moved out of *Carpha*, but are they closely related to *Carpha* and are these changes justified? (3) What are the relationships among the different species within *Carpha*?

Materials and methods

Cladistic analyses of morphological data

Species sampled

Within Schoeneae, 16 species of *Carpha* recognised by phenetic analyses (Zhang 2002; Zhang *et al.* 2006) and 29 species of relatives of *Carpha* were chosen as ingroups for cladistic analysis. A total of 262 herbarium specimens of 45 species sampled for ingroups are listed in Appendix 2 (available as an accessory publication on the web). The

sample included all species that were described in *Carpha* at various times (Appendix 1) with the exception of *Carpha schweinfurthiana* Boeck. That species has very different features from other species in *Carpha* (Nelmes 1953), and is now placed in *Coleochloa*, which is very distantly related to *Carpha* (Muasya *et al.* 1998). The sample also included species from all genera that were considered to be close relatives of *Carpha* (Clarke 1897–1898, 1902; Kükenthal 1939b, 1939c, 1940a; Goetghebeur 1986; Bruhl 1995; Zhang 2002; Zhang *et al.* 2004a) and from other genera of the tribe Schoeneae. Two specimens of *Tetraria capillaris* (Appendix 2) showed great differences in their morphology. For example, one had flowers with a perianth and the other had flowers without a perianth. Hence, they were treated separately in the cladistic analyses. A specimen of *Costularia pilisepala* (*L. J. Brass 8802*) from New Guinea showed some differences from the other two specimens (*W. L. Chew 4966*, *M. S. Clemens 51062*) from Borneo such as in having curling leaves and a dense inflorescence. This specimen (*L. J. Brass 8802*) was also treated separately in the cladistic analyses and labelled as '*Costularia pilisepala2*'.

Two species (six specimens) of *Rhynchospora* in the tribe Rhynchosporae, which is considered to be closely related to Schoeneae, and two species (five specimens) of *Scleria* in the tribe Sclerieae, which is supposed to be more distantly related (Bentham 1883; Koyama 1961; Schultze-Motel 1964; Hooper 1973; Goetghebeur 1998), were chosen as outgroups (Appendix 2).

Characters

Ninety-four morphological characters (37 quantitative and 57 qualitative) were included in this cladistic analysis (Table 1), representing aspects of growth habit, and vegetative and reproductive morphology. The annotated characters are listed in DELTA format (Dallwitz *et al.* 1999) in Appendix 3 (available as an accessory publication on the web).

Morphological observations were made with Stemi 2000 Zeiss (Zeiss, Jena, Germany) or Leica MZ75 (Leica, Heerbrugg, Switzerland) dissecting microscopes. Glumes were removed carefully from base to apex of a spikelet to reveal details of 'rachilla' and flowers. Herbarium material was softened by boiling in water with a drop of domestic detergent where necessary. Characters related to spikelet, flower and nut morphology, and those involving measurements of less than 1 cm were measured with an ocular micrometer in dissecting microscopes at 10–20 \times . Otherwise, measurements were made with a ruler. Nuts from herbarium specimens, after removal of selected perianth parts where necessary, were mounted on stubs using double-sided tape, sputter-coated with gold using a SEM coating unit E5100, and viewed under a JEOL JSM-5800LV scanning electron microscope (JEOL, Tokyo, Japan) operated at 15 kV.

The value of each of the quantitative characters for each species was the mean value of sampled specimens. For qualitative characters, states recorded for each species were used.

Character coding and weighting

The 37 quantitative characters (i.e. characters 3, 5, 6, 17, 18, 22–24, 27, 29–31, 34, 38, 40, 42–47, 53, 55, 59, 63,

Table 1. Morphological characters and coded character states used in the cladistic analyses

Ordered characters are indicated. See Appendix 3 for character explanation and units

No.	Character
1.	Rhizome: absent (0), present (1).
2.	Lifeform: annual (0), perennial (1).
3.	Plant height from ground level to top of plant, including inflorescence (ordered).
4.	Culm shape in cross-section: triangular (0), narrow-elliptical or fusiform (1), obtusangular-circular (2).
5.	Fertile node number (see Reid and Arnold 1984) (ordered).
6.	Sterile node number (cauline leaves; see Reid and Arnold 1984) (ordered).
7.	Leaf sheath colour: brownish includes yellow-green to brown (0), reddish includes red to dark red (cf. <i>Schoenus andinus</i> , <i>S. rhynchosporoides</i> , <i>S. antarcticus</i>) (1).
8.	Ligule: absent (0), present (1).
9.	Ligule whether ciliate: glabrous (0), ciliate (1).
10.	Contraflagellum: absent (0), present (cf. <i>Scleria levis</i>) (1).
11.	Pseudopetiole: absent (0), present (1).
12.	Leaf blade whether curling (see Curtis 1984): curled for at least one third of its length (0), only leaf tips curled (1), not curled (2).
13.	Leaf blade whether spirally twisted: not spirally twisted (0), spirally twisted (e.g. the leaves of <i>Cyathochaeta diandra</i> , <i>C. avenacea</i> and some of <i>C. clandestina</i>) (1).
14.	Leaf whether rigid: not rigid (0), rigid (1).
15.	Leaf blades with a median stomate-less longitudinal band adaxially between two faint or obvious veins (Wilson 1993): absent (0), present (1).
16.	Leaf blade shape in cross-section at mid-third: V-shaped (0), subcircular-circular (1), thinly crescentiform or flat (includes shallowly corrugate) (2), thickly crescentiform (includes sub-triangular, thickly V-shaped and subhemispherical) (3).
17.	Mature longest leaf blade length (ordered).
18.	Mature widest leaf blade maximum width (ordered).
19.	Involucral bract sheath colour: brownish includes yellow-green to brown (0), reddish includes red to dark red (cf. <i>Schoenus andinus</i> , <i>S. rhynchosporoides</i> , <i>S. antarcticus</i>) (1).
20.	Involucral bract type: ovate (i.e. bract-like) (0), linear-lanceolate (i.e. leaf-like) (1).
21.	Ovate involucral bracts type: ovate without long apices (0), ovate with long leaf-like apices (1).
22.	Proximal involucral bract length including sheath (ordered).
23.	Proximal involucral bract blade maximum width (ordered).
24.	Inflorescence length (ordered).
25.	Spikelets, whether all enclosed by involucral bracts: not all enclosed by involucral bracts (0), all enclosed by involucral bracts (1).
26.	Spikelets, whether densely clustered: densely clustered (0), loosely clustered (1).
27.	Head(s) number per inflorescence (see Clarke 1897–1898) (ordered).
28.	Shape of the head(s) formed by spikelets: ovoid (0), oblong-ellipsoid (1), globose (2), obovoid or obconical or fan-shaped (3).
29.	Spikelet pedicel length (spikelet pedicel is enclosed by primary involucral bract sheaths) (ordered).
30.	Spikelet secondary pedicel length (spikelet pedicel is not enclosed by primary involucral bract sheaths) (ordered).
31.	Spikelet number per inflorescence (ordered).
32.	Basal spikelets: absent (0), present (cf. the species of <i>Trianoptiles</i>) (1).
33.	Male only spikelets: absent (0), present (1).
34.	Female-fertile spikelet length (excluding pedicel) (ordered).
35.	Glume colour: brownish includes yellow green to brown (0), reddish includes red to dark red (cf. <i>Schoenus andinus</i> , <i>S. rhynchosporoides</i>) (1).
36.	Glume arrangement: spiralled (0), distichous (1).
37.	Lower glumes relative length to upper glumes within a spikelet: shorter than upper glumes (0), longer than upper glumes (1).
38.	Glume number per spikelet (ordered).
39.	Glumes whether persistent: all glumes persistent (0), lower sterile glumes persistent (1), all glumes deciduous (2).
40.	Proximal sterile glumes number (ordered).
41.	Uppermost glume: fertile (0), sterile (1).
42.	Proximal fertile glume length (including any awn) (ordered).
43.	Proximal fertile glume maximum width (ordered).
44.	Second fertile glume length (including any awn) (ordered).
45.	Second fertile glume maximum width (ordered).
46.	Third fertile glume length (including any awn) (ordered).
47.	Third fertile glume maximum width (ordered).
48.	'Rachilla', whether elongated above fertile flower: not elongated above fertile flower (0), elongated above fertile flower (1).
49.	'Rachilla', whether adnate to fertile glume base: not adnate to fertile glume base (0), adnate to fertile glume base (1).
50.	Bisexual flowers: absent (0), present (1).
51.	Female only flowers: absent (0), present (1).
52.	Male only flowers: absent (0), present (1).
53.	Flower number per female-fertile spikelet (including all kind of flowers: bisexual, male and female flower in spikelet) (ordered).
54.	Perianth: absent (0), present (1).
55.	Perianth member number (ordered).

