TAXONOMIC RELATIONSHIPS AND PHOTOSYNTHETIC PATHWAYS
IN THE CYPERACEAE

by

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DECLARATION

The work presented in this thesis is my own, except where otherwise acknowledged.

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ABSTRACT

An automated data bank of the sedge genera of the world has been developed using the DELTA system, covering all 122 genera of the Cyperaceae via 374 characters including standard morphological and anatomical features plus aspects of synonymy, nomenclature, taxonomy, photosynthetic pathways, ecology, and distribution. A diskette of the INTKEY version of the data bank is presented for use on MS-DOS microcomputers, providing facilities for interactive identification and data retrieval.

A comprehensive classification of the family into two subfamilies and 12 tribes was derived with aid of automated cladistic and phenetic analyses of the descriptions. The relationships of the Arthrostylideae and Hypolytreae remain contentious, while those within the Scirpeae are still poorly resolved.

Comparative and developmental morphological observations on floral morphology in *Eleocharis*, *Schoenoplectus* and *Lepidosperma* accords with the traditional, ranalean interpretation of their flowers.

*Eleocharis* and *Abildgaardia* are variable for photosynthetic pathway, in addition to *Cyperus* and *Rhynchospora*. The ‘one cell distant’ criterion accurately predicts C₄ pathway in sedges, with the exception of *Eleocharis*. A checklist of C₃ and C₄ sedges is based on reports for 947 species and lists data on all the genera except *Oreobolopsis* and *Rhynchocladium*.

C₄ acid decarboxylation assays of 30 species from 12 genera of sedges revealed the existence of NAD-ME *Eleocharis* species with novel C₄ (eleocharoid) anatomy. Other C₄ sedges are NADP-ME and possess chlorocyperoid, fimbristyloid or rhynchosporoid anatomy.

NAD-ME C₄ and C₃-like C₃-C₄ intermediate *Eleocharis* exhibit abundant mitochondria, and chloroplasts with well stacked grana, in their PCR/bundle sheath cells. These PCR chloroplasts have well developed peripheral reticulum and abundant starch grains. All sedges examined, regardless of photosynthetic pathway and anatomical type have a suberized lamella in the mestome sheath position. Ultrastructural features of sedges are sufficiently well preserved in dried material to allow prediction of biochemical pathway from herbarium material.
Presentation

Chapters 4-7 and 9 are basically in the form of papers intended for publication, each with its own introduction and discussion. An earlier version of Chapter 6 has already been published (Bruhl et al. 1987), but the thesis version incorporates additional data and text improvement. Chapters 2 and 3 provide the framework for the automated generic database presented as Appendix 3. Chapter 8 introduces the automated database, exemplifying applications. It also provides a printed key to the sedge genera of the world, generated automatically from the database.

Tables and illustrations with captions appear at the end of each chapter, and the references are pooled at the end of the thesis. Three microfiche appendices 1-2 and 4 (pertinent to Chapters 5-9) and Appendix 3 (in the form of a floppy diskette) are lodged in the inside of the back cover. The format used is that of the CSIRO Journals.
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Chapter 1

Introduction

The Cyperaceae are a cosmopolitan family of monocotyledonous plants with about 5100 species. The historically important paper-making plant, papyrus (Cyperus papyrus) is well known from legend and for its use in horticulture. Apart from their historical local economic and cultural importance, a few sedges are economically significant at the global scale. These include the pernicious agricultural weed Cyperus rotundus, and commercial Chinese water-chestnuts (Eleocharis dulcis). Ecologically, the Cyperaceae are very important, particularly in wet habitats at almost all latitudes. They include Carex, which with about 2500 species is one of the largest genera of flowering plants; and the family is the focus of a great deal of systematic effort in its own right. Interest in Cyperaceae is engendered across biological disciplines by the occurrence of both C\textsubscript{3} and C\textsubscript{4} photosynthetic pathways.

The family is widely acknowledged as posing peculiar difficulties for classifiers, as indicated by Metcalfe (1971):

"The main difficulty about the classification of the Cyperaceae when the subject is approached solely along traditional lines is that the flowers are very small, the exact morphology of their parts is often obscure, and the morphology of the inflorescences is difficult to interpret."

Light microscopy of whole mounts and serial sections have failed to resolve these problems, and it has been imperative to extend the taxonomic criteria to include anatomy, physiology and biochemistry.

The main aims of this project were to investigate the broad outline of the classification of the Cyperaceae and to acquire an automated database of more general utility. Practical considerations led to sampling around the generic level on a world scale. Chapter 2 explains the choice of taxa included in my database, with qualifying comments on them as necessary, and draws attention to many contentious taxonomic issues.

Chapter 3 sets out the character list in an annotated and illustrated form. The rationale for inclusion of characters, for recognition of states and dealing with matters of terminology is discussed within in the framework of a DELTA system treatment. The list cover all the recognized "standard" morphological and anatomical characters, and many additional characters dealing with embryo morphology, photosynthetic pathways,
vegetative ultrastructure, and parasites. "Characters" expressing geographical
distribution, nomenclature, taxonomy and ecology have been included to broaden the
scope of the database for general application.

The difficulties in interpreting floral morphology in the Cyperaceae prompted a
novel developmental SEM approach (Chapter 4). Representatives of five sedges were
investigated with the aim of resolving disparate interpretations of sedge flowers: are they
conventional flowers with a perianth surrounding the androecium and gynoecium, or
do they represent a collection of flowers (synanthia)? Is there evidence to support the
anthoid theories of Meeuse as adopted by Goetghebeur (1986)?

Variation in photosynthetic pathways has received much attention in the
Cyperaceae, but mostly in an anatomical/taxonomic context. In developing the generic
database, compilation of basic data was seen as an essential prerequisite for addressing
variation in photosynthetic pathways in more detail (Chapter 5; Appendix 2). Initially
some time was spent in researching the literature towards a more detailed assessment
of C$_3$ and C$_4$ in Cyperaceae in relation to distribution in Australia. The appearance of a
paper on this topic (Takeda et al. 1985) rendered my efforts in this direction redundant.

A biochemical, physiological and ultrastructural survey was undertaken to assess
the range of variation in photosynthetic pathway across the Cyperaceae (Chapters 6-8).
Interesting variation in vegetative anatomy (Chapter 6) inspired wider sampling of
Eleocharis from herbarium collections and led to the discovery of C$_4$ and putative C$_3$-C$_4$
intermediate species in this genus (previously thought to be wholly C$_3$). Limitations on
the material available in the short term, and a wish to continue pursuing the main aims
of the project, precluded a comprehensive study at this time.

At the commencement of this project, no recent worldwide treatment of the genera
of the Cyperaceae was available. In 1986 Goetghebeur published his thesis (a twelve-
year study) which represents primarily a taxonomic synthesis of inflorescence, floral
and embryo morphology, with some additional features including general vegetative
morphology (though with little anatomy). His treatment of floral morphology follows
Meeuse's anthoid theories. Coverage of the genera was thorough, and cladistic analyses
(contentious in incorporating some biogeographical characters) were undertaken by
hand. Goetghebeur's work has been particularly useful as a reliable and detailed source
of nomenclatural information and as a modern comprehensive treatment with which my
analyses could be compared (Chapter 9).
Chapter 2

Taxa included in the automated database of the sedge genera of the world

Introduction

The main aims of the present study were to investigate the broad outlines of the classification of the Cyperaceae, and simultaneously to acquire a database of more general utility. It was evidently essential to prepare descriptions on a world scale, and the most practical approach was to sample around the generic level. Where alternative generic circumscriptions are available I have generally opted for the one which seemed best suited to the present purpose. By contrast with the generally far broader generic concepts of Koyama (1961, 1962, 1972), narrower circumscriptions at the lowest practicable level have generally been preferred, not because one would necessarily want to recommend their general acceptance, but because a) the descriptions are likely to contain less variability, and thus be more suitable for classificatory analyses; b) they permit incidental investigation of questions relating to generic circumscriptions; c) it is easier to coalesce descriptions, should this seem desirable for other purposes (cf. Chapter 9), than to separate them; d) they are more likely to represent monophyletic taxa; and e) narrower groups approach closer to the ideal of species level descriptions. In the last context it will be seen (see character #337, Appendix 1 and Chapter 8) that the descriptions include 51 monotypic or ditypic genera, 30 'genera' with 3-9 species, 20 with 10-49 species, 10 with 50-99 species, and 10 with 100 or more species. For the same reasons, several large genera (Carex and Cyperus) have been represented here by subgeneric descriptions.

Goetghebeur (1986) has recently provided an account, in Flemish, of the genera of the Cyperaceae, and most of the generic circumscriptions adopted here conform with his. However, I have accepted as genera a number of taxa (e.g. Anosporum, Erioscirpus, Lophoschoenus and Vesicarex) which Goetghebeur considered only as variants of sensu lato genera. I have also divided some genera largely on the basis of photosynthetic pathway variation (e.g. Eleocharis and Rhynchospora) and described the variants separately, in order to explore the association of photosynthetic pathway related features with others. Goetghebeur (1986) provides historical and nomenclatural information for each genus. Metcalfe (1971), Haines and Lye (1983) and Tucker (1987) provide
comments on generic circumscriptions of sedge genera, and together with Goetghebeur (1986) they provide extensive lists of relevant literature (see also character #366 in Appendix 1).

There follow comments on those taxa included in the DELTA database (Appendices 1 and 3) for which some qualification seems necessary (for example, where generic concepts differ from those of Goetghebeur, 1986). A comprehensive listing of synonyms and relevant literature references for each genus is provided in Appendix 1 (characters #1-2 and 366), and this information is readily available via the automated database which constitutes Appendix 3.

**Annotated list of sedge genera**

**Abildgaardia** Vahl (the C₄ species): Abildgaardia, Fimbristylis and Bulbostylis have been variously treated as one, two or three genera (Vahl 1805; Kunth 1837; see also Goetghebeur and Coudijzer 1984 for more detailed nomenclatural discussion), depending largely upon the use and interpretation of embryological and micromorphological characters. When treated in the broad sense, they have been lumped under *Fimbristylis* (e.g. Bentham 1883; Koyama 1961). More often, *Abildgaardia* has been included in *Fimbristylis*, with *Bulbostylis* recognized separately (e.g. Clarke 1902; Wilson 1983). Lye (1973) and Haines and Lye (1983), however, included *Abildgaardia* in *Bulbostylis*.

**Abildgaardia** (the C₃ species): Includes two species (see also Chapter 5) originally described under *Fimbristylis* (Gordon-Gray 1966), and later transferred, without explanation, to *Abildgaardia* (Lye 1971). Although Gordon-Gray (1966 p.137) suggested that the relationship between the two species was "not particularly well marked", when later she assessed the differences between *Abildgaardia, Fimbristylis* and *Bulbostylis* (1971) she presented them next to one another in her sequence of *Abildgaardia* species though originally she separated them (1965) in line with Kern’s sectional arrangement of *Fimbristylis* (1955: *F. hygrophila* in Section *Abildgaardia* and *F. variegata* in Section *Fuscae*). Subsequently Goetghebeur and Coudijzer (1984), in a regional treatment, and Goetghebeur (1986), in a generic treatise, corroborated Lye’s nomenclatural decision regarding the placement of *A. hygrophila*. *Abildgaardia variegata* has horizontally-elongated pericarp epidermals. It was not sampled by Goetghebeur and Coudijzer (1984), though it would key out to *Fimbristylis* in their regional treatment.
Acriulus Ridley: Has seesawed taxonomically in and out of Scleria (Ridley 1883; Clarke 1902, 1908; Kern 1963; Franklin Hennessy 1985). Franklin Hennessy (1985) recognized it only at sectional rank in a taxonomic revision based on a morphological and anatomical study of the southern African species of Scleria. Acriulus is represented as a separate description in this study to provide extra scope for assessing the relationships between Scleria and Diplacrum (see below).

Alinula J. Raynal: Similarities between the species of Alinula and Cyperus malawicus led Haines and Lye (1983) to reduce Alinula to a subgenus of Cyperus. Goetghebeur (1986) included Cyperus malawicus in Alinula, along with two Ascolepis species, on the basis of floral ground-plan.

Anosporum Nees: Recognized by Clarke (1908) and by Haines and Lye (1983) at subgeneric rank. Goetghebeur (1986) described it separately, but only as a variant of Cyperus.


Baumea Gaudichaud: Baumea, Machaerina and Cladium are each recognized here as genera, following Blake (1969) and Goetghebeur (1986).

Blysmopsis Oteng-Yeboah: A monotypic genus (Oteng-Yeboah 1974) split from Blysmus on the basis of vegetative anatomy and micromorphology.


Bulbostylis Kunth: See the comments above under Abildgaardia (the C₄ species).

Carex Linnaeus subgenus Primocarex Kuekenthal, subgenus Vignea (P. Beauvois) Kuekenthal, subgenus Carex, subgenus Indocarex Baillon: Kuekenthal’s (1909) and Goetghebeur’s (1986) recognition of four subgenera of Carex, followed here, was based largely on inflorescence features. See Tucker (1987) for additional references.

Carpha Banks and Solander ex R. Brown: Treated here in the broad sense, i.e. including Asterochaete (cf. Haines and Lye 1983; Goetghebeur 1986; but contrast Metcalfe 1971).

Cladium P. Browne: As recognized here, comprises four species (cf. Goetghebeur 1986), whose limits remain contentious (see Tucker 1987 and references therein).

Costularia C.B. Clarke: Recognized here in the sense of Raynal’s (1974) treatment of Costularia subgenus Costularia. Seberg (1986, 1988a-b) argued in favour of a modification of Kuekenthal’s (1939-1940) three subgenera: i.e. Costularia,
Chamaedendron and Lophoschoenus. By contrast, Goetghebeur (1986) treated Costularia in the broad sense. A reassessment of the species is needed to clarify the generic limits.