Table 1. (continued)

No.	Character
56.	Perianth whorls: one whorl (0), two whorls (1).
57.	Perianth members whether inner whorl and outer whorl more or less equal in length: inner whorl more or less equal in length to outer whorl (0), inner whorl much longer than outer whorl (1).
58.	Perianth members whether more or less equal in length within a whorl: obviously unequal in length within a whorl (0), more or less equal in length within a whorl (1).
59.	Maximum perianth length (ordered).
60.	Perianth member type: bristles (0), scales (1).
61.	Perianth members, whether glabrous: glabrous (0), not glabrous (scabrous or with some hairs) (1).
62.	Perianth bristles whether plumose: plumose (0), scabrous (1).
63.	Plumose perianth trichomes maximum length (ordered).
64.	Plumose perianth scabrous zone maximum length (ordered).
65.	Perianth members whether trifid: not divided (0), trifid (1).
66.	Perianth members whether twisted at maturity: not twisted (0), twisted (1).
67.	Perianth scales whether with a dense tuft of hairs on the adaxial surface: without a dense tuft of hairs on the adaxial surface (0), with a dense tuft of hairs on adaxial surface (cf. <i>Trianoptiles stipitata</i>) (1).
68.	Perianth members whether base fused into a band: base not fused into a band (0), base fused into a band (cf. <i>Cyathocoma hexandra</i>) (1).
69.	Perianth member, whether forming a disc at base of fruit: absent (0), present (cf. <i>Scleria</i> , there is a disc at base of fruit, usually falling with the mature nut) (1).
70.	Perianth: deciduous from spikelet (0), persistent on spikelet (1).
71.	Stamen number per flower (ordered).
72.	Stamen filaments whether persistent around fruit: deciduous separately from fruit (0), persistent around fruit (1).
73.	Anthers colour: anthers green-yellow (0), anthers red-brown (1).
74.	Anther length excluding apical appendage (ordered).
75.	Anther apical appendage length (ordered).
76.	Anther apical appendage maximum width (ordered).
77.	Stigma number (ordered).
78.	Style base: not enlarged (0), enlarged (1).
79.	Style base: deciduous (0), persistent (1).
80.	Persistent style base length (ordered).
81.	Persistent style base maximum width (ordered).
82.	Fruit number per spikelet (ordered).
83.	Fruit shape in the broadest lateral view: elliptic (0), obovate (1), ovate (2), subcircular-circular (3), lanceolate to narrow-oblong (4).
84.	Fruit shape in cross-section: trigonous (1), subcircular to circular (2), biconvex (3), crescentiform (cf. species of <i>Cyathochaeta</i>) (4).
85.	Fruit colour at maturity: white (1), red (2), brown (pale brown to dark brown) (3).
86.	Fruit whether with tapered apex: without tapered apex (0), with tapered apex (cf. <i>Oreobolus oxycarpus</i>) (1).
87.	Fruit whether with loose outermost layer (see Wilson 1993): without loose outermost layer (0), with loose outermost layer (cf. <i>Gymnoschoenus sphaerocephalus</i>) (1).
88.	Fruit surface whether reticulate: not reticulate (0), reticulate (1).
89.	Fruit surface whether rugose (see Bruhl 1995): not rugose (0), rugose (1).
90.	Fruit surface whether punctulate: not punctulate (0), punctulate (1).
91.	Fruit length (excluding stalk and persistent style base) (ordered).
92.	Fruit maximum diameter (ordered).
93.	Gynophore: absent (0), present (cf. <i>Mesomelaena graciliceps</i>) (1).
94.	Fruit stalk length (ordered).

64, 71, 74–77, 80–82, 91, 92, 94) were coded by the gap weighting method (Thiele 1993) because this coding method uses range-standardisation and retains information on both the rank order of states and the sizes of the gaps between states (Thiele 1993; Kitching *et al.* 1998). Among currently available methods for coding quantitative data, gap weighting is among the best at retaining phylogenetic information as argued by Lee *et al.* (2001).

To maximise the utilisation of the raw data, a suitable state number of each quantitative character for gap weighting should be a maximum that must be within the maximum number of states allowed by the computer program (Kitching *et al.* 1998). In this study, the state number was determined to be 24 for the following reasons. The first is that it is under the limit of

26 and 32 imposed by MacClade (Maddison and Maddison 1992) and by PAUP* (Swofford 2000) respectively. The second is that after gap weighting, qualitative characters must be weighted to maintain parity with quantitative characters, i.e. the qualitative character should be weighted to have the same maximum state value (i.e. 24) as quantitative characters, and the number ensures an integer weight for each qualitative character for convenience in weighting. Qualitative characters in this study (Table 1 and Appendix 3) have 2–5 states. The binary-state qualitative characters (0, 1) were weighted by 24, three-state characters (0, 1, 2) by 12, four-state characters (0, 1, 2, 3) by eight and five-state characters (0, 1, 2, 3, 4) by six. The full morphological data set for cladistic analysis is available on request from the authors.

Cladistic analyses

The data set including all ingroups and outgroups was analysed phylogenetically using PAUP* 4.0b8 (Swofford 2000) for Windows. The quantitative characters and qualitative characters were treated as ordered and unordered respectively in the analysis. The characters were polarised by the outgroup method. Heuristic searches were conducted using maximum parsimony with TBR branch swapping. Random-taxon addition (1000 replicates) was employed to search for multiple islands of trees. Branch length for trees was calculated using the accelerated transformation optimisation (ACCTRAN; the default). Bootstrapping analysis (Felsenstein 1985) using heuristic search with random addition on 1000 bootstrap replicates was performed in PAUP* to determine relative support for various clades found in the parsimony analysis. Jackknife analysis (Farris *et al.* 1996) using random addition on 1000 jackknife replicates of heuristic search with 37% of characters deleted per run was also performed in PAUP*.

After analysis, the position of the outgroup taxon *Rhynchospora* violated the initial assumption of ingroup monophyly (see Fig. 1). To investigate whether this result is affected by character polarity, i.e. outgroup taxa, an analysis excluding two species of *Scleria* and using only two species of *Rhynchospora* as outgroups was conducted using the same methods of character coding and weighting and cladistic analysis described above.

Cladistic analyses of combined morphological and molecular data

Sampling

The species sampled in the molecular data (Zhang 2002; Zhang *et al.* 2004a) were basically a subset of those sampled for the morphological data here. Only the species sampled for both data sets were included in this combined analysis: *Carpha alpina*, *C. capitellata*, *C. curvata*, *C. filifolia*, *C. glomerata*, *C. nitens*, *C. nivicola*, *C. rodwayi*, *Cyathochaeta diandra*, *Gahnia sieberiana*, *Gymnoschoenus sphaerocephalus*, *Oreobolus distichus*, *O. pumilio*, *Ptilothrix deusta*, *Schoenoides oligocephalus*, *Schoenus paludosus*, *S. turbinatus*, *Trianoptiles solitaria*, *Tricostularia pauciflora* and outgroups *Rhynchospora brownii* and *R. corymbosa*. Of these species with more than one sample in the molecular data set, only the samples *J. J. Bruhl 1719* (*Carpha glomerata*), *J. J. Bruhl 1880B* (*Carpha alpina*), *J. J. Bruhl 1718* (*C. capitellata*), *J. J. Bruhl 1894* (*C. curvata*), *J. J. Bruhl 1868A* (*C. nivicola*), *J. J. Bruhl 1890A* (*C. rodwayi*) and *J. R. Hosking 1765* (*Trianoptiles solitaria*) were used in the combined cladistic analyses.

Characters

The same 94 morphological characters (37 quantitative and 57 qualitative) used in morphological analyses and the same alignment sequences used by Zhang (2002) and Zhang *et al.* (2004a) were combined in this cladistic analyses.

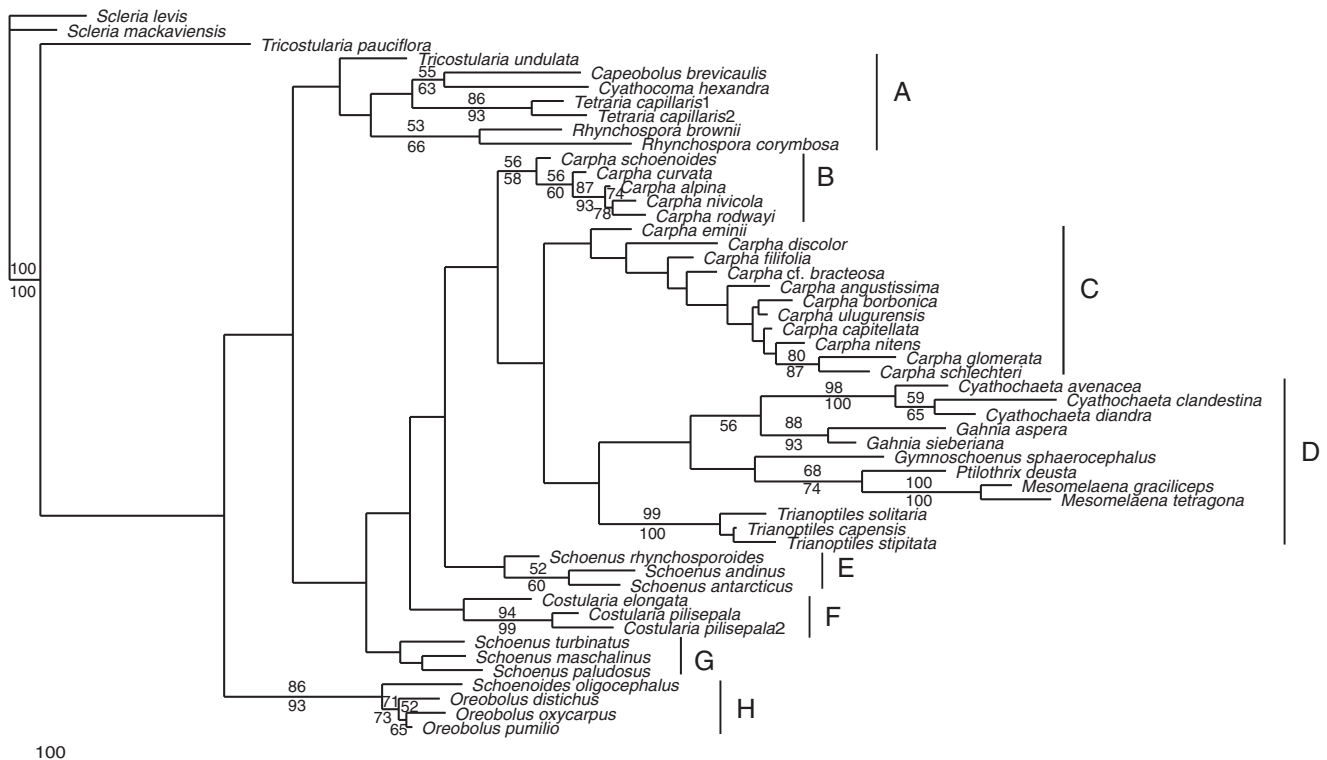


Fig. 1. The most parsimonious tree (length = 6821 steps, $CI = 0.3127$, $RI = 0.6036$) from the cladistic analysis of morphological characters included all ingroups (within Schoeneae) and outgroups (two species each of *Scleria* and *Rhynchospora*). Bootstrap values (>50%), for 1000 replicate analyses, are presented above the branches. Jackknife values (>50%), for 1000 replicate analyses, are presented below the branches. The major clades are labelled A–H.

Character coding and weighting

The 37 quantitative characters were coded using the same gap weighting (Thiele 1993) method referred to above. Qualitative characters were weighted using the same procedure as described earlier. A weight of 24 was applied to each molecular character to maintain the same weights as assigned to the 94 morphological characters, i.e. each molecular character was treated as a four-state character and weighted by eight. The combined data set for cladistic analysis is available on request from the authors.

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 incongruence length difference (ILD) test (Farris et al. 1994). The PTP test for the presence or absence of phylogenetic signal of two data sets was performed with 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 performed with PAUP* 4.0b8 (Swofford 2000) for Windows.