Costularia brevicaulis C.B. Clarke: This species has been included in both Costularia (sensu lato: Clarke 1897, 1898; Kuekenthal 1939b, see also Goetghebeur 1986) and Tetraria (Clarke 1894; Levyns 1947), while Seberg (1988a) included it in his informal group approximating to Costularia subgenus Chamaedendron. To test its relationships, Costularia brevicaulis was described separately here (Chapter 9).

Courtoisina Sojak: The change from Courtoisia Nees to Courtoisina was a nomenclatural necessity (Sojak 1979). Lye (1983) and Haines and Lye (1983) confer only subgeneric rank on its two constituents.

Crosslandia W.V. Fitzgerald: An Australian monotypic genus with rather variable inflorescences. Goetghebeur (1986) proposed a second species to include the anthelate individuals.

Cyathocoma Nees: Has been generally recognized as Macrochaetium (e.g., Reid 1985, but see Goetghebeur 1986).


Cyperus Linnaeus subgenus Pycnostachys C.B. Clarke: Recognized here as circumscribed by Lye (1981) and Haines and Lye (1983), but their name, Cyperus subgenus Protocyperus, is illegitimate (Tucker 1987). Cyperus decidualus was treated by Clarke (1879) under Mariscus and by Kuekenthal (1936) under Cyperus subgenus Mariscus, because its spikelets are generally deciduous at maturity. However, Druyts-Voets (1970) found that C. deciduus has 'eucyperoid' (or 'C3') anatomy. Haines and Lye (1983 p.166) transferred it to Cyperus subgenus Protocyperus on the basis of its "eucyperoid anatomy and digitately arranged spikelets". Further, both its wingless rachillae (Kuekenthal 1936 p.473) "Rhachilla lata rigida exata" and the proliferous inflorescence (Haines and Lye 1983) are attributes more typical of Cyperus subgenus Pycnostachys than of Mariscus. I have, therefore, incorporated C. deciduus in the description of Cyperus subgenus Pycnostachys.

Cyperus Linnaeus subgenus Cyperus: Following Goetghebeur (1986), the C4 genera 'Sorostachys', 'Galilea' and 'Juncellus' have been included under Cyperus subgenus Cyperus. By contrast, the C3 Anosporum has been treated separately (see above). It would be prudent to await species treatments or judicial exclusion of certain species before recognizing the former three 'genera'. For example, Juncellus may prove...
worthy of recognition at the generic rank, after the removal at least of *Cyperus alopecuroides*.

**Diplacrum** R. Brown: *Diplacrum* species have often been presented in floras (e.g. Kern 1974) under *Scleria*. Eiten (1976a) has expounded on the floral and inflorescence differences between them.

**Eleocharis** R. Brown (the C₃ species): The monotypic genera ‘Chamaegyne’ and ‘Chillania’ have not been recognized as distinct from *Eleocharis* by either Eiten (1976b) or Goetghebeur (1986). Both segregates are said to have C₃ anatomy (Goetghebeur 1986), but the anatomical description for ‘Chamaegyne’ (Suessenguth 1952) seems an inadequate basis for this conclusion.

**Eleocharis** R. Brown (the C₄ species): The C₄ species were treated separately in this study to test whether their distinction, in terms of photosynthetic pathways (see Bruhl et al. 1987), is associated with differences in other features (Chapter 9). Currently this group includes three species (one with three subspecies). *Helonema* was reduced to synonymy with *Eleocharis minima* by Eiten (1976b), a species closely related to the C₄ species (see Svenson 1937), but its vegetative anatomy has not been investigated (see also Goetghebeur 1986).

**Eleogiton** Link: Frequently included in *Isolepis* (e.g. Wilson 1981; Haines and Lye 1983), or in *Scirpus* when that genus is treated in the broadest sense (e.g. Kern 1974). If Wilson (1981) is correct, and *Eleogiton* represents an aquatic specialization of *Isolepis*, they would be expected to appear as sister taxa in classificatory analyses (Chapter 9).

**Eriophoropsis** Palla: A monotypic ‘satellite’ genus of *Eriophorum*, recognized on anatomical grounds (Palla 1896), has sometimes been accorded subgeneric rank (Raymond 1954; Oteng-Yeboah 1974).

**Erioscirpus** Palla: Another ‘satellite’ of *Eriophorum* recognized by Palla (1896). The embryos of the two species illustrated by Goetghebeur (1986 p.308 Fig. 8.3.2E-F) are distinctly ellipsoid, by contrast with the turbinate-type of the other *Eriophorum* species illustrated.

**Ficinia** Schrader: Employed here in the broad sense (except for separate recognition of the following taxon) for pragmatic reasons, including the lack of a recent comprehensive revision of the genus. By contrast, Nees (1834) recognized seven genera all now included in *Ficinia*.

**Ficinia** Schrader subgenus *Sickmannia* C.B. Clarke: *Sickmannia* has variously been treated as a genus (Nees 1834; Levyns 1947, 1950), a subgenus (Clark 1898) or a
subsection (Pfeiffer 1921). It was described separately here to provide a contrast with *Ficinia* (sensu lato).

**Fimbrystylis** Vahl: See the comments above under *Abildgaardia*.


**Hemicarpha** Nees: Goetghebeur (1986) detailed separately the species of *Hemicarpha*, *Rikliella* and *Lipocarpha*, but recognized only the last as a genus. The genera were originally defined largely on the basis of spikelet morphology: *Rikliella* with subtending bracts only, *Hemicarpha* with subtending bracts and spikelet prophylls but no floral bracts, and *Lipocarpha* with subtending bracts, spikelet prophylls and floral bracts. In the present study the three genera are treated separately.

**Hymenochaeta** P. Beauvois ex Lestiboudois: A monotypic segregate of *Scirpus* comprised of *H. grossa*.

**Isolepis** R. Brown: Another segregate from *Scirpus*, which is gaining broader acceptance (cf. Wilson 1981; Haines and Lye 1983; Goetghebeur 1986), but still given only sectional status by some (e.g. Walters 1980; Tucker 1987). The generic limits of *Isolepis* are not clear-cut; ‘*I. nodosa*’ and ‘*I. prolifera*’, in particular, are controversial in terms of embryo and hypogynium attributes (see Wilson 1983). To avoid prejudging their generic relationships, these two species were excluded from the present descriptions (Chapter 9).

**Kobresia** Willdenow: Gilly’s (1952) proposal of a family for this genus has received no subsequent support (cf. Kern 1958; Metcalfe 1971; Kukkonen 1983; Goetghebeur 1986).


**Lagenocarpus** Nees: Includes *Cryptangium*, by contrast with Metcalfe (1971).

**Lepironia** L.C. Richard: Kern (1974) reduced *Lepironia mucronata* to synonymy with *L. articulata*, now the sole species of this genus.

**Lipocarpha** R. Brown: Treated here as distinct from both *Hemicarpha* and *Rikliella* (see above).

**Lophoschoenus** Stapf: Included here in the sense of Raynal’s (1974) treatment of *Costularia* subgenus *Lophoschoenus*. Metcalfe’s (1971) sample of *Lophoschoenus* included *L. fragilis*, which is treated under *Costularia* in the present study (cf. Seberg 1988a).

**Machaerina** Vahl: See comments above under *Baumea*. 
Mapaniopsis C.B. Clarke: Not examined.

Mariscus Vahl: Treated here as a subset of Kuekenthal's (1936) Cyperus subgenus Marsicus, with the exclusion of most of section Aristati (whose species constitute Courtoisina, Queenslandiella, and Monandrus). I have followed Haines and Lye (1983) in treating Mariscus deciduus under Cyperus subgenus Pycnostachys (see above), but have included in Mariscus their subgenera of Cyperus, Bulbomariscus and Bulbocaulis.

Micropapyrus Suessenguth: After discussing the evidence available from the literature, Goetghebeur (1986) included Micropapyrus in Rhynchospora, but its vegetative anatomy had not been investigated (cf. Metcalfe 1971). It was described separately in the present study, to permit reassessment of its relationships (Chapter 9).

Monandrus P. Vorster: Monandrus is not yet validly published (Goetghebeur 1986). It is included here to cope with part of Cyperus section Aristati, and is equivalent to Cyperus subgenus Aristomariscus (Lye 1983; Haines and Lye 1983).

Morelota Gaudichaud: Comprises M. affinis and M. gahniformis (cf. Gahnia above).

Nemum Desvaux ex Hamilton: Not examined.

Nelmesia Van der Veken: Not examined.

Oreobolopsis T. Koyama and Guaglianone: Oreobolopsis is a recently described monotypic genus from Bolivia (Koyama and Guaglianone 1987), and has not been examined here.

Oreobolus R. Brown: In a recent revision of Oreobolus, Seberg (1986, 1988a-b) removed Oreobolus oligocephalus, creating the monotypic genus Schoenoides (see below).

Pleurostachys Brongniart: Not examined.

Rhynchochladium Koyama: Not examined.

Rhynchospora Vahl corr. Willdenow: Rhynchospora includes C₃ species and two C₄ types (chlorocyperoid and rhynchosporoid; Takeda et al. 1980; Bruhl et al. 1987; Ueno and Koyama 1987). The C₄ genera Remirea and Sphaerocyperus were at times included in Rhynchospora, but are now generally recognized as distantly related genera (see Metcalfe 1971; Haines and Lye 1983; Goetghebeur 1986). To test the taxonomic soundness of Rhynchospora in the face of the remaining variation in photosynthetic pathways, the chlorocyperoid and rhynchosporoid species of Rhynchospora have been described separately (Chapter 9).

Rikliella J. Raynal: See comments above under Hemicarpha.
Schoenus Linnaeus: *Schoenus paludosus* and *S. pauciflora* are referred here to *Tricostularia* (see below). *Schoenus (Elynanthus) grandiflorus* may be misplaced here, and it has been omitted from the data pending a *de novo* examination.

Scirpoïdes SÈguier: The generic limits of Scirpoïdes are not clear-cut: for example, ‘*Isolepis nodosa*’ and ‘*I. prolifera*’ have been referred to *Scirpoïdes* (see Wilson 1983). To avoid prejudging their generic relationships, these two species were excluded from the present descriptions (Chapter 9).


Scleria Sergius: See the comments above under Acriulus.

Sumatroscirpus Oteng-Yeboah: Not examined.

Syntrinema Pfeiffer: Included by Goetghebeur (1986) in *Rhynchospora*, on the evidence only of published descriptions, and exclusive of anatomical evidence. It was described separately in the present study, to permit reassessment of its relationships (Chapter 9).

Trichoschoenus J. Raynal: Not examined.

Tricostularia Nees: See Schoenus above.

Tylocarya Nelmes: Kern (1958) submerged this monotypic genus in *Fimbristylis*. Goetghebeur (1986) described it separately, but as a ‘variant’ of *Fimbristylis*.

Vesicarex Steyermark: Goetghebeur (1986) described *Vesicarex* separately, but as a ‘variant’ of *Carex*. 
Chapter 3

Organizing the taxonomic descriptive data

Introduction

The content of the character list developed in this study (see below) was determined by the main objectives of the work. These were, by taking advantage of the options available via the DELTA system (Dallwitz 1980; Dallwitz and Paine 1986; Partridge et al. 1986; Dallwitz and Zurcher 1988):

1) to conduct phenetic and cladistic classificatory analyses, for comparison with existing classifications and if necessary proposing a new or revised one;

2) to provide a flexible capability for identifying Cyperaceae to generic level, offering scope (for example) for identifying sterile or fragmentary material; and

3) to set up an information retrieval system providing opportunities (a) to explore associations of taxonomic groupings with morphological and anatomical characters and with topics of general interest such as variations in photosynthetic pathways, ecology and biogeography, and (b) to explore interrelationships of these aspects independently of taxonomy — for example, it should be possible to explore host/parasite relations directly in relation to particular anatomical and physiological features.

The need was for a detailed list of morphological and anatomical characters, supplemented by ‘characters’ to cope with nomenclature (#1-2), cytology (#333), host specificities of pathogenic fungi (#334-336), numbers of species per genus (#337), geographical distributions (#338-356), taxonomy (#357-359 and 393-374), ecology (#360-364), miscellaneous comments (#365), relevant literature references (#366), and listing of specimens sampled (#367-368), plus ‘familial characters’ (#369-372) for outgroup comparisons.

Critical to achieving these objectives is the quality of the character list in recognizing appropriate characters and valid character state definitions. The list (see below) was developed de novo, though Watson’s character list for the grass genera of the world (Watson and Dallwitz 1988) provided the basic model. Care was taken to include all characters which have been considered important in sedge classification, and many have been introduced which are new in this context. The latter include many describing culm (#57-107) and leaf blade (#108-162) anatomy and photosynthetic pathway variation (#163-167). Many of the character state definitions represent standard botanical or cyperological usage, or are self-explanatory. The list is extensively cross-
referenced with illustrations, and additional notes relevant to individual characters are presented in the list appended to this section. Chapter 4 carries some detailed discussion pertinent to interpretation of some especially problematical aspects of floral and inflorescence morphology involved in characters 168-267, while chapters 7-9 relate specifically to characters 91-98, 107, 144-151, 153, and 162-167. Interpretations of characters, delimitation of character states and choices of terminology naturally reflect personal preferences, but I have tried to balance the needs a) to conform so far as possible with accepted usage, b) to provide scientifically accurate descriptions in a framework of properly exclusive character states, and c) to incorporate data from literature which is often defective in these respects. I have aimed at consistency over use of descriptive terms in different parts of the list (e.g. disposition of the sexes: #168, 178, 183, and 200; and form of the inflorescence: #177 and 184). On the other hand, I have opted to accept the ideas of homology implicit in some terms, in particular "spikelet prophyll" and "floral bract" were used rather than the generalized terms, ‘bracts’, ‘glumes’ and ‘scales’. Although Metcalfe (1971) provided the basis for the terminology of vegetative anatomy used here, some aspects of his interpretation of silica bodies (which often constitute an obvious feature of vegetative anatomy) remain controversial, and many of his quantitative characters (particularly those relating to sclerenchyma and vascular bundles, e.g. #100-104 and 154-158) have here been interpreted more broadly as qualitatives, the better to accommodate generic rather than specific descriptions. Not all features represented as "variable" within the family by Metcalfe were found to be so in the present study. Thus, he listed nine genera with "stomata tending to be tetracytic" (pp.541-542), but only one tetracytic stoma was seen during the present study. In some species, not all in genera listed by Metcalfe, epidermals adjacent to the stomata appear superficially to be part of the stomatal apparatus, but thinner walls of the subsidiaries clearly differentiate the latter from the general epidermals. His distinction between stomata "irregularly distributed" and "in longitudinal files" seems largely to reflect the relationship between width of the intercostal zones (dealt with here in terms of the relative width of the epidermal zones, #57 and #108) and stomatal abundance (employed here in absolute terms only for the culms: i.e. #69). Metcalfe’s character states seem in this instance merely to represent the extremes of a continuum.

Any attempt at rational classification demands that at least some characters be both applicable and fully recorded across the group under consideration, and I have tried to maximize these for Cyperaceae (e.g. #25, 40-41, 43, 49, 66, 168-169, 185 and 203). Inevitably, however, many characters which demand inclusion are not recordable across the board, being ambiguous in relation to some taxa (e.g. in those with capitate or spike-
like inflorescences the inflorescence prophylls, #19, may be indistinguishable from spikelet prophylls, and have then been left unscored), and many others depend on the applicability of or knowledge of their 'controlling' characters (e.g. if the leaves are elaminate, leaf-blade characters are inapplicable: 25,1:28-38:108-162). It is sobering to contemplate that of the 20 androecial and hypogynial characters (#268-287), each potentially applicable to all the 132 descriptions (see Chapter 2), the mean of missing values (including unknowns) is 29 ±8 descriptions; while the 36 leaf blade characters (#127-162) are unavoidably inapplicable to a mean of 63 ±4 descriptions. The extent of 'missing data' is not surprising, but it is significant in that some classificatory methods require a complete data matrix (e.g. Principal Components Analysis), and in that variability is inevitably underestimated, especially with respect to poorly scored characters. "Unwarranted comparisons" in relation to unknowns and inapplicables are also inevitable (Sneath and Sokal 1973; though these comparisons have been rationalized in terms of 'underlying synapomorphies': Saether 1979, but see Cranston and Humphries 1988; see also Chapter 9).

The reliability of descriptions and of taxonomic conclusions derived from them is largely a function of sample sizes. Barely scored characters (e.g. #219 and 272) and descriptions of large genera (e.g. Bulbostylis, Lagenocarpus and Carex) are the most likely to be misleading in this respect. A balance needs to be made between the necessity of generalizing from small samples and the ideal of scoring each species for every character. Some little-scored characters (e.g. #285-286: pollen characters) may be more use after further sampling. Other characters (e.g. #290: style, whether terete) may be somewhat unreliable due to the indiscriminate use of fresh and herbarium material, while yet others are certainly very reliable regardless (e.g. epidermal features, silica body characters and anatomical characters relating to photosynthetic pathways). My assessment of the reliability of the characters in the present descriptions, in general terms, is expressed in the 'character reliabilities' listed in the TOINT and TOKEY files (Chapter 8).

The character list and the descriptions will lend themselves readily to updating and improvements, according to future requirements and as new data become available. In what follows, I provide an annotated and illustrated version of the current character list; and Appendix 1 comprises the DELTA 'generic' descriptions, translated into English using this list in association with CONFOR.
Methods and Materials

Descriptive data

Most of the morphological and anatomical data were obtained from herbarium material, but fresh material was examined where available. Herbaria abbreviations (see general descriptions in Appendix 1) follow Holmgren et al. (1981), and vouchers (#367-368) cross-reference with those in Appendix 1. Only the first collector is given, together with the collection number or date of collection and the herbarium abbreviation. Where collectors' information is not present, absent or indecipherable, only the herbarium abbreviations and sheet numbers are listed.

General morphological observations were made under a stereo- microscope (Wild M5). Where necessary, herbarium material was softened by boiling in water with Teepol. Compound microscopy was carried out with a Leitz Orthoplan (bright-field, cross-polarized and phase-contrast illumination) or a Wild M11 (bright-field). Photomicrographs were taken using either a Wild M400 or a Leitz Orthoplan/Orthomat. Whole mount micromorphological preparations, such as styles and stamens, were made from fresh or rehydrated material, mounted on glass slides in water, 50% glycerol, or Hoyer’s solution.

Anatomical preparations of mature culms were made from the mid-third of the culm internode immediately below the inflorescence, and leaf preparations were taken from the mid-third of mature laminae. Herbarium material was first rehydrated in water with Teepol. Culm and leaf epidermes were prepared, softening when necessary in 12% lactic acid for 1-5 mins, by scraping the inner tissues away from sagittal sections with a razor-blade. Swelling of preparations was enhanced in KOH (2-5% for 1 min). Preparations were stained in 0.05% Toluidine Blue O in acetate or benzoate buffer (Feder and O’Brien 1968) or in Melzer’s reagent, and mounted on glass slides in 50% glycerol or Hoyer’s mountant, respectively. The shape of the subsidiaries in surface view (#72 and 123) was ascertained in optical section, with their outer walls in sharp focus.

Anther measurements (#272 and 277) were made with an eyepiece graticule in either a stereo microscope or compound microscope. Endothecial thickening (#284) preparations were made either by boiling anthers or anther sacs discarded from pollen preparations (see below) in 12% lactic acid for 2 to 5 mins, teasing them apart on a glass slide and covering with Hoyer’s mountant. Fresh or dried pollen was prepared for cell (‘nuclei’) counting (#286) following Gardner and Rattenbury (1974).
The presence and features of stigmatic papillae (#298-300) were assessed from whole-mount preparations in water for fresh material, or in KOH (2-5%) solution for dried samples. Hand-cut transverse sections of fruits (#316-320) were stained in Melzer's reagent and mounted in Hoyer's solution. Embryos (#321-332) were prepared according to Van der Veken (1965), except that the bleaching step was found to be redundant.

The ecological data (#360-364) have been compiled from herbarium labels and from the literature, supplemented by original field observations.

Automated descriptions

Automated descriptions were organized under the DELTA (DEscription Language for TAxonomy, Dallwitz and Paine 1986) system which has been designated by the International Union of Biological Sciences Commission for Plant Taxonomic Databases (formerly TADWG) as the international standard for the transfer of taxonomic descriptive information. This is a flexible computer system for storing and processing taxonomic descriptions, and provides user friendly, free-format data entry. Sample files and diagnostic error checking programs are provided. VAX/VMS (750/11, Vaxstation 2000 and 3100) computers were used, but the system can also be used on MS-DOS and Prime computers. All types of 'characters' can be encoded, including unordered and ordered binary and multistates, real and integer numerics, and text. Common character states can be dealt with implicitly, requiring only the unusual state to be explicitly scored.

The DELTA format-conversion program CONFOR automatically checks the consistency with one another of all the files and permits reordering the characters (in the character list and the items files); the encoded descriptions can be translated into natural language (e.g. English) and into formats required for other programs, including KEY (Dallwitz and Paine 1986) for computer generation of identificatory keys, PAUP (Swofford 1985, for cladistic analyses), DIST (Dallwitz 1989 unpublished, which produces distance matrices for use in phenetic and principle coordinates analyses), and INTKEY (Dallwitz and Paine 1989, an innovative identification/data interrogation program). DELTA is compatible with TYPSET (Dallwitz and Zurcher 1988), a computer typesetting program by which PostScript and camera ready copy can be generated.
NOMENCLATURE
#1. <Synonyms: i.e. ‘genera’ included in the current description: data mostly from Goetghebeur 1986>/
#2. = <Sensu lato genus: i.e. genus in which this taxon might reasonably be (or sometimes is) included>/

HABIT, VEGETATIVE MORPHOLOGY
#3. <Habit>/
1. ‘long-rhizomatous’ <Plates 1.1-2>/
2. ‘long-stoloniferous’ <i.e. exhibiting the “runners” of Haines and Lye 1983> <Plates 1.3, 1.7>/
3. caespitose <Plates 1.1, 1.5-6>/
   • ‘Long-rhizomatous’: a more or less horizontal axis with more than one internode clearly visible between the vertical shoots, as in ginger.
   ‘Long-stoloniferous’: only one horizontal internode (often greatly developed) is visible between the vertical shoots, and rooting is restricted to the nodes, cf. strawberries.

#4. <Habit>/
1. epiphytic <e.g. Everardia>/
2. ‘terrestrial’ <implicit>/
   • ‘Terrestrial’ here includes lithophytic.

#5. <Longevity of plants>/
1. annual <Plates 1.5–6, 1.9>/
2. perennial <Plates 1.1, 1.8, 2.3>/
   • ‘Perennial’ plants have old dead culms and/or rhizomes, whereas annuals have only the senesced early leaves of the current year’s growth at the base (cf. Macfarlane 1979).

#6. Plants <whether possessing a ‘trunk’, i.e. a caudex>/
1. with a ‘trunk’ <Plates 1.4, 1.8>/
2. without a ‘trunk’ <implicit> <Plate 1.9>/
• A "trunk" (giving a pseudoarborescent appearance) may be composed of a rather loose mat of old leaf sheaths and roots in *Everardia*, possibly devoid of secondary growth. A similar but more solid construction with some secondary growth occurs in *Microdracoides*. The woody trunk in *Gahnia* (Staff and Clifford 1987) represents anomalous secondary growth. The character is evidently homoplasious, but comparative anatomical studies are required to break it down into its constituents.

**#7. Plants <whether shoots dimorphic>/**

1. differentiated into separate sterile <laminate> and fertile <elaminate> shoots

   <Plate 2.1>/

2. not differentiated into sterile and fertile shoots <implicit>/

• Many authors, e.g. Kern (1974), describe the culms as "central" or "axillary" (see also #15) according to the general appearance of their relative positions. However, those plants with culms apparently "originating from the side of the plant" or "axillary", in fact typically possess a series of elaminate leaves at their base. Therefore the culm is central to its elaminate leaves. Such fertile shoots are usually diminutive, by comparison with the sterile laminate shoots, and are often displaced sideways; thus the culms superficially appear to be axillary. I have preferred to describe this feature in terms of the differentiation of the shoots, rather than their superficial placement. The character should not be confused with the contrast between 'vegetative shoots' and 'vegetative culms' within *Carex* (Reznicek and Catling 1986).

**#8. Plants <whether possessing a fenugreek odour>/**

1. with a fenugreek odour/

2. without a fenugreek odour <implicit>/

• In a few genera of the Cypereae, a fenugreek (*Trigonella foenum-graecum*) odour is readily detectable in fresh and (especially) herbarium material.

**#9. Plants <especially the roots and rhizomes: whether faintly lemon-scented, see Getliffe 1983>/**

1. <faintly> lemon-scented *Kyllinga>/

2. not lemon-scented <implicit>/

• *Kyllinga* species are all faintly lemon-scented (Getliffe 1983). This feature is paralleled in many other flowering plant families, but in the Cyperaceae is seemingly confined to *Kyllinga*. 
Plants <whether possessing 'spines', i.e. strong, stiff, sharp-pointed, 'woody', multicellular processes, see also Hewson 1988>/

1. 'spiny' <e.g. *Reedia* > <Plate 21.3>/
2. without spines <implicit>/

- The spines represent extensions of the margin of leaves and other organs into hooks, each topped by a prickle-hair almost completely composed of silica. The precise placement of the prickle-hair and the fact that the presence of spines correlates with very broad leaves suggests that the feature involves homoplasy. A closer study of the development and differences between the spines of the taxa in which they occur is warranted.

Plant indumentum <culms, leaves, and or sheaths: colour>/

1. purple <*Bisboeckelera*> /
2. not purple <implicit>/

- The colour of indumentum should not to be confused with the colour of the surrounding epidermis. Prickle-hairs and other forms of indumentum in the Cyperaceae are typically colourless (though the long hairs in *Gymnoschoenus* discolour brown-black with age). By contrast, the indumentum itself in the material seen of *Bisboeckelera* is mostly purple, as is much of the surrounding epidermis.

Vegetative shoots <relative to cauline sheaths: whether extravaginal or intravaginal>/

1. extravaginal <*Cladium*> <Plate 4.7>/
2. intravaginal <implicit>/

- Extravaginal growth at the base of sedges is relatively common. However, it is associated with the upper culm only in *Cladium*.

Lateral shoots <whether originating at the base of the uppermost culm internodes>/

1. originating only at the base of the uppermost culm internode <i.e. the shoots bear prophylls: e.g. *Oreobolus*> <Plates 2.4–5>/
2. originating below the base of the uppermost culm internode <i.e. the shoots originating in the axils of basal leaf sheaths – implicit>/

- Seberg (1988a p. 126) states that "the vast majority of the Cyperaceae innovate their shoot-systems by lateral shoots in the axils of leaves close to or beneath the surface of the substrate" while (e.g.) *Oreobolus* produces "lateral shoots ... immediately below the inflorescences." These states, however, are not strictly exclusive. Instead I specify the origin of the lateral shoots as at or
below the base of the uppermost culm internode, this being delimited by the first vegetative leaf below the inflorescence. Seberg (1988a) also points out that the growth pattern of the plants with the lateral shoots originating only at the base of the culms, as in Oreobolus, "raise(s) the plants up above the substrate". However, many tussock- or cushion-forming species with their lateral shoots originating below the base of the culm internodes, are similarly raised above the substrate.