Cladistic analyses

Maximum parsimony analysis, bootstrap analysis and jackknife analysis of the combined data were carried out by the same methods as described above.

Results

Cladistic analyses of morphological data

Maximum parsimony analysis of the full morphological data set including all ingroups and outgroups resulted in one most parsimonious tree (Fig. 1), 6821 steps long, with a retention index of 0.6036 and consistency indices of 0.3272 including, and 0.3127 excluding, autapomorphies. To easily describe results, the major clades are labelled as A to H in Fig. 1.

The position of the outgroup taxon *Rhynchospora* violated the initial assumption of ingroup monophyly; it nested in Schoeneae. The clade formed by *Rhynchospora* and all the sampled species of Schoeneae has 100% bootstrap support (BS) and jackknife support (JN) (Fig. 1).

Cladistic analysis of the data set that excluded the two species of *Scleria* and used only two species of *Rhynchospora* as outgroups also resulted in one most parsimonious tree (Fig. 2), 6405 steps long, with a retention index of 0.6060 and consistency indices of 0.3297 including, and 0.3143 excluding, autapomorphies. This tree presented the same topology as in Fig. 1, but rooted with different taxa. The bootstrap and jackknife analyses also gave essentially the same results as in Fig. 1. Thus, all subsequent descriptions and discussions on BS and JN are based on the results presented in Fig. 1.

The bootstrap and jackknife analyses indicated that some clades were strongly supported, but others were relatively to very weakly supported by the data (Figs 1, 2). All traditional genera sampled formed monophyletic clades except for *Carpha*, *Schoenus* and *Tricostularia*. Most of these clades,

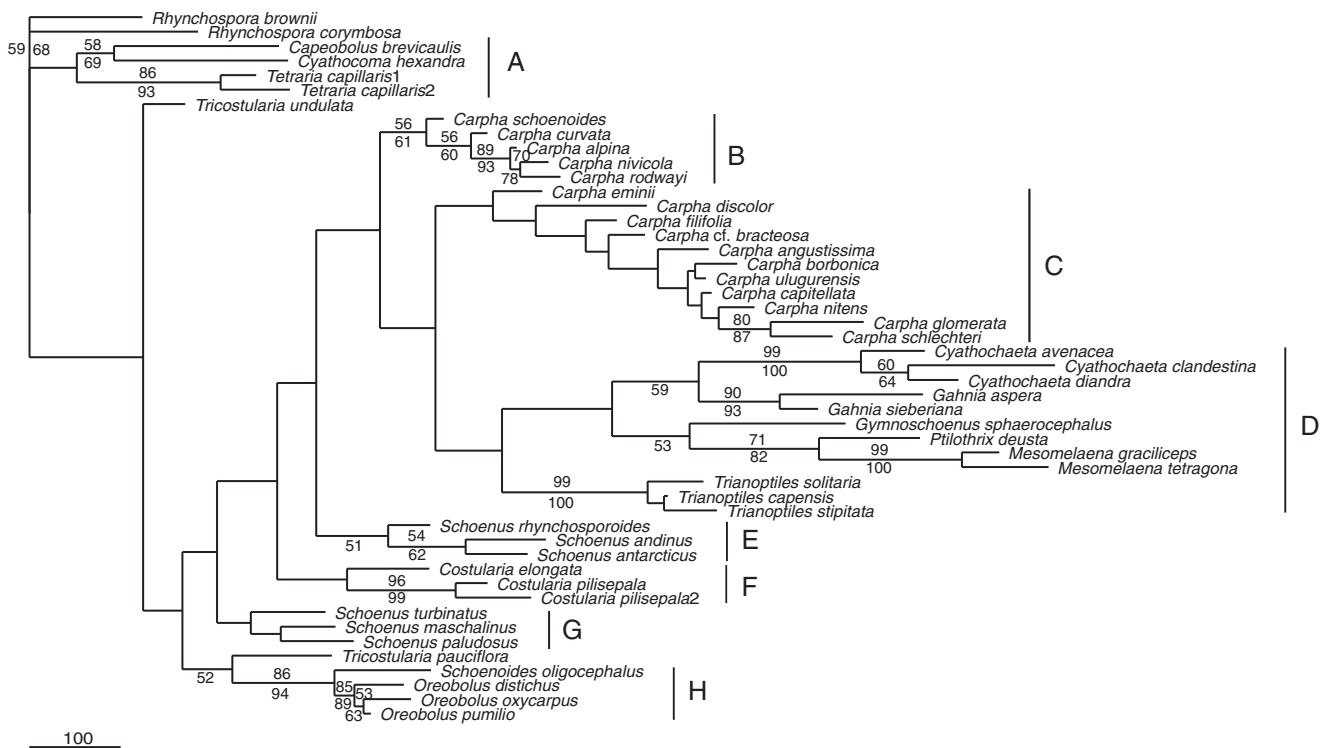


Fig. 2. The most parsimonious tree (length = 6405 steps, $CI = 0.3297$, $RI = 0.6060$) from the cladistic analysis of morphological characters included all ingroups (within Schoeneae) and outgroups (two species of *Rhynchospora*, i.e. excluding *Scleria* spp.). Bootstrap values (>50%), for 1000 replicate analyses, are presented above or on the left of the branches. Jackknife values (>50%), for 1000 replicate analyses, are presented below or on the right of the branches. The major clades (except A) are labelled the same as in Fig. 1.

such as *Tetraria*, *Cyathochaeta*, *Gahnia*, *Mesomelaena* and *Trianoptiles*, had over 86% BS and JN. Only the *Costularia* clade was without support (Figs 1, 2).

Within clade A in Fig. 1, *Capeobolus* and *Cyathocoma* came together in a group (55% BS and 63% JN), sister to which was *Tetraria* and then *Rhynchospora* (Figs 1, 2) but without support. The two specimens of *Tetraria capillaris* came together with 86% BS and 93% JN. Clade A in Fig. 2 consists of *Capeobolus*, *Cyathocoma* and *Tetraria* where *Rhynchospora* was used as an outgroup.

Carpha was separated into two clades, B and C (Figs 1, 2), indicating that *Carpha* is paraphyletic. Clade B consists of *C. alpina*, *C. curvata*, *C. nivicola*, *C. rodwayi* and *C. schoenoides* with 56% BS and 58% JN. Within this clade, the phylogenetic relationships among the five species were fully resolved with 56% or more BS and JN for each relationship (Figs 1, 2). *Carpha schoenoides* was sister to the rest of the species in this clade. *Carpha curvata* was closer to the other three species than was *C. schoenoides*. *Carpha alpina* was sister to the clade formed by *C. nivicola* and *C. rodwayi*.

Clade C was formed by all the other species of *Carpha*. The phylogenetic relationships among these species within clade C were not supported by bootstrap or jackknife except the relationship of *C. glomerata* and *C. schlechteri*, which were sister species with 80% BS and 87% JN. *Carpha capitellata* and *C. nitens* with *C. glomerata* and *C. schlechteri* formed a clade, and this was sister to the clade formed by *C. borbonica* and *C. ulugurensis*, and then, *C. angustissima*, *C. cf. bracteosa*, *C. filifolia* and *C. discolor* joined successively. *Carpha eminii* was basal to all other species within this clade.