#14. Culms <whether dimorphic – not to be confused with dimorphic shoots>/
1. dimorphic <i.e. with readily distinguishable sterile and fertile ‘culms’ – e.g. Websteria> <Plates 1.3, 1.7>/
2. monomorphic <implicit>/
   • Dimorphic culms are known to occur only in the elaminate, hydrophytic Egleria and Websteria. The abundant sterile culms are fine, hair-like and photosynthetic. Their high surface-to-volume ratio probably bestows a high diffusion potential, and they seem (unsurprisingly) to be astomatal.

#15. Culms <whether central or ‘axillary’: presence of a prophyll on the culm at the base of the uppermost internode indicates ‘axillary’>/
1. central <Plates 2.1, 2.4>/
2. ‘axillary’ <Plates 2.3, 4.1>/
   • Central culms bear leaves. When the culms are ‘axillary’ a prophyll or prophylls are present at the base of the culm internode immediately below the inflorescence. The prophyll keels are on the external, abaxial surface facing away from the culm (e.g. Microdracoides; by contrast with Seberg, 1988a p. 126). This attribute should not be confused with character #13, where leafy shoots bear prophylls, e.g. in Oreobolus, and the keels of the prophyll adjoin the culm.

#16. Culms <whether fibrous or herbaceous>/
1. fibrous <to ‘woody’ and persistent>/
2. herbaceous <not woody, never persistent>/
   • Herbaceous culms are readily torn with one twist-and-cutting action between the fingers and thumbs of both hands.

#17. Culms <whether possessing complete septa>/
1. with complete septa <includes septate-nodulose> <Plates 3.5–6>/
2. without complete septa <implicit>/
   • Dissection of the culm is necessary to confirm the presence of complete septa. However, they are usually obvious in dried or herbarium specimens. In
the field, they can usually be detected by running the culm between forefinger and thumb. A number of genera are variable for this feature, which is more useful for identification than classification.

#18. Culms <whether armed with prickle-hairs, i.e. unicellular, short, sharp trichomes, cf. Metcalfe 1971 p.12>/
1. armed with prickle-hairs/
2. without prickle-hairs/
   • Many taxa possess culm prickle-hairs only immediately below the inflorescence. Check the entire length of the culm.

#19. Culms <maximum height>/
   cm high/
   • Most of my data for heights of culms, or flowering stems, have been collected from floras or monographs, and the values usually include the inflorescence and continuous leafy cauline internodes, down to the base of the plant.

#20. Culms <mid-culm internode: maximum diameter>/
   mm in diameter/
   • The mid-culm internode is taken to be the internode immediately below the lowest node of the inflorescence.

#21. Culms <whether by the aggregation of leaf bases>/
1. enlarged basally by the aggregation of the leaf bases <Plate 2.7>/
2. not enlarged basally by the aggregation of the leaf bases/
   • The leaf-bases may be thickened and clustered together to give the base of the plant a pseudobulbous appearance, even though the cauline component is not swollen.

#22. Culms <whether bulbous at the base>/
1. bulbous <at the base> <Plate 2.9>/
2. not bulbous <at the base: implicit>/
   • The culm-base itself may be enlarged. The base may either be fleshy, as in Fuirena umbellata, serving as a food storage organ, or woody, as in Exocarya sclerioides, where the function is not obvious.

#23. Tubers <whether present>/
1. present <Plate 2.8>/
2. absent <implicit>/
   • Tubers are separated from the culm by a stolon or rhizome, but otherwise resemble or are equivalent to a bulbous culm-base. The world’s worst weed,
Cyperus rotundus, owes much of its reproductive potency to the production and dissemination of tubers (Willis 1987). The tubers of Eleocharis dulcis provide a commercial crop in Asia (Kern 1974).

#24. Vernation <ptyxis of Dahlgren and Clifford 1981>/
1. conduplicate <includes plicate> <Plates 3.3–4>/
2. ‘curved’ <includes parallel> <Plates 3.1–2>/
   • ‘Conduplicate’ and ‘curved’ vernation are equivalent terms to ‘folded in the bud’ and ‘rolled in the bud’ respectively. The vernation may be determined directly by cutting across a young shoot and examining the cut surface pattern, or indirectly via the shape of the trans-section of mature leaves.

#25. Leaves <whether reduced to sheaths or laminate>/
1. ‘elaminate’ <i.e., with reduced laminae, or represented by sheaths> <Plates 1.1–3, 1.7>/
2. laminate <Plates 1.2, 1.8>/
   • Leaves with only short mucronate or awn-like laminae are scored as ‘elaminate’.

#26. Leaves <phyllotaxis>/
1. spirally disposed <comment if pentastichous>/
2. distichous <comment if spirodistichous> <Plates 3.4, 4.2>/
3. tristichous <Plates 3.2–3>/
   • Most genera possess either tristichous (76) or distichous (33) leaves. However, in at least some of the ‘spirally disposed’ forms the phyllotaxis may eventually prove to be spirodistichous or spirotristichous. Most of the taxa unscored for this character are elaminate or possess very few leaves per culm. Here, the arrangement of the primary inflorescence bracts may provide a useful indication of the phyllotaxis. Phyllotaxes of orders higher than three, e.g. Fuirena, have been scored as ‘spirally disposed’.

#27. Leaves <whether cauline or radical>/
1. cauline <Plates 1.2, 4.6>/
2. radical <Plate 1.9>/
   • Cauline leaves are present when nodes and internodes are clearly visible along the flowering stem. Cauline leaves should not be confused with primary inflorescence bracts, which subtend floral axes, nor with radical or basal leaves whose sheaths extend some distance along the culm, as in Blysmus or Machaerina.
22

• It is convenient to recognize the three forms of laminate leaves (Oreobolus-like ‘pseudopetiolate’ leaves, Mapania-like ‘petiolate’ leaves, and sessile leaves) to emphasize (in particular) the apparently independent origin of the first two types. ‘Pseudopetiolate’ leaves are divided into three sections. A crimping or slight change in shape between the leaf apex and sheath, often accompanied by a change in indumentum, delimits the leaf-blade from the ‘pseudopetiole’. The sheath constitutes the third section. Further complications are sometimes apparent, as in Schoenoides, where several constrictions delimit more than one lamina-like portion above the ‘pseudopetiole’). The lamina is taken here to end at the base of the lowermost constriction. The adaxial surface of the ‘pseudopetiole’ is more or less concave. ‘Pseudopetioles’ are more widespread than Seberg (1986, 1988a-b) suggested, and may prove occur in yet further genera. ‘P etiolate’ leaves are also differentiated into three sections, but here, the lamina tapers more or less markedly to form the petiolate mid-portion. The adaxial surface of the ‘petiole’ is usually irregular or contorted (contrast Kern 1974 p. 467 Fig. 9 who shows the petiole as a unifacial structure). ‘Pseudopetiolate’ leaves (‘pseudopetioles’ plus laminae) are more or less lance-like, while ‘petiolate’ leaves are more strap-shaped. Sessile leaves are simply differentiated into distal leaf-blade and proximal leaf-sheath portions.

• This character was introduced to recognize a unique attribute of Cymophyllus, but represents a quantitative rather than a qualitative character.

#29. Leaf margins <whether translucent and achlorophyllous>/

1. translucent and colourless <Cymophyllus> <Plate 2.6>/
2. not translucent and colourless <implicit>/

#30. Leaf margins <whether undulate>/

1. undulate <in the plane parallel to the leaf surface – Cymophyllus> <Plate 2.6>/
2. not undulate <implicit>/

#31. Leaf blades <whether bifacial or unifacial>/

1. bifacial <Plates 3.2–3>/
2. unifacial <includes cylindrical> <Plate 3.4>/
Upper faces are different from lower faces in bifacial, or dorsiventral leaves. 'Unifacial' leaf blades have identical upper and lower faces or simply one 'face', as in the case of cylindrical leaves.

#32. Leaf blades <maximum width in mid-third>/
  mm wide/
  - Refers to fully developed leaves, either cauline or radical. Primary inflorescence bracts are best avoided. Most data are from floras or monographs.

#33. Leaf blades <whether with conspicuous transverse septa>/
  1. with readily visible transverse septa <state whether these are partial or complete>/
  2. without readily visible transverse septa/
  - 'Readily visible' septa, constituting ridges in dried or herbarium specimens, can be seen with the unaided eye.

#34. Leaf blade septa <whether visible adaxially or abaxially>/
  1. visible adaxially/
  2. visible abaxially/
  - This and the preceding character should probably be reserved for identificatory purposes, as the character appears to be generally consequent on thick, broad leaves. Superficial invisibility of septa, however, is not reliable evidence of the absence.

#35. Leaf blade margins <whether armed with prickle-hairs>/
  1. armed with prickle-hairs/
  2. without prickle-hairs/
  - Prickle-hairs (Metcalfe 1971 p. 12: "prickles") are short unicellular outgrowths of the epidermis, each with a sharp conical or pyramidal apex. They are typically highly silicified, and sometimes grade in size into much longer unicellular trichomes. Prickle-hairs are almost always antorse, though they are retrorse in the scandent Scleria boivinii.

#36. Leaf blades <whether with a keeled midrib>/
  1. with a keeled midrib <Plates 18.1, 19.3–4>/
  2. without a keeled midrib/
  - This character indicates whether the main vein of a dorsiventral leaf forms a keel on the abaxial surface. Leaves are scored "with a keeled midrib" where the midrib portion is enlarged relative to the lateral portions of the laminae, as seen in transection. Most V-shaped leaves (see #127) are 'keeled'.

#37. Leaf blades <when dry: whether markedly infolded, markedly revolute or neither>/

1. markedly infolded <i.e. involute or convolute> when dry <Plate 3.2>/
2. markedly revolute when dry/
3. ‘flat’ <i.e. neither revolute nor involute> when dry <implicit>/

- Leaf blades that are hinged about the midrib, such that the opposing adaxial surfaces are brought together when the leaves dry, are scored as ‘flat’. This is referred to by comment only.

#38. Leaf blades <whether deciduous or persistent>/

1. deciduous <along an abscission zone> <Plates 1.4, 3.9, 4.1>/
2. <more or less> persistent <implicit>/

- Deciduous laminae, like complete septa, occur sporadically in one or two species of a number of distantly related taxa. Their presence, in certain closely related Costularia species, and the Trilepideae, is nevertheless of more taxonomic interest.

#39. Leaf bases <whether breaking down into fibres>/

1. breaking down into fibres <Plate 2.7>/
2. not breaking down into fibres/

#40. Leaf sheaths <whether open to base or tubular>/

1. open to the base/
2. tubular <Plates 4.4, 4.6, 4.8–9>/

- Tubular sheaths may be torn with age or split by the growth of enclosed leaves and culms. To avoid misinterpretation due to subsequent splitting of once-tubular sheaths, young leaves should be examined.

#41. Leaf sheaths <whether the margins overlapping distally>/

1. with overlapping margins distally <Plates 4.7–8>/
2. with entire margins <Plates 4.4, 4.6, 4.9>/

- If the radical leaves are absent from the specimen or difficult to inspect, the lower primary inflorescence bract sheaths may provide the requisite information. Caution is necessary, however, as the portion of the sheath with overlapping margins may decrease as more distal sheaths are examined, until the sheaths are entire. The junction of the leaf sheath margins may be prominently thickened and this provides a clue to the presence of obscurely overlapped margins.
#42. Leaf sheaths <whether with free lateral limbs>/
1. with free lateral limbs/
2. without free lateral limbs/
   ● These lobes, on each side of the sheath, were not accepted by Dahlgren and Clifford (1982) as stipules.
#43. <Leaf> sheath apices <shape>/
1. n-shaped <i.e. forming a "contraligule"> <Plates 4.6, 4.9>/
2. 'truncate' <includes U-shaped> <Plate 4.4>/
3. V-shaped <Plates 4.7–8>/
   ● The term "contraligule" has often been used in the Cyperaceae (e.g. Koyama and Maguire 1965; Haines and Lye 1983), and simply denotes n-shaped leaf sheath apices. It is, however, not equivalent to the term as applied to grasses (cf. Watson and Dallwitz 1988). Beware of torn sheaths, which sometimes spuriously appear V-shaped; and sheaths with only slightly overlapping margins, which may superficially appear truncate when they are in fact V-shaped. Ideally, only intact leaf sheath apices should be scored.
#44. <Leaf> sheath apices <whether indumented>/
1. indumented <Plates 4.4, 4.8–9>/
2. glabrous <Plate 4.6>/
   ● Score only the actual sheath apices, rather than the whole sheaths, although both often share the same state.
#45. <Leaf> sheath apices <indumentum form; cf. Hewson 1988>/
1. 'pilose'/
2. 'puberulous'/
3. 'scabrous' <i.e. constituting prickle-hairs>/
   ● ‘Pilose’ with long, soft, thin hairs with a length:breadth ratio of more than 5:1. ‘Puberulous’ with short hairs with a length:breadth ratio of about 2:1 to 5:1. ‘Scabrous’ with short sharp hairs, i.e. prickle-hairs, with a length:breadth ratio up to 2:1.
#46. Leaf sheath fronts <whether different in texture>/
1. similar in texture to the backs <and to the blades> <Plates 4.4, 4.6>/
2. differing in texture from the backs <and from the blades> <Plates 3.8, 4.5>/
   ● This character is usually best determined for the distal portion of the sheaths. Gradual changes in texture towards the sheath margins are best ignored. The radical and cauline sheaths may differ for this attribute. In my observations, "similar" may mean that the fronts and the backs are both
membranous, or that both are cartilaginous. This is another character is best omitted from classificatory analyses.