According to the topologies (Figs 1, 2), clades D, E and F were closer to *Carpha* (i.e. clade B and C) than other clades but without BS and JN.

Within clade D (Figs 1, 2), *Ptilothrix* and *Mesomelaena* were sisters (68% BS and 74% JN), sister to which were *Gymnoschoenus* (no support), then the clade formed by *Cyathochaeta* and *Gahnia* (also no support), and then *Trianoptiles* (also no support).

Species of *Schoenus* formed two clades E and G (Figs 1, 2) indicating that *Schoenus* was polyphyletic. Species of *Costularia* formed clade F, but without support. Within this clade, *C. pilisepala2* and *C. pilisepala* formed a well-supported (94% BS and 99% JN) clade.

Clade H was a well defined monophyletic group formed by all the sampled species of *Schoenoides* and *Oreobolus* (86% BS and 93% JN), and within this clade *Schoenoides* was sister to *Oreobolus*.

The analyses (Figs 1, 2) also indicated that *Tricostularia* was polyphyletic, with its two representatives in different clades.

Cladistic analyses of combined morphological and molecular data

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 heterogeneous ($P = 0.001$), 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, 11 528 steps long, with a retention index of 0.6374 and consistency indices of 0.6626 (0.5512 excluding autapomorphies) (Fig. 3). The BS and JN for the clades, especially for the two clades of *Carpha*, generally increased in the cladogram resulting from the combined data set compared with the morphological data sets analysed (Figs 1, 2) and molecular analysis (Zhang 2002; Zhang *et al.* 2004a), although the ILD test showed significant incongruence between the two data sets.

Using two species of *Rhynchospora* as outgroups to root the phylogeny, a well-supported clade (100% BS and JN) formed by all species sampled in Schoeneae was revealed. Like the results derived from morphological data alone (Figs 1, 2), the analysis of the combined data (Fig. 3) showed *Carpha* was paraphyletic and grouped species of *Carpha* into two clades. One clade was consistent with clade B in Figs 1 and 2 with 99% BS and 100% JN, whereas the other clade was consistent with clade C in Figs 1 and 2 with 53% BS and 57% JN. Within these two clades of *Carpha*, *C. alpina* was sister to *C. curvata* with 67% BS and 76% JN, *C. nivicola* was sister to *C. rodwayi* with 75% BS and 85% JN, and the relationships of *C. filifolia*, *C. capitellata*, *C. glomerata* and *C. nitens* were consistent with the relationships seen in Figs 1 and 2.

Trianoptiles plus all species of *Carpha* formed a well-supported clade (100% BS and 100% JN), and within this clade, *Trianoptiles* was sister to the clade formed by *C. filifolia*, *C. capitellata*, *C. glomerata*, and *C. nitens* with 50% BS and 60% JN.

Like the results derived from morphological data alone (Figs 1, 2), *Oreobolus* and *Schoenoides* formed a well-supported clade (100% BS and JN) in the analysis of combined data, and within this clade *Schoenoides* was sister to *Oreobolus*. The clade formed by *Oreobolus* and *Schoenoides* was sister to the clade formed by *Carpha* and *Trianoptiles*, but without support.

The analysis of combined data also revealed the close relationship of *Cyathochaeta*, *Gahnia*, *Gymnoschoenus* and *Ptilothrix*. *Cyathochaeta* and *Ptilothrix* came together in a group (59% BS and 61 JN), sister to which was *Gahnia* (84% BS and 93 JN) and then *Gymnoschoenus* (without support). This analysis also indicated that *Schoenus* was not a monophyletic genus, with the two species sampled being paraphyletic (Fig. 3).

Comparing the results from the analysis of the combined data sets with those derived from morphological data alone (Figs 1–3), the differences between the two analyses were 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.

Discussion

The morphological data show a high degree of homoplasy as indicated by *CI* values of 0.3127 (51 taxa) and 0.3142 (49 taxa) respectively in the two morphological analyses of this study, which are among the lowest (indicative of a high

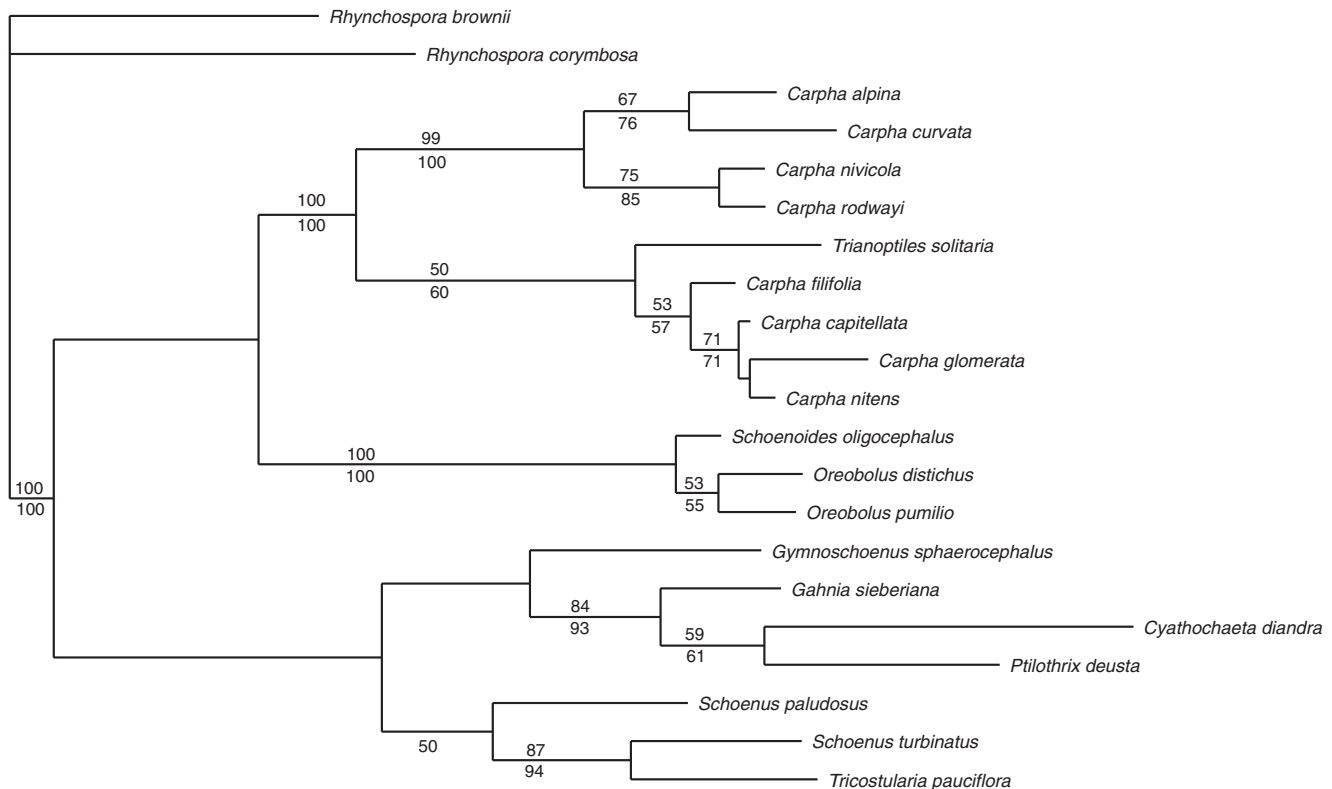


Fig. 3. The most parsimonious tree from cladistic analysis of combined morphological and molecular data of *Carpha* and its relatives, using *Rhynchospora* as outgroup. Bootstrap values (>50%), for 1000 replicate analyses, are presented above the branches. Jackknife values (>50%), for 1000 replicate analyses, are presented below the branches.

level of homoplasy) of the values reported in previous studies with a comparable number of taxa (Givnish and Sytsma 1997; Lowrey *et al.* 2001). The high level of morphological homoplasy within Schoeneae in this study is consistent with a previous morphological analysis of Cyperaceae with a comparable number of taxa (Muasya *et al.* 2000), which reported a *CI* of 0.28 (64 taxa). The high level of morphological homoplasy of Schoeneae may explain the lack of strong support for some of the clades within this assemblage.

Tribal limits of Schoeneae

The analysis of the full morphological data set including all ingroups and outgroups has *Rhynchospora* nested in Schoeneae (Fig. 1). The clade formed by *Rhynchospora* and all sampled species of Schoeneae in Fig. 1 is monophyletic with 100% BS and JN. The cladistic analysis of the morphological data set that excluded two species of *Scleria* and used only two species of *Rhynchospora* as an outgroup (Fig. 2) provided the same topology (i.e. the same relationship between species of *Rhynchospora* and species of Schoeneae) as in Fig. 1, indicating that the relationship between *Rhynchospora* and Schoeneae is not affected by outgroup taxa. Therefore, the analyses of morphological data indicate that Schoeneae is not monophyletic if *Rhynchospora* is separated from this tribe. The cladistic analysis of combined morphological and molecular data grouped all the sampled species of Schoeneae into a monophyletic

group using two species of *Rhynchospora* as outgroup members (Fig. 3), but this more limited combined analysis did not include species of *Scleria*, *Capeobolus*, *Cyathocoma* or *Tetraria*. Thus, the combined analyses did not provide a good test of corroboration and the conclusions 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. However, Goetghebeur (1998) suggested the need for a further division of Schoeneae due to the variation in embryo types among different genera of the tribe. 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.

Some generic and species definitions and limits within Schoeneae

The present analyses (Figs 1–3) indicate that, except for *Carpha*, *Schoenus* and *Tricostularia*, all currently recognised genera sampled form monophyletic clades. Most of these clades have strong BS and JN.

Carpha is paraphyletic and forms two clades in both the analyses of morphological and combined morphological and molecular data (Figs 1–3). One clade is composed of all

or sampled species of *Carpha sensu stricto* (Hooker 1860, 1867; Bentham 1878, 1883; Wilson 1986, 1993, 1994a, 1994b) with 56% BS and 58% JN or 99% BS and 100% JN respectively in morphological analyses and combined analysis. The other clade includes all or sampled species of the rest of the species of *Carpha sensu lato* that corresponded to the definition of *Asterochaete* (Nees 1834; Kunth 1837; Steudel 1855; Levyns 1950) without support or with 53% BS and 57% JN respectively in morphological analyses and combined analysis. This suggests *Carpha* should be separated as two different genera. The two clades also appeared in cladistic analyses based on DNA sequence data alone (Zhang 2002; Zhang *et al.* 2004a), suggesting 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 recognised *Carpha sensu lato*. This division into two genera is consistent with the previous views of some authors (Levyns 1947, 1950; Wilson 1986, 1993, 1994a, 1994b).

Schoenus is a large genus (~100 species) and the character state that has been used to distinguish this genus from other genera is the possession of the elongated and prominently zigzag internodes above the fertile nodes of the 'rachilla' (Clarke 1902; Kern 1974; Wilson 1993; Goetghebeur 1998). However, this character state (Table 1) is not shared by all species of *Schoenus*. Three species in the morphological analyses, *Schoenus rhynchosporoides*, *S. paludosus* and *S. turbinatus*, do not have elongated and prominently zigzag upper internodes of the 'rachilla' (also see Zhang *et al.* 2004b, fig. 5b–d for the 'rachilla'). Both the analyses based on morphological and combined data, even with the small sample, indicates the non-monophyletic status of *Schoenus* (Figs 1–3). This result is consistent with the molecular analyses (Zhang 2002; Zhang *et al.* 2004a). To reliably resolve the relationships and determine the limits of *Schoenus*, more thorough sampling and further analyses are required.

The analyses based on morphological data (Figs 1, 2) indicate that *Tricostularia* is polyphyletic. *Tricostularia* has been distinguished from other genera by its deciduous scale perianth and functionally male lower flower (Kern 1974; Wilson 1993; Goetghebeur 1998). The character of spikelets with a male flower is not shared by all species in *Tricostularia*. *Tricostularia undulata* does not have male-only flowers. Spikelets with a male flower (Table 1) occur in *Capeobolus brevicaulis*, *Carpha schlechteri*, *Costularia pilisepala*, *Schoenus paludosus* and *Tricostularia pauciflora* in this study. A perianth of scales (Table 1) is not a unique character for *Tricostularia* either, and is not shared by all members of the genus; for example, the perianth of *Tricostularia undulata* is composed of bristles rather than scales as defined in this study (Appendix 3), although Kern (1974) called them scales. Bruhl (1995, p. 210) noted that, 'the generic limits of *Tricostularia* warrant further attention'. More sampling and further studies are needed to define the limits of *Tricostularia* and clarify its phylogenetic relationships.

The South African endemic species *Capeobolus brevicaulis* was previously treated as *Costularia brevicaulis* (Clarke 1897–1898; Kükenthal 1939a; Browning and Gordon-Gray 1996) or *Tetraria brevicaulis* (Clarke 1894; Levyns 1947, 1950). It was amalgamated with *Costularia* in Seberg's (1986, 1988) cladistic analyses, but it failed to pair with *Tetraria* or

Costularia in Bruhl's (1995) analyses. Browning and Gordon-Gray (1999, p. 218) established a new genus, *Capeobolus*, for it because it differs from *Costularia* and *Tetraria* by its 'low growth form, reduced cryptic inflorescence, short non-plumose perianth outgrowths and shape and positioning of the embryo within the fruit'. Our cladistic analyses of morphological data found *Capeobolus* to be isolated from *Costularia* and *Tetraria* (Figs 1, 2). This result is consistent with Bruhl's (1995) findings and supports separating *Capeobolus* from *Costularia* and *Tetraria* as done by Browning and Gordon-Gray (1999).