#47. Leaf sheath fronts <texture>/
1. ‘hyaline’ <i.e. transparent>/
2. ‘membranous’ <i.e. translucent>/
3. ‘cartilaginous’ <i.e. tough and opaque> <Plates 4.4, 4.6, 4.8>/

#48. Leaf sheath fronts <colour>/
1. colourless <includes white>/
2. pallid-brown <includes yellow-brown>/
3. green/
4. red-brown <includes dark-brown>/
5. blackish <including purple and dark-red> <Plate 1.9>/

- For identification, it may be wise to enter the range of possible states, and eliminate only those states which are obviously mismatches; e.g. if the sheaths appear pallid-brown, scoring as 48,2-3 avoids a mismatch due to fading from green.

#49. Ligules <abaxial, whether present>/
1. present <Plates 3.7, 4.3, 4.5>/
2. absent/
- The sedge ligule is an adaxial projection from the top of the leaf sheath, comparable with the adaxial ligule of grasses. Simple discontinuities in texture between the sheath and lamina are not scored as ligules, but are commented on.

#50. Ligules <distally, whether limbed>/
1. with a free limb <Plates 3.7, 4.5>/
2. without a free limb/
- This character refers to the flange of tissue constituting the ligule, and not its indumentum.

#51. Ligules <maximum length of free limb>/
   mm long/
- This character is as yet poorly scored.

#52. Ligules <whether partial or entire>/
1. partial <Plate 3.8>/
2. entire <Plates 3.7, 4.5>/
- Partial ligules are easily overlooked. The junction of the leaf sheaf apex and the lamina should be carefully inspected for overlap of the sheath onto the
adaxial surface of the lamina, thus indicating the presence of a ligule. Some ligules appear notched with age. Such ligules have, for the present, been scored as complete, qualified by the comment "emarginate".

#53. Ligules <shape/>
1. acute <Plate 4.3>/
2. obtuse <Plate 3.7>/

#54. Ligules <distally, texture>/
1. 'membranous' <i.e. translucent> <Plate 4.5>/
2. 'chartaceous' <i.e. opaque> <Plate 3.7>/

#55. Ligules <distally, whether indumented>/
1. indumented <Plate 4.5>/
2. glabrous/

#56. Ligules <distally, indumentum form>/
1. 'pilose' <Plate 3.9>/
2. 'puberulous'/
3. 'scabrous' <i.e. constituting prickle-hairs>/
   • Terms as for #45 above.

CULM EPIDERMIS

#57. Culm epidermal zones <mid-third of the uppermost internode below the inflorescence: relative width>/
1. wider costally than intercostally <Plates 7.3, 11.9>/
2. <costal and intercostal> of equal width <Plates 5.8, 12.1>/
3. wider intercostally than costally <Plates 5.5–6, 6.1, 7.6>/
4. absent <Plates 5.1, 5.4, 7.1, 11.2>/
   • The width of the costal zones is defined by the width of the strands and/or girders contiguous with the epidermis.

#58. <Culm> intercostal zones <whether differentiated into alternating narrow stomatal zones and wide astomatal zones>/
1. differentiated into alternating <relatively> narrow stomatal zones and wide astomatal zones <Actinoschoenus> <Plates 5.2, 9.1>/
2. undifferentiated <implicit>/
   • State 1 is unique to Actinoschoenus.

#59. <Culm> intercostal cells <whether regular and rectangular or irregular>/
1. regular and rectangular <Plates 5.2, 5.7, 6.5–7, 7.2>/
2. irregular <at least in places, e.g. around the stomata> <Plates 5.1, 5.6, 7.8>/
• Ignore curved faces contiguous with the lateral ends of the stomata.

#60. <Culm> intercostal cell anticlinal walls <whether sinuate or straight in outer optical section>/
1. sinuate <Plates 5.2, 5.7, 6.3, 6.5, 7.2>/
2. straight <Plate 6.1>/
• Many taxa have mid-culm epidermes with the anticlinal walls superficially straight. However, by comparison with grasses, careful focussing of the intact walls or inspection of the walls along tear-lines will often reveal that they are sinuate.

#61. <Culm> epidermal cell outer walls <whether thickened; not scored for cells with conical silica bodies>/
1. thick <and lignified> <Plates 8.6, 9.7, 11.7>/
2. moderately thickened <Plate 8.1>/
3. thin/
• Thick walled: the outer wall is half or more of the height of the cells; moderately thick walled: possessing an obvious secondary wall less than half the height of the epidermals; and thin walled: without an obvious secondary wall, the outer wall only as thick as the outer walls of the epidermals containing conical silica bodies. Currently both costal and intercostal cells are assessed. Restriction of the character to only intercostal cells may reveal more useful character state distributions.

#62. <Culm> epidermal cells in transverse section <whether radially elongated>/
1. <noticeably> ‘radially elongated’ <Plates 8.3, 11.3, 11.8>/
2. <more or less> isodiametric <Plate 8.2>/
• The mid-culm epidermals are ‘radially elongated’ when the radial walls of the epidermal are more than twice as long as the periclinal walls, and the epidermals are larger than the underlying mesophyll cells.

#63. Culms <mid-third of uppermost internode, whether indumented>/
1. indumented <Plates 7.3, 10.8>/
2. glabrous <Plates 5.3, 5.5, 10.4>/

#64. Culms <indumentum: form>/
1. ‘papillose’ <i.e. constituting erect papillae> <Plates 7.1, 10.6, 21.9>/
2. ‘scabrous’ <Plates 7.3, 7.7>/
3. ‘pilose’ <Plate 7.5>/
• Rounded, finger-like or nipple-like projections of epidermals (one per cell) constitute ‘papillae’, see also #45 above (cf. Hewson 1988).
#65. <Culm> indumentum <distribution>/
   1. intercostal <Plates 7.7, 21.9>/
   2. costal <Plate 21.9>/

#66. <Culm> silica bodies <whether present>/
   1. present <Plates 6.4, 6.8>/
   2. absent/
      • ‘Particulate’ silica and the silica directly associated with prickle-hairs is not scored, though the former may be commented upon.

#67. <Culm> silica bodies <location, with respect to the epidermis>/
   1. luminal/
   2. embedded in the outer periclinal wall/
   3. ‘external’ <i.e. forming cones seated on the epidermis> <Plates 7.2, 9.1>/
      • As bridge-shaped and wedge-shaped silica bodies (Metcalfe 1971) intergrade, they are treated here as equivalent and scored as ‘embedded in the outer periclinal wall’. These silica bodies are difficult to discern. They may be artifacts of slightly sunken, dome-topped epidermals. In any case, I have scored the attribute consistently. Seberg (1988a p. 128) cites Metcalfe (1971) in distinguishing the position and size of the ‘external’ silica bodies of Actinoschoenus from those of Oreobolus. However, Metcalfe’s (1971 p. 68 Fig. 10D) illustration of Actinoschoenus silica bodies is uninterpretable, and does not match my observations on this genus. The ‘external’ silica bodies of Actinoschoenus and Oreobolus appear identical, except those of the former are considerably larger.

#68. <Culm> ‘luminal’ silica bodies <type>/
   1. conical <with their bases on the proximal periclinal epidermal wall above sclerenchyma> <Plates 6.4, 8.1>/
   2. globular <free or attached to the anticlinal walls>/
      • The conical silica bodies, as with other opaline silica bodies, do not stain. However, the organic foot often does stain and then is a prominent marker for them.

#69. Culms <mid-third of uppermost internode, whether possessing stomata>/
   1. with stomata <implicit>/
   2. ‘without stomata’ <Plate 6.1>/
      • If no stomata are seen in ten square millimetres of epidermal tissue, the culm is scored ‘without stomata’.
#70. <Culm> stomata <position relative to the epidermals – best seen in transverse section>/
1. sunken <Plate 8.6>/
2. flush <Plates 10.7, 11.7, 12.2>/
3. raised <Plates 7.4, 8.7, 9.7>/
   • Papillae and hairs are ignored in estimating the level of the epidermals.

#71. <Culm> stomata <whether obscured by projections from the adjacent epidermal cells, not to be confused with erect papillae>/
1. obscured by projections from the adjacent epidermal cells <Plates 5.5–6, 7.6, 8.6>/
2. not obscured by projections from the adjacent epidermal cells <Plates 5.8, 8.2>/
   • Refers to horizontal projections and adjacent papillae that are inclined over the stomata. Adjacent, erect papillae, and distant erect papillae are ignored.

#72. <Culm> subsidiaries in surface view <shape>/
1. ‘triangular’ <i.e. with concave sides> <Plate 5.7>/
2. ‘dome-shaped’ <i.e. with convex sides>/
3. ‘rectangular’ <i.e. with the outer anticlinal walls parallel> <Plates 6.2, 6.6>/
   • By comparison with the grasses, many taxa are variable for this feature.

#73. <Culm> subsidiaries in transverse section <size relative to the adjacent epidermal cells>/
1. smaller than the adjacent epidermal cells <Plate 8.2>/
2. similar in size to the adjacent epidermal cells <Plate 12.3>/
3. larger than the adjacent epidermal cells <Plate 11.4>/

#74. <Culm> subsidiaries in transverse section <shape>/
1. square or horizontal-rectangular/
2. ‘vertical-rectangular’ <includes curved-rectangular> <Plate 10.5>/
3. lachrymose <Plates 8.2, 8.7, 11.4, 12.3>/

#75. <Culm> substomatal chambers <whether lined with bridging sclereids>/
1. lined with <bridging> sclereids <Reedia and Gymnoschoenus>/
2. without sclereids <implicit> <Plate 12.3>/
   • Bridging sclereids occur in the stems of many Restionaceae but are of very limited occurrence in Juncus. They are uncommon in the Cyperaceae, where they link Gymnoschoenus with Reedia. Metcalfe (1971), however, did not draw the parallel between the bridging sclereids in these families, nor between
the two sedge genera, describing the former (p. 298) as "scleroded cells" and the latter (p. 417) as "with thicker walls than their neighbours".

**CULM ANATOMY**

#76. Culm trans-section at mid-third of the uppermost internode, terms after Metcalfe 1971/

1. triangular/
2. quadrangular <Plate 9.7>/
3. pentagonal/
4. polygonal/
5. circular <Plate 3.6>/
6. truncate circular <Plate 9.5>/
7. broadly elliptical <Plates 9.3, 9.6>/
8. ‘narrow elliptical’ <or fusiform> <Plate 9.2>/

#77. Culms at mid-third of uppermost internode, whether from their inception hollow or solid/

1. initially hollow <Plates 3.5–6>/
2. initially ‘solid’ <includes ‘reticulate’ and ‘spongy’> <Plates 9.6, 11.1>/
   • Culms which are hollow from their inception are usually associated with the presence of complete septa. Culms where the pith is reticulate (i.e. the parenchymatous cells form a net-like pattern about large intracellular spaces) have been scored as solid, even when the reticulum is poorly developed, as in *Websteria* and some *Eleocharis* species.

#78. Culms at mid-third of uppermost internode whether hollow with age/

1. <solid when young> hollow with age/
2. remaining ‘solid’ <with age>/
   • This character serves an identificatory role, and should not to be confused with the preceding.

#79. Culms at mid third, whether medullated/

1. medullated <i.e. with a pith> <Plates 9.2–8, 11.1, 12.1>/
2. not medullated <Plate 9.1>/
   • Non-medullated culms, i.e. without pith, are found in *Actinoschoenus* and *Ficinia*. Hollow culms are bordered by pith. Culms where the pith is reticulate are scored as medullated, even when the reticulum is poorly developed, as in *Websteria* and some *Eleocharis* species.
#80. <Culm> pith <whether with 'translucent tissue'>/
1. with 'translucent tissue' <Plates 8.5, 10.1, 11.2, 12.8>/
2. without 'translucent tissue' <Plate 9.3>/
• 'Translucent tissue' implies heterogeneity of the pith, and includes that component which is clearly distinguishable from the whole, in texture (the 'translucent tissue' being thinner-walled) or by the degree of formation of intercellular air spaces (these usually more pronounced in the 'translucent tissue').

#81. <Culm> pith <whether with air cavities: excluding any central hole>/
1. with air cavities <Plates 9.3, 10.1, 12.8>/
2. without air cavities/
• 'Air-cavities' usually result from breakdown of the 'translucent tissue'. However they may also reflect development of lacunae (indicated by the comment that the pith is 'reticulate').

#82. Culms <whether photosynthetic>/
1. photosynthetic <implicit>/
2. 'not <appreciably> photosynthetic' <Plates 9.3, 10.2>/
• Applies only to fertile culms. Taxa scored as 'not photosynthetic' (i.e. without appreciable development of chlorenchyma) have all been examined in herbarium material only. Observations on fresh material may reveal at least some development of chlorenchyma, but the difference between *Websteria* and *Eleocharis* is evidently not an artifact of preservation.

#83. <Culm> mesophyll 'translucent tissue' <whether present>/
1. present <Plates 10.1, 12.1>/
2. absent <Plates 8.3, 11.7>/
• Mesophyll 'translucent tissue' is distinguished from pith 'translucent tissue' (perhaps rather arbitrarily) by being contiguous with or surrounded by chlorenchyma. The mesophyll 'translucent tissue' may vary in constitution from 'balloon cells' to stellate aerenchyma.