Schoenoides oligocephalus was first described by Curtis (1984) as *Oreobolus oligocephalus*. It resembles *O. pumilio* in habit. Later, Seberg (1986) set up a monotypic genus *Schoenoides* for it because it differs from other species of *Oreobolus* in having almost capitate inflorescences and usually having two flowers per spikelet, rarely three or one, rather than a single flower per spikelet. Recently Goetghebeur (1998) merged *Schoenoides* back into *Oreobolus*. The results of our cladistic analyses based on morphological and combined data (Figs 1–3) indicated that *Schoenoides* is sister clade to *Oreobolus*; *Schoenoides* and *Oreobolus* together form a single well-supported clade (86% BS and 93% JN in the analyses based on morphological data, and 100% BS and 100% JN in the analysis based on combined data). The estimate of phylogeny based only on molecular data (Zhang 2002; Zhang *et al.* 2004a) had *Schoenoides* nested in *Oreobolus*. Thus, we conclude that the better treatment is to place *Schoenoides* back in *Oreobolus* as done by Goetghebeur (1998).

Koyama (1961) sank *Costularia* in *Tetraria*, and this was followed by Gordon-Gray (1995). The cladistic analyses based on morphological data showed the sampled species of the two genera formed two distant clades (Figs 1, 2). This result is consistent with previous cladistic analyses (Goetghebeur 1986; Bruhl 1995) and anatomical studies (Metcalf 1971), and indicates that both genera should be maintained.

Although the two specimens of *Tetraria capillaris* grouped together as expected with 86% BS and 93% JN in cladistic analyses of morphological data, the evident differences in their morphology suggest a further study, especially phenetic analysis with more samples, to determine species limits. Similarly, *Costularia pilisepala* and *C. pilisepala*2 formed a well-supported (94% BS and 99% JN) clade as expected in cladistic analyses of morphological data, but heterogeneities in their morphology might suggest a further study using phenetic analysis with more samples to determine species limits.

Phylogenetic relationships of Carpha and its relatives

Cladistic analyses of morphological data indicated that *Capeobolus* and *Cyathocoma* formed a clade with 55% BS and 63% JN, sister to which is *Tetraria* (clade A in Figs 1, 2). *Tetraria* being closer to *Cyathocoma* is consistent with the results of Goetghebeur's (1986) analysis.

Cladistic analyses of morphological data grouped *Cyathochaeta*, *Gahnia*, *Gymnoschoenus*, *Ptilothrix* and *Mesomelaena* (clade D in Figs 1, 2). This agrees with Goetghebeur's (1986) analysis with the exception of *Gahnia*, which failed to form a clade with the other four genera

in his analysis. The close relationships of *Cyathochaeta*, *Ptilothrix*, *Gahnia* and *Gymnoschoenus* were also shown in cladistic analyses of combined morphological and molecular data (Fig. 3). Within this group, *Cyathochaeta* is sister to *Gahnia*, which is consistent with Bruhl's (1995) analyses, and *Gymnoschoenus*, *Ptilothrix* and *Mesomelaena* formed a clade, which is consistent with Goetghebeur's (1986) analysis. The close relationship of *Gymnoschoenus*, *Ptilothrix* and *Mesomelaena* was previously recognised by Bentham (1878), who included the two small genera *Gymnoschoenus* and *Ptilothrix* in *Mesomelaena*, and by Kükenthal (1939c, 1940a).

Cladistic analyses of morphological data indicated that clade D forms a clade with *Carpha* (clades B and C). Although without BS and JN, the topologies indicate that the genera *Trianoptiles*, *Gymnoschoenus*, *Mesomelaena*, *Ptilothrix*, *Cyathochaeta* and *Gahnia* within Clade D are close to *Carpha*. That *Trianoptiles* has a close relationship with *Carpha* is strongly supported by the cladistic analysis of combined data (Fig. 3), where *Trianoptiles solitaria* and all sampled species of *Carpha* formed a clade with 100% BS and JN, and also supported by the studies of Goetghebeur (1986), Bruhl (1995), Zhang (2002) and Zhang *et al.* (2004a). *Trianoptiles* was once treated as a subgenus of *Carpha* by Kükenthal (1939b). The close relationship of *Gymnoschoenus* and *Mesomelaena* with *Carpha* was previously recognised by Kükenthal (1940a), as was the close relationship of *Ptilothrix* (*Ptilanthelium* auct.) with *Carpha* (Kükenthal 1939c; Bruhl 1995). Many early systematists (Brown 1810; Kunth 1837; Steudel 1855; Boeckeler 1874; Clarke 1908, 1909; Pfeiffer 1931) included the single species of *Ptilothrix* in *Carpha* (Appendix 1).

One of the clades (E) formed by some South American species of *Schoenus* in the cladistic analyses of morphological data is close to *Carpha* although without BS and JN, while the other clade (G) formed by the remaining species of *Schoenus* is more distant from *Carpha* (Figs 1, 2). Clarke (1902) and Kükenthal (1939b) previously noted that *Carpha* had a close relationship with *Schoenus*. Clarke (1902, p. 483) wrote that, 'This genus differs from *Schoenus* only by the lowest nut-bearing glume having the next glume close over it, not separated by an elongate curved joint of the rachilla as is the case in *Schoenus*'. In fact, the three species in clade E were once included in *Carpha* (Philippi 1857–1858; Clarke 1901; Pfeiffer 1927) (Appendix 1). This study indicates that some species (clade E) in the polyphyletic genus *Schoenus* have a closer relationship to *Carpha* than others.

Costularia (clade F) is also close to *Carpha* (Figs 1, 2) in the cladistic analyses of morphological data and this agrees with the result of Goetghebeur (1986). Kükenthal (1939b, p. 101) recognised this relationship and wrote, 'Die Blütenverhältnisse zeigen annähernd dasselbe Bild wie bei *Costularia*. ... Wie *Costularia* hat *Carpha* fast durchweg gestauchte, gerade und schmale Scheinachsen mit dicht übereinanderstehenden Gipfelblüten'.

The topologies based on morphological data indicate that *Oreobolus* and *Schoenoides* are more distant from *Carpha* than are *Costularia*, *Cyathochaeta*, *Gahnia*, *Gymnoschoenus*, *Mesomelaena*, *Ptilothrix*, *Schoenus* and *Trianoptiles* (Figs 1, 2). This is not surprising because these two genera have very different features from *Carpha*, especially in the morphology

of their flowers. However, the analysis based on combined morphological and molecular data suggested that *Oreobolus* and *Schoenoides* are closer to *Carpha*, which is consistent with the analyses of Goetghebeur (1986) and Bruhl (1995). Differences in these relationships occurred at the nodes that were without support in both analyses.

Although the topologies show many aspects of relationships of *Carpha* and its relatives to be in agreement with previous studies, the weak support or lack of support for some clades requires other sources of data, such as other genes and embryo morphology, be gathered to re-evaluate and test these relationships.