#84. <Culm> mesophyll air cavities <whether present>/
1. present <Plates 8.7, 10.1, 12.1>/
2. absent <Plates 8.3, 11.7>/
• Mesophyll air cavities are usually derived as a result of the breakdown of the 'translucent tissue', however they may also be a product of the breakdown of stellate chlorenchyma or very loosely packed spongy mesophyll (and are commented as such).
#85. <Culm> tannin idioblasts <whether present>/
   1. present <Plate 8.6>/
   2. absent/

#86. <Culm> tannin idioblasts <distribution>/
   1. epidermal <Plates 6.6, 8.4>/
   2. in the chlorenchyma <Plates 8.6, 9.1–2, 12.8>/
   3. in the pith <Plates 9.4, 9.8, 10.2>/
   4. in the ‘translucent tissue’/

#87. Culms <whether with a hypodermis>/
   1. with a hypodermis <Plates 9.3, 10.2–3, 11.2>/
   2. without a hypodermis <Plates 8.7, 9.6, 11.7–9>/
      • The hypodermis as interpreted here includes only achlorophyllous parenchyma, contiguous with the epidermis, excluding any bundle sheath extension cells, and never including sclerenchyma. The hypodermis may be equivalent to a multiple epidermis. By contrast, Metcalfe (1971, e.g. p. 18) scores both "translucent" and "sclerenchymatous" subepidermal layers as constituting hypodermis. These two tissue types are better regarded as being of independent origin, and subepidermal sclerenchyma is dealt with separately below.

#88. <Culm> vascular bundles <whether contiguous with chlorenchyma>/
   1. contiguous with chlorenchyma <Plates 10.4, 10.7>/
   2. not contiguous with chlorenchyma/
      • State one includes vascular bundles completely or partially embedded in the chlorenchyma.

#89. <Culm> vascular ‘rings’ completely embedded in chlorenchyma <number>/
#90. <Culm> vascular ‘rings’ partially embedded in chlorenchyma <number>/
#91. Culm vascular bundle sheaths <primary bundles: number>/
      • Primarily included for identificatory purposes, this character refers to the sheaths of the primary bundles. Parenchymatous bundle sheaths (PBS), mestome sheaths, and sheaths of boundary layer cells that are large and chlorenchymatous are each scored as one sheath. A sheath, e.g. a PBS, more than one cell wide, still contributes only one to the total sheath number. A mestome sheath is always present.
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#92. <Culm> boundary layer cells <primary bundles: relative to bundle parenchyma cells, whether 'large' or 'small'> /
1. 'large' <Plates 10.7, 10.9, 11.5> /
2. 'small' /
• The boundary layer cells (or border parenchyma) are parenchymatous cells contiguous with the inner periclinal walls of the mestome sheath.

#93. <Culm> boundary layer cells <primary bundles: whether chlorenchymatous>/
1. chlorenchymatous <Plates 10.7, 11.5>/
2. 'non-chlorenchymatous' <i.e., never with abundant chloroplasts>/
• The boundary layer cells are scored as non-chlorenchymatous even if a few chloroplasts are present, as long as they are decidedly less abundant than in the mesophyll cells.

#94. <Culm> boundary layer cells <of the primary bundles: whether 'complete' or interrupted>/
1. forming a 'complete' sheath/ 
2. interrupted by metaxylem/ 
• Any gaps in the boundary layer cells in the region of protoxylem lacunae have been ignored when assigning to state 1. The boundary layer cells are parenchymatous. Where thick-walled mestome sheath like cells occur between the mestome sheath proper and the metaxylem vessel elements they are counted as part of the mestome sheath and the boundary layer cells are scored as interrupted.

#95. <Culm> mestome sheaths <primary bundles: whether chlorenchymatous>/
1. chlorenchymatous/ 
2. 'non-chlorenchymatous' <i.e., never with abundant chloroplasts>/
• The mestome sheath is always present and complete, though its extent may be obscured by contiguous fibres. At the light microscope level it is usually readily recognizable by its walls, which are thicker than the adjacent boundary layer cells and parenchymatous bundle sheath and/or chlorenchyma cells, or by its brightness when viewed between cross-polarizers. Ultrastructurally, a suberized lamella can be seen. The mestome sheath is scored as non-chlorenchymatous even if a few chloroplasts are present, as long as they are decidedly less abundant than in the mesophyll cells.
#96. <Culm> parenchymatous bundle sheaths <primary bundles: external to the mestome sheath, whether present>/
1. present <Plate 8.7>/
2. absent/
   • When present, the parenchymatous bundle sheath is located contiguous to the outer walls of the mestome sheath, and distinguished from the adjacent mesophyll cells by in shape and often by a different abundance of chloroplasts. In transverse section the outer periclinal wall of the PBS cells are generally rounded, and intercellular airspaces are smaller than amongst the mesophyll or ‘primary carbon assimilation’ (PCA) cells. Seen in longitudinal section the PBS are longer than the adjacent mesophyll or PCA cells.

#97. <Culm> parenchymatous bundle sheaths <primary bundles: whether chlorenchymatous>/
1. chlorenchymatous/
2. ‘non-chlorenchymatous’ <i.e., never with abundant chloroplasts> <Plate 9.6>/
   • The PBS is scored as non-chlorenchymatous even if a few chloroplasts are present, as long as they are decidedly less abundant than in the mesophyll cells.

#98. <Culm> parenchymatous bundle sheaths <primary bundles: configuration>/
1. complete <Plates 9.6, 12.3>/
2. interrupted by fibres <Plates 11.4, 11.8>/
3. only adjacent metaxylem vessels <Plate 10.9>/
4. ‘irregular’ <regardless of whether the bundles are fully embedded in chlorenchyma>/
   • When the PBS, is ‘interrupted by fibres’, both adaxially and abaxially, it may superficially appear to be ‘only adjacent metaxylem vessels’. In these cases the PBS is scored as the former. By contrast, those taxa with the PBS only adjacent metaxylem vessels also have at least some PCA and/or pith cells contiguous with the mestome sheath.

#99. <Culm> parenchymatous bundle sheaths <whether with extensions>/
1. with extensions <Plate 10.1>/
2. without extensions/
   • Only PBS extensions that are more or less contiguous with the epidermis are scored.
#100. <Culm> sclerenchyma <distribution>/
   1. comprising peripheral strands/
   2. comprising girders <Plate 11.4>/
   3. forming <inner and/or outer> caps on the vascular bundles <Plate 11.1>/
      • Strands are composed of clustered, or more rarely solitary, fibres. They are
        usually contiguous with the epidermis, but are commented upon if not. Girders
        are contiguous with both the epidermis and a vascular bundle. The
        sclerenchyma contiguous with the vascular bundles but isolated from the
        epidermis by other tissue types constitute caps. The mestome sheath is not
        scored as part of the sclerenchyma.

#101. <Culm> sclerenchyma <i.e. caps and girders: whether in direct contact with all
       of the vascular bundles>/
   1. not in direct contact with all of the vascular bundles <Plates 10.4, 11.5,
      12.6>/
   2. in direct contact with all of the vascular bundles <Plates 12.5, 12.7>/

#102. <Culm> sclerenchyma <i.e. the caps and/or girders: whether coalescing to form
       a ‘ring’>/
   1. coalescing to form a ‘ring’ <Plates 8.4, 9.7, 11.6>/
   2. not coalescing to form a ‘ring’ <Plate 9.5>/
      • The ‘ring’ may be incomplete, but is then commented upon.

#103. <Culm> strands <whether all aligned with the vascular bundles>/
   1. all aligned with the vascular bundles/
   2. not all aligned with the vascular bundles <Plate 8.5>/

#104. <Culm> sclerenchyma groups <i.e. the strands and girders> to vascular bundles,
       ratio/
   1. less than 1:1 <Plates 9.7, 12.4>/
   2. 1:1/
   3. greater than 1:1 <Plates 8.5, 9.5>/

#105. <Culm> spongy mesophyll <whether present>/
   1. present <Plates 9.2, 11.5–6>/
   2. absent <Plates 11.7>/
      • Brick-shaped PCA cells (which are commented upon when present) and
        other regularly shaped mesophyll cells that are not vertically aligned with the
        epidermis are scored as spongy mesophyll.
#106. <Culm> palisade mesophyll <whether present>/
   1. present <Plates 8.2–3, 8.8, 9.2, 11.7>/
   2. absent <Plates 11.5–6>/
   • Palisade mesophyll comprises perpendicularly elongated (chlorenchyma) cells relative to the surface of the leaves (Jackson 1971 p. 263). Brick-shaped PCA cells are not scored as forming palisade, though in some C₄ species these cells may appear to constitute a palisade.

#107. Culm ‘maximum cells-distant count’ <after Hattersley and Watson 1975: excluding the parenchymatous bundle sheath>/
   1. one <indicative of C₄> <Plates 10.7, 10.9, 12.6>/
   2. more than one <indicative of C₃> <Plates 9.2, 12.2>/
   • The one cell distant criterion (Hattersley and Watson 1975 p. 325) of grasses states that "in C₄ species no chlorenchymatous mesophyll cell is separated from the nearest PBS cell by more than one other chlorenchymatous mesophyll cell". In the Cyperaceae, the mestome sheath, any nonchlorenchymatous cells and PBS cells are ignored. The first exceptions to the ‘maximum cells-distant count’ criterion in the Cyperaceae have been found in C₄ Eleocharis. However, outside Eleocharis, this criterion provides a very reliable basis by which to assign sedges as C₃ or C₄.

LEAF BLADE EPIDERMIS

#108. Abaxial leaf blade epidermal zones <relative width>/
   1. wider costally than intercostally/
   2. <costal and intercostal> of equal width <Plates 15.2>/
   3. wider intercostally than costally <Plates 13.1, 13.6, 13.8, 15.1, 15.5, 16.1, 17.8>/
   4. absent <Plate 13.5>/
   • See #57 above.

#109. Abaxial <leaf blade> epidermal cells <whether regular and rectangular or irregular>/
   1. regular and rectangular <Plates 16.1–2, 16.8>/
   2. irregular <at least in places, e.g. around the stomata> <Plates 13.4–5, 14.2–4, 15.6, 16.5>/
   • See #59 above.
#110. Abaxial <leaf blade> epidermal cell anticlinal walls <whether sinuate or straight in outer optical section>/
1. sinuate <Plates 13.2, 14.1>/
2. straight/
   • See #60 above.
#111. Abaxial <leaf blade> epidermal cell outer walls <whether thickened; not scored for Si cells>/
1. thick <and lignified> <Plates 18.7, 21.8>/
2. moderately thickened <Plate 21.1>/
3. thin <Plate 17.4>/
   • See #61 above.
#112. Leaf blades <mid-third, excluding prickle-hairs along the margins, whether indumented>/
1. indumented <Plates 13.2, 14.1, 15.3>/
2. ‘glabrous’ <Plate 13.1>/
#113. Leaf blades <mid-third; indumentum: form>/
1. ‘papillose’ <i.e. constituting erect papillae> <Plates 14.3, 14.5, 14.8, 15.4, 17.6>/
2. ‘scabrous’ <Plate 15.3>/
3. ‘pilose’ <Plates 14.1, 15.3, 24.3>/
   • See #64 above.
#114. The leaf blade indumentum <distribution>/
1. intercostal <Plates 13.2, 15.4>/
2. costal <Plate 14.1>/
#115. The leaf blade indumentum <location>/
1. abaxial <Plates 14.3, 14.5>/
2. adaxial <Plates 14.5, 15.3, 19.5>/
#116. <Leaf blade> trichomes <mid-third; whether unicellular>/
1. unicellular <Plates 13.2, 14.3, 15.3>/
2. multicellular <Plate 14.6>/
   • "Multicellular trichomes" provides a catch-all state for identification, as dome-shaped, elongated multiseriate, and uniseriate types are included.
#117. <Leaf blade> silica bodies <whether present>/
1. present <Plates 15.8, 21.4>/
2. absent/
   • See #66 above.
#118. *Leaf blade* silica bodies *location, with respect to the epidermis*:
1. *luminal* *Plates 21.3–4*;
2. embedded in the outer periclinal wall *Plate 18.6*;
3. ‘external’ *i.e. forming cones seated on the epidermis* *Plate 21.7*;
   • See #67 above.

#119. *Leaf blade* ‘luminal’ silica bodies *type*:
1. conical *with their bases on the proximal periclinal epidermal wall above sclerenchyma* *Plates 13.3, 21.4*;
2. globular *free or attached to the anticlinal walls* *Plates 13.5, 13.7, 14.4, 17.2*;
   • See #68 above.

#120. Leaf blades *stomata: distribution*:
1. hypostomic *i.e. with stomata confined to the abaxial surfaces*;
2. epistomic *i.e. with stomata confined to the adaxial surfaces*;
3. amphistomic *i.e. with stomata over both surfaces*;
   • The extent of the abaxial epidermis is defined by the presence of vascular bundles with phloem facing that epidermis. Thus, unifacial leaves, with a complete layer of bundles, and an epidermis with stomata, are scored as hypostomic.

#121. *Leaf blade* stomata *position relative to the epidermals – best recorded in transverse section*:
1. sunken *Plate 17.6*;
2. flush *Plate 21.6*;
3. raised *Plates 17.4, 17.7, 20.6*;
   • See #70 above.

#122. *Leaf blade* stomata *whether obscured by projections from the adjacent epidermal cells, not to be confused with erect papillae*:
1. obscured by projections from the adjacent epidermal cells *Plates 14.8, 15.2, 15.4, 17.6*;
2. not obscured by projections from the adjacent epidermal cells *Plates 14.2, 14.5, 17.7*;
   • See #71 above.

#123. *Leaf blade* subsidiaries in surface view *shape*:
1. ‘triangular’ *i.e. with concave sides* *Plates 13.5, 15.7, 16.3, 16.7–8*;
2. ‘dome-shaped’ *i.e. with convex sides* *Plates 13.2, 16.2, 16.4*;
3. ‘rectangular’ *i.e. with outer anticlinal walls parallel* *Plate 14.2*;
• See #72 above.

#124. <Leaf blade> subsidiaries in transverse section <size relative to adjacent epidermal cells>/
1. smaller than the adjacent epidermal cells <Plates 17.4, 17.7>/
2. similar in size to the adjacent epidermal cells/
3. larger than the adjacent epidermal cells <Plate 17.5>/

#125. <Leaf blade> subsidiaries in transverse section <shape>/
1. square or horizontal-rectangular <Plate 17.7>/
2. 'vertical-rectangular' <includes curved-rectangular> <Plate 21.9>/
3. lachrymose <Plate 21.7>/

#126. <Leaf blade> substomatal chambers <whether lined with bridging sclereids>/
1. lined with <bridging> sclereids <Reedia and Gymnoschoenus> <Plates 19.6, 19.8>/
2. without sclereids <implicit>/
• See #75 above.

LEAF BLADE ANATOMY

#127. Leaf blade trans-section <mid-third; terms after Metcalfe 1971>/
1. 'V-shaped' <with or without a median adaxial groove> <Plate 18.1>/
2. 'flanged V-shaped' <includes inversely W-shaped, and plicate> <Plate 3.3>/
3. 'thinly crescentiform' <includes shallowly corrugate, and flat> <Plates 3.2, 18.2>/
4. 'thickly crescentiform' <includes sub-triangular, thickly V-shaped, and subhemispherical> <Plates 18.3–4>/
5. circular/
6. 'elliptical' <includes constricted elliptical, tetragonal, sub-cruciform, and winged fusiform> <Plate 3.4>/

• Metcalfe (1971 p. 7) described 16 transection leaf shapes. These have been reduced to a manageable number of states by recognizing broader, more inclusive states. Only Metcalfe’s "V-shaped; pseudo-dorsiventral" state has been rejected outright. Established for Cladium, Metcalfe applied the term where the laminae appear more or less similar above and below except in the median region, and where the vascular bundles are mostly 'inverted'. The pseudo-dorsiventral state (see Metcalfe 1971 p. 10) is highly interpretive, and there is no developmental evidence to support the historical infolding of the vascular bundles (Fisher 1971). In any case, as the morphological variation is
dealt with via a number of other characters (e.g. #120, 127 and 141) the state is redundant. Metcalfe (1971 p. 8) states that "the whole external surface must be covered by the true epidermis, the real adaxial epidermis having been lost", but this is simply not the case; at least the median portion of the topologically adaxial surface is undoubtably ‘truly’ adaxial in origin. States 1 and 2, 3 and 4, and 5 and 6 respectively, intergrade to some extent.

#128. Leaf blades <ribbing>/

1. with distinct, prominent adaxial ribs <these of two or more size orders – \textit{Gahnia} > Plates 3.7, 18.2>/
2. ‘adaxially <more or less> flat’ <ignore mid-rib and main lateral ribs – implicit> <Plate 18.1>/

\textit{Gahnia} leaves have distinct, prominent adaxial ribs. This attribute supports the separation of \textit{Morelotia}, which has adaxially flat leaves, from \textit{Gahnia} (cf. Blake 1969; but contrast Metcalfe 1971).

#129. <Leaf blade> hypodermis <whether present>/

1. present < Plates 18.7, 19.7>/
2. absent < Plates 17.1, 20.2>/

• See #87 above.

#130. <Leaf blade> hypodermis <distribution>/

1. abaxially ‘complete’ < Plates 20.1, 20.3>/
2. abaxially about the main lateral veins only < Plate 19.7>/
3. adaxially ‘complete’ < Plates 18.3–5, 19.6, 19.8>/
4. adaxially median only < Plates 19.3–4, 20.7, 21.6>/

• In scoring ‘complete’ the interruption of the hypodermis by sclerenchyma and stomata is ignored. The variation might have been better expressed as several binary characters.

#131. <Leaf blade> hypodermis <number of tiers>/

tiered/

• This character may be of limited use at the generic level, for classification and diagnosis, but is of some value for identification.

#132. <Leaf blade> hypodermal cells <whether larger than the adjacent epidermal cells>/

1. <distinctly> larger than the adjacent epidermal cells < Plates 20.3, 20.7>/
2. not larger than the adjacent epidermal cells < Plates 20.8>/
When the hypodermal cells are at least twice as large as the adjacent epidermal cells they are considered "distinctly larger". This feature, noted in Hypolytrum by Koyama (1966), exhibits discontinuity across the family.

#133. <Leaf blade> 'bulliform cells' <whether present/>
1. present <Plates 20.1, 21.6>/
2. absent <Plate 20.7>/

I define bulliform cells as those conspicuous epidermals that are more than twice as large as the underlying chlorenchyma cells and far larger than any fibres. The bulliforms are usually relatively thin-walled and often radially elongated, and may constitute 'hinge cells'. Metcalfe (1971) generally restricts use of the term 'bulliforms' to cover 'hinge cells', but apparently bases some decisions on position rather than anatomy (see Metcalfe 1971 pp. 422-430: Rhynchospora). He also accepted some subepidermal cells as bulliforms (p. 22), whereas I treat them only as hypodermal.

#134. <Leaf blade> 'bulliform cells' <distribution/>
1. covering the abaxial surface/
2. abaxially, only over the main lateral veins <Plate 19.1>/
3. covering the adaxial surface <Plates 19.3, 20.4>/
4. adaxially, median only/

States 1 and 3 ignore the interruption of the bulliform cells by small epidermals overlying sclerenchyma and of course, stomatal complexes. This character should probably be reappraised as several binary characters for classificatory analyses.

#135. <Leaf blade> 'translucent tissue' <whether present or absent/>
1. present <Plates 17.2–3, 20.1, 21.8>/
2. absent <Plate 17.6>/

'Translucent tissue' constitutes undifferentiated, translucent cells usually distinguishable from hypodermis by being thinner-walled or by the extent of intercellular air spaces (these usually more pronounced in the 'translucent tissue').

#136. <Leaf blade> 'translucent tissue' <distribution>/
1. intervascular <Plates 17.2, 21.8>/
2. <more or less> adaxial to vascular bundles <Plates 17.1 18.5>/
3. <more or less> abaxial to vascular bundles <Plate 20.1>/

In 'unifacial' leaves where the bundles form a 'ring' and surround the 'translucent tissue', the 'translucent tissue' has been treated as adaxial.
#137. <Leaf blade> mesophyll air cavities <whether present>/
   1. present <Plates 17.2, 17.4, 21.8>/
   2. absent <Plates 20.5>/
   • see #84 above.

#138. <Leaf blade> tannin idioblasts <whether present>/
   1. present/
   2. absent/

#139. <Leaf blade> tannin idioblasts <location>/
   1. epidermal <Plates 14.4, 16.6>/
   2. in the chlorenchyma <Plate 20.2>/
   3. in the hypodermis/
   4. in the 'translucent tissue'/

#140. <Leaf blade> vascular bundles <arrangement>/
   1. 'in one row' <includes Kyllinga-type> <Plates 19.6, 19.8, 20.2>/
   2. 'zig-zagged' <e.g. Everardia> <Plate 20.3>/
   3. 'in multiple rows' <e.g. Remirea>/
   4. forming 'ring' or 'horseshoe' patterns <e.g. Mariscus>/
   • 'Vascular bundles in one row' deliberately ignores the presence of secondary bundles abaxial to the primary bundle (#142), and the occasional occurrence of similarly oriented superimposed bundles, but includes those cases where the bundles constitute a single, continuous ring. 'Zig-zagged bundles' usually involves bundles of different size-classes.

#141. <Leaf blade> vascular bundles <whether 'inverted'>/
   1. 'inverted' <Plates 17.1, 18.3, 21.8>/
   2. not 'inverted' <implicit>/
   • 'Inversion' is indicated by apposition of xylem in opposite or adjoining bundles.

#142. <Leaf blade> midrib <vascularization>/
   1. with a secondary bundle abaxial to the primary bundle <Plate 18.8>/
   2. without a secondary bundle abaxial to the primary bundle <implicit> <Plate 20.6>/
   • Midribs with a secondary bundle abaxial to the primary bundle occur in some C₄ taxa, where the small secondary bundle 'maintains' the 'maximum cells-distant count' at one.
#143. <Leaf blade> midrib <with respect to the vascular bundles, fibres, and chlorenchyma: whether symmetrical>/
   1. anatomically symmetrical <Plates 18.8, 20.6, 20.8>/
   2. anatomically asymmetrical <Plate 20.7>/

   • The discontinuities in this character may be taxonomically more useful at the species level than at the generic rank, judging from the concurrence of my observations with those in the literature.

#144. Leaf blade vascular bundle sheaths <primary bundles: number>/

   • See #91 above.

#145. <Leaf blade> boundary layer cells <primary bundles: relative to bundle parenchyma cells, whether ‘large’ or ‘small’>/
   1. ‘large’ <Plates 17.8, 21.7>/
   2. ‘small’ <Plates 21.1, 21.2>/

   • See #92 above.

#146. <Leaf blade> boundary layer cells <primary bundles: whether chlorenchymatous>/
   1. chlorenchymatous <Plate 17.8>/
   2. ‘non-chlorenchymatous’ <never with abundant chloroplasts>/

   • See #93 above.

#147. <Leaf blade> boundary layer cells <primary bundles: whether complete or interrupted>/
   1. forming a complete sheath/
   2. interrupted by metaxylem <Plate 17.8>/

   • See #94 above.

#148. <Leaf blade> mestome sheaths <primary bundles: whether chlorenchymatous>/
   1. chlorenchymatous <Plate 18.7>/
   2. ‘non-chlorenchymatous’ <never with abundant chloroplasts> <Plates 17.8, 21.1–2, 21.7>/

   • See #95 above.

#149. <Leaf blade> parenchymatous bundle sheaths <primary bundles: whether present>/
   1. present <Plates 17.8, 20.1, 21.1>/
   2. absent <Plate 18.8>/

   • See #96 above.
#150. <Leaf blade> parenchymatous bundle sheaths <primary bundles: whether chlorenchymatous>/
1. chlorenchymatous/
2. ‘non-chlorenchymatous’ <never with abundant chloroplasts> <Plates 21.1–2, 21.7>/
   • See #97 above.

#151. <Leaf blade> parenchymatous bundle sheaths <primary bundles: whether complete, interrupted, only adjacent metaxylem vessels, or irregular>/
1. complete <Plates 17.3–4>/
2. interrupted by fibres <Plates 19.8, 21.1, 21.7>/
3. only adjacent metaxylem vessels <Plates 17.8, 21.5>/
4. ‘irregular’ <regardless of whether the bundles are fully embedded in chlorenchyma>/
   • See #98 above.

#152. <Leaf blade> parenchymatous bundle sheaths <whether with extensions>/
1. with extensions <Plates 17.2, 17.4, 20.4, 21.1–2>/
2. without extensions <Plate 17.3>/
   • The PBS extensions may be adaxial or abaxial. Score only extensions that are more or less contiguous with the epidermis.

#153. <Leaf blade> ‘distinctive-cells’ <whether present>/
1. present/
2. absent <implicit>/
   • ‘Distinctive cells’ are a rare feature in sedges, known only from two C<sub>4</sub> Rhynchospora species. They constitute clusters of ‘photosynthetic carbon reduction’ (PCR) cells unaccompanied by vascular tissue, which ‘maintain’ the ‘maximum cells-distant count’ at one (cf. Watson and Dallwitz 1988 Fig. 211: ‘circular cells’).

#154. <Leaf blade> sclerenchyma <form>/
1. forming strands <above and/or below the vascular bundles>/
2. forming <adaxial and/or abaxial> girders <Plates 21.1, 21.4–6>/
3. forming caps <above and/or below the vascular bundles> <Plate 21.1>/
   • See #100 above.

#155. <Leaf blade> sclerenchyma <i.e. caps and girders; whether in direct contact with all of the vascular bundles>/
1. not in direct contact with all of the vascular bundles <Plates 17.8, 18.8>/
2. in direct contact with all of the vascular bundles/
#156. <Leaf blade> sclerenchyma <girders or caps of the main veins: whether ‘encasing’ parenchyma/>
1. ‘encasing’ parenchyma <Plate 19.7>/
2. not encasing parenchyma <implicit>/
   • Baas (1969) records ‘translucent cells opposite the principal vascular bundles’ in Hypolytrum, Paramapania, Mapania, and Thoracostachyum floribundum, but not T. bancanum. My material exhibited them in Hypolytrum, Mapania, and Principina, but not Thoracostachyum.

#157. <Leaf blade> strands <whether all aligned with the vascular bundles>/
1. all aligned with the vascular bundles <excluding marginal groups>/
2. not all aligned with the vascular bundles <Plate 21.8>/

#158. <Leaf blade> sclerenchyma groups <i.e. the strands and girders> to vascular bundles, ratio/
1. less than 1:1 <Plate 20.2>/
2. 1:1/
3. greater than 1:1 <Plate 21.8>/

#159. <Leaf blade> spongy mesophyll <whether present>/
1. present <Plates 17.6, 21.7–8>/
2. absent/
   • See #105 above.

#160. <Leaf blade> palisade mesophyll <whether present>/
1. present <Plate 17.6>/
2. absent <Plates 21.7, 21.8>/
   • See #106 above.