Phylogenetic relationships of species within Carpha

Carpha is separated into two clades, *Carpha sensu stricto* and *Asterochaete*, in our cladistic analyses (Figs 1–3). Within the *Carpha sensu stricto* clade, the sister relationship of *C. nivicola* and *C. rodwayi* is identified by both cladistic analyses based on morphological data and on combined data, which is consistent with the molecular data analysis (Zhang *et al.* 2004a). The cladistic analyses based on combined data (Fig. 3) identify the sister relationship of *C. alpina* and *C. curvata*, which is also consistent with the molecular data analyses (Zhang *et al.* 2004a), but analyses based on morphological data alone (Figs 1, 2) indicates that *C. curvata* is sister to the clade formed by *C. alpina*, *C. nivicola* and *C. rodwayi*. Cladistic analyses based on morphological data show *C. schoenoides* as sister to the other four species in this clade. *Carpha schoenoides* is restricted to South America, and is disjunct from other species of *Carpha*.

Within clade C (Figs 1, 2), the phylogenetic relationships among these species are fully resolved based on morphological data, but with no support except for the relationship of *C. glomerata* and *C. schlechteri*, which are sister species with 80% BS and 87% JN. This lack of support for relationships within clade C requires the use of further sources of data, such as other genes and embryo ontogeny and form, to re-evaluate and test these relationships.

In summary, the morphological data show a high degree of homoplasy, which may explain the lack of strong support for some of the clades within this assemblage. This study reveals that Schoeneae (Bruhl 1995) is not a monophyletic tribe because *Rhynchospora* nests in Schoeneae and forms a monophyletic group with all sampled species of Schoeneae (100% BS and JN) (Fig. 1). A further study of the broader Schoeneae (Goetghebeur 1998) is needed to determine tribal limits. *Carpha* is paraphyletic and forms two clades, consistent with the definitions of *Carpha sensu stricto* (Hooker 1860, 1867; Bentham 1878, 1883; Wilson 1986, 1993, 1994a, 1994b) and *Asterochaete* (Nees 1834; Kunth 1837; Steudel 1855; Levyns 1950) respectively, supporting the division of *Carpha* into two genera: *Carpha sensu stricto* and *Asterochaete*. The study indicates the polyphyletic status of *Schoenus* and *Tricostularia*; suggests merging of *Schoenoides* back into *Oreobolus*; supports separation of *Capeobolus brevicaulis* from *Costularia* or *Tetraria*; and shows the distant relationship of *Costularia* and *Tetraria*. The study resolves relationships between *Carpha* and its relatives, with limited or no support in some cases, but many aspects of these relationships are in agreement with previous studies. The study also fully resolves

the phylogenetic relationships in *Carpha*, but there is lack of support in some clades, especially within clade C (Figs 1, 2). This lack of support for some clades highlights the need for other sources of data, such as other genes, embryo morphology and ontogenetic development, to further evaluate and test these relationships.

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Appendix 1. Summary of nomenclatural history of species included in *Carpha* at various timesFor detailed taxonomic history of *Carpha*, see Zhang (2002) and Zhang *et al.* (2006)

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.Clark var. <i>angustissima</i> (Cherm.) Kük. → <i>Carpha angustissima</i> Cherm./ <i>Carpha eminii</i> (K.Schum.) C.B.Clark var. <i>angustissima</i> (Cherm.) Kük.
<i>C. antarctica</i> (Hook.f.) C.B.Clark	<i>Chaetospora antarctica</i> Hook.f. → <i>Carpha antarctica</i> (Hook.f.) C.B.Clark → <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>Tetralia 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>Tetralia 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>explicator</i> C.B.Clark	<i>Carpha aubertii</i> Nees ex Boeck. var. <i>explicator</i> C.B.Clark → <i>Carpha costularioides</i> C.B.Clark → <i>Costularia elongata</i> (Kunth) Kük. → <i>Tetralia 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.Clark	<i>Elynanthus borbonicus</i> Steud. → <i>Carpha borbonica</i> (Steud.) C.B.Clark
<i>C. bracteosa</i> C.B.Clark	<i>Carpha bracteosa</i> C.B.Clark → <i>Carpha capitellata</i> (Nees) Boeck. var. <i>bracteosa</i> (C.B.Clark) Kük. → <i>Carpha capitellata</i> (Nees) Boeck. → <i>Carpha bracteosa</i> C.B.Clark/ <i>Carpha capitellata</i> (Nees) Boeck. var. <i>bracteosa</i> (C.B.Clark) Kük.
<i>Carpha capensis</i> (Steud.) H.Pfeiff.	<i>Ecklonia 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.Clark) Kük.	<i>Carpha bracteosa</i> C.B.Clark → <i>Carpha capitellata</i> (Nees) Boeck. var. <i>bracteosa</i> (C.B.Clark) Kük. → <i>Carpha capitellata</i> (Nees) Boeck. → <i>Carpha bracteosa</i> C.B.Clark/ <i>Carpha capitellata</i> (Nees) Boeck. var. <i>bracteosa</i> (C.B.Clark) 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.Clark	<i>Carpha aubertii</i> Nees var. <i>explicator</i> C.B.Clark → <i>Carpha costularioides</i> C.B.Clark → <i>Costularia elongata</i> (Kunth) Kük. → <i>Tetralia 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>Asterochaete elongata</i> Kunth → <i>Carpha elongata</i> (Kunth) Boeck. → <i>Costularia elongata</i> (Kunth) Kük. → <i>Tetralia elongata</i> (Kunth) T.Koyama → <i>Costularia elongata</i> (Kunth) Kük.
<i>C. eminii</i> (K.Schum.) C.B.Clark	<i>Oreograstis eminii</i> K.Schum. → <i>Carpha eminii</i> (K.Schum.) C.B.Clark
<i>C. eminii</i> (K.Schum.) C.B.Clark var. <i>angustissima</i> (Cherm.) Kük.	<i>Carpha angustissima</i> Cherm. → <i>Carpha eminii</i> (K.Schum.) C.B.Clark var. <i>angustissima</i> (Cherm.) Kük. → <i>Carpha angustissima</i> Cherm./ <i>Carpha eminii</i> (K.Schum.) C.B.Clark 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.Clark	<i>Carpha graciliceps</i> C.B.Clark → <i>Ptilanthelium graciliceps</i> (C.B.Clark) Kük. → <i>Mesomolaena graciliceps</i> (C.B.Clark) K.L.Wilson
<i>C. hexandra</i> Nees	<i>Carpha hexandra</i> Nees → <i>Tetralia hexandra</i> (Nees) Kük. → <i>Cyathocoma hexandra</i> (Nees) J.Browning
<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.

Appendix 1. (continued)

Name published under <i>Carpha</i>	Original name, and subsequent name changes, ending with name current at start of project
<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.

Appendix 2. Voucher specimens used in cladistic analyses of morphological data

Appendix 3. Annotated characters listed in DELTA format used in cladistic analyses

These Appendices are available as accessory publications on the web.