#161. <Leaf blade> palisade mesophyll <whether abaxial or adaxial>/
1. abaxial/
2. adaxial/

#162. Leaf blade ‘maximum cells-distant count’ <after Hattersley and Watson 1975: excluding the parenchymatous bundle sheath>/
1. one <indicative of C₄> <Plate 17.8>/
2. more than one <indicative of C₃> <Plate 20.6>/
   • See #107 above.
PHOTOSYNTHETIC PATHWAY

#163. <Photosynthetic pathway: of the culms, leaves or inflorescence bracts, predicted anatomically or via $^{13}$C or $\Gamma$ values, or established biochemically>/

1. C$_3$/
2. C$_3$-C$_4$ intermediate/
3. C$_4$

#164. <C$_4$> anatomical type <of the culms and/or leaves, determined from the primary vascular bundles>/

1. fimbristyloid/
2. chlorocyperoid/
3. eleocharoid/
4. rhynchosporoid/

- The C$_4$ anatomical types are described in terms of primary vascular bundles, the latter being recognized by the possession of meta- and proto-xylem, often associated with a protoxylem lacuna. Fimbristyloid C$_4$ anatomy comprises three bundle sheaths: the inner border parenchyma cells are large and chlorenchymatous, constituting the PCR tissue, and interrupted laterally by the metaxylem vessel elements; the mestome sheath of small, a-chlorenchymatous, thick-walled cells; and a complete (unless interrupted by sclerenchyma) PBS, which is usually smaller and less chloroplast laden than the surrounding PCA tissue (a PBS also surrounds the secondary bundles). Chlorocyperoid C$_4$ anatomy is essentially similar, but here the PBS is restricted to one or a few cells lateral to the metaxylem vessel elements, or, in a few genera, is completely absent (and is always absent from the secondary bundles). The border parenchyma cells also constitute the PCR tissue in eleocharoid C$_4$ anatomy, but are usually not interrupted by the metaxylem vessel elements, and the PBS is absent. The mestome sheath constitutes the PCR site in rhynchosporoid C$_4$ species, and the PBS is present but irregularly incomplete.

#165. <C$_4$> biochemical type <as determined by enzyme assay: data from Ueno et al. 1986, and Bruhl et al. 1987. Species samples in parentheses>/

1. NAD-ME/
2. NADP-ME/

#166. $^{13}$C value range <literature sources in parentheses>/

- Data as yet not incorporated, but available in Appendix 2.

#167. $\Gamma$ value range <literature sources in parentheses>/

- Data as yet not incorporated, but available in Appendix 2.
INFLORESCENCE AND FLOWERS

#168. Plants <whether plants monoecious, with bisexual spikelets, or dioecious>/

1. <bisexual, but> monoecious, with all spikelets unisexual <Plates 22.4, 25.5, 28.7>/

2. bisexual, with <at least some> bisexual spikelets <Plates 22.2, 23.8>/

3. dioecious <with separate male and female individuals>/

#169. Plants <whether having hermaphrodite flowers, not to be confused with the presence or absence of hermaphrodite spikelets>/

1. with <at least some> hermaphrodite flowers <Plate 30.6>/

2. without hermaphrodite flowers/

#170. 'Basal spikelets' <whether present, i.e. whether the plants are amphicarpic>/

1. present <Plates 22.1, 22.3>/

2. absent <implicit>/

- 'Basal spikelets', when present, constitute a second class of spikelets proximal to the distant terminal or aerial spikelets. Where the inflorescence constitutes spikelets clustered only close to the ground, as in *Volkiella*, basal spikelets are absent. Plants with basal spikelets are generally amphicarpic. Cheplick’s (1987) review overlooks the Cyperaceae, despite the existence of various published accounts of amphicarpy in the family, cf. Chermezon 1929; Svenson 1939; Haines 1971; Raynal 1976; Haines and Lye 1977). *Crosslandia* may not be amphicarpic, as my preliminary observations indicate no class-size differences between the fruits of the aerial and basal spikelets. However, Goetghebeur's (1986 p. 416 Fig. 8.6.4E-G) line drawing (without scale) of an embryo from a basal spikelet is larger than those from aerial spikelets.

#171. ‘Basal spikelets’ <position relative to ground level>/

1. borne above ground/

2. subterranean <Plates 22.1, 22.3>/

- Most basal spikelets are borne at about ground level, solitary in the axils of basal sheaths (Haines 1971; Raynal 1976). The sheath may form an erect, elongated tube enclosing a very long style (e.g., *Trianoptiles*). In some of the C₄ species of *Eleocharis*, the basal spikelets form on an elongated culm as do the aerial spikelets, but they are positively geotropic, buried completely underground, and are not associated with notable development of the style or leaf sheaths.
#172. ‘Basal spikelets’ <sex>/
1. female <Plate 22.1>/
2. bisexual/
   • In *Eleocharis* the basal spikelets possess anthers as well as a gynoecium. Although it is not certain whether these males are functional, I have described them as bisexual. Indeed, whether basal spikelets are sexual or apomictic is unknown.

#173. Inflorescence <whether always restricted to a solitary spikelet>/
1. <always restricted to> a solitary spikelet <Plates 1.3, 1.7, 22.2, 24.4>/
2. <at least sometimes> comprising more than a solitary spikelet <implicit> <Plate 1.8>/
   • Occasional reduction to a solitary spikelet in forms normally characterized by more complex inflorescences perhaps relates to resource availability rather than genotype, and I have felt obliged to ignore such supposed ‘depauperate’ material in relation to characters #175-176, 178, 180-191, 194-197, and 206.

#174. Inflorescence <whether proliferous>/
1. proliferous <Plate 23.3>/
2. not proliferous <implicit>/

#175. Inflorescence <primary axis: whether elongated>/
1. elongated <Plates 1.8, 22.6>/
2. contracted <the primary rachides not visible> <Plates 22.4–5, 23.1, 23.4>/
   • The primary rachides constitute the nodes and internodes above the lowest primary inflorescence bract. The culm below is ignored.

#176. Inflorescence <whether terminal or pseudoaxillary>/
1. terminal <Plates 22.4, 23.1, 23.5>/
2. pseudoaxillary <with the subtending bract apparently continuing the axis> <Plates 22.5, 23.6>/
   • Although this character can usually be scored unambiguously, intermediate states sometimes occur, and have been scored as ‘variable’.

#177. Inflorescence <borne on the main axis: overall form – terms modified after Müller-Doblies 1987>/
1. ‘conipaniculate’ <i.e. paniculate> <Plates 1.2, 1.8, 22.7>/
2. ‘planipaniculate’ <i.e. corymbose>/
3. anthelate <Plates 1.9, 23.4, 24.7>/
4. capitulate <Plates 1.1, 2.2, 22.4–5, 23.1>/
Planipaniculate (corymbose) inflorescences are dome-shaped, with the youngest (distal) branches constituting the central peak. Anthelate inflorescences are funnel-shaped with the youngest (distal) branches close to the base of the inflorescence. Literature descriptions do not usually make this distinction (see, e.g. Kern 1974).

#178. Inflorescence <overall disposition of the sexes>/
1. gynandrous <i.e. with the female-only spikelets distal>/
2. androgynous <i.e. with the male-only spikelets distal> <Plate 22.4>/
3. with the sexes mixed <implicit> <Plate 23.1>/

#179. Inflorescence <type: from Goetghebeur 1986>/
1. Hypolytrum-type/
2. Scirpus-type/
3. Eleocharis-type <Plates 1.3, 1.7>/
4. Schoenoplectus-type/
5. Isolepis-type/
6. Ficinia-type/
7. Fimbristylis-type/
8. Abildgaardia-type/
9. Cyperus-type <Plates 23.1–4>/
10. Ascolepis-type/
11. Lipocarpha-type/
12. Dulichium-type <Plate 1.2>/
13. Arthrostyletis-type/
14. Rhynchospora-type/
15. Lagenocarpus-type <Plates 1.7, 25.5>/
16. Trilepis-type <Plates 1.3>/
17. Scleria-type <Plates 28.7>/
18. Diplacrum-type/
19. Carex-type <Plates 22.5>/

#180. <Inflorescence> branching pattern <of the main axis: data mostly from Goetghebeur 1986>/
1. ‘normal’ <Plate 23.2>/
2. ‘prophyllar’/

Meert and Goetghebeur (1979) set out three branching patterns for the Cyperaceae, founded on the ideas of Haines (1966) and Haines and Lye (1972). These are applicable to both the main axis and the lateral branches
Where the inflorescence bracts subtend a single lateral branch the branching pattern is ‘normal’. The ‘prophyllar’ branching pattern involves the repeated production of lateral branches in the axil of prophylls. This gives rise to the characteristic fascicled appearance of the branches as seen in *Lagenocarpus*. Anisophyllly or ‘tandem’ branching is a variant of ‘prophyllar’ branching, where successive branches originate in the axil of the opposing keel of successive prophylls, thus appearing zig-zagged or cymoid.

**#181. Lateral inflorescence branching pattern**<data mostly from Goetghebeur 1986>/
1. ‘normal’/
2. ‘prophyllar’ <Plate 1.8>/
3. anisophyllous <equivalent to Goetghebeur’s 1986 ‘tandem branching pattern’>/

- See #180 above.

**#182. Lateral inflorescence branches**<whether contracted>/
1. elongated <Plates 1.8, 22.6, 23.2, 23.4>/
2. contracted <the secondary rachides not visible>/

**#183. Lateral inflorescence branches**<disposition of the sexes>/
1. gynandrous <i.e. with the female-only spikelets distal>/
2. androgynous <i.e. with the male-only spikelets distal>/
3. with the sexes mixed <implicit>/

**#184. Lateral branch inflorescences**<form – terms modified after Müller-Doblies 1987>/
1. ‘conipaniculate’ <i.e. paniculate> <Plate 1.8>/
2. ‘planipaniculate’ <i.e. corymbose> <Plate 22.7>/
3. anthelate <Plates 2.1>/
4. capitate <Plates 1.9, 23.4>/

- See #177 above.

**#185. Lateral inflorescence branch bases**<whether enclosed or exposed>/
1. enclosed <by sheathing bases of bracts> <Plates 22.6, 24.3>/
2. exposed <not enclosed by sheathing bases of bracts> <Plate 23.2>/

- Minute sheaths which do not enclose the lateral branch bases (e.g. in *Cyperus*) are ignored.

**#186. Primary inflorescence bracts**<whether foliose or scale-like>/
1. foliose <Plates 1.2, 22.5, 22.7, 23.1, 23.6>/
2. scale-like <Plate 22.4>/
• Many floras refer to primary inflorescence bracts as being "culm-like" or "leaf-like". This is often unsatisfactory, because in Cyperaceae the terms are not mutually exclusive. Here, ‘foliose’ means possessing a ‘lamina’, and ‘scale-like’ is essentially ‘elaminate’.

#187. Primary inflorescence bracts <whether graded in length or with one bract much longer>/
1. graded in length <Plate 23.1>/
2. with one much longer <Plate 22.5>/

• When two distinct sizes class can be determined (the first with one large bract and the second with much shorter bracts which are all similar in length), the primary inflorescence bracts are scored ‘with one much longer’. When there is no obvious discontinuity in sizes (all similar in length, or becoming progressively smaller distally) they are ‘graded in length’.

#188. Primary inflorescence bracts <whether spathe-like>/
1. spathe-like <Reedia>/
2. not spathe-like <implicit>/

#189. Primary inflorescence bracts <‘phyllotaxis’>/
1. spirally disposed/
2. distichous <or spirodistichous>/
3. tristichous <or spirotristichous> <Plates 1.9, 23.1>/

• The comments under #26 are relevant here.

#190. Primary inflorescence bracts <whether deciduous>/
1. deciduous <e.g. Oreobolus> <Plate 22.9>/
2. persistent <implicit>/

#191. Primary inflorescence bracts <whether armed with prickle-hairs>/
1. armed with prickle-hairs/
2. without prickle-hairs/

#192. Rachis <whether rod-shaped>/
1. rod-shaped <Reedia>/
2. not rod-shaped <implicit>/

#193. Rachis <whether ‘widened’ via clustering of the rachilla bases>/
1. ‘widened’ <via clustering of the rachilla bases, e.g. Alinula>/
2. not widened <via clustering of the rachilla bases – implicit> <Plate 25.2>/

#194. Inflorescence prophylls <whether present throughout the inflorescence>/
1. present <Plates 22.6, 23.2>/
2. absent/
• Where the lateral inflorescence bracts are enclosed by sheaths, these may have to be dissected to examine the inflorescence prophyll characters.

#195. Inflorescence prophylls <whether possessing an adaxial pulvinus>/
   1. adaxially pulvinate <Plate 23.2>/
   2. epulvinate <Plate 22.6>/

#196. Inflorescence prophylls <whether tubular>/
   1. tubular <Plates 22.6, 23.2>/
   2. bract-like/

#197. Subtending bracts <within the inflorescence: whether imbricate>/
   1. non-overlapping/
   2. imbricate <Plate 22.5>/

#198. ‘Synanthia’ <whether present>/
   1. present <Plates 22.5, 22.8>/
   2. absent/

• This character is included to cope with mapanioid taxa, with superficially flower-like spikelets (contrast Goetghebeur 1986: "anthoids"). These spikelets are composed of a terminal female and proximal anthers, either or both subtended by floral bracts, together with male-fertile or sterile prophylls. The prophyll usually comprises two lateral, keeled portions.

#199. Terminal spikelets <whether present: after Goetghebeur 1986>/
   1. present/
   2. absent/

• When spikelet prophylls are present, terminal spikelets are usually readily identified as those spikelets distant from their prophylls due to the interposition of lateral spikelets.

FEMALE-FERTILE SPIKELETS

#200. Female-fertile spikelets <disposition of the sexes, see Eiten 1976a>/
   1. gynandrous <i.e. with the female flowers distal>/
   2. androgynous <i.e. with the male flowers distal> <Plate 26.4>/
   3. mesogynous <i.e. with female flowers proximal and distal to the male flowers>/
   4. with only hermaphrodite flowers <implicit>/

• Although none of these states is redundant, the last may perhaps be better treated as the basis for a separate character.
#201. Female-fertile spikelets <shape>/
1. shortly ovate/
2. elliptical/
3. lanceolate/
4. linear/
5. obovate/
   • Examine at or before anthesis to avoid changes in shape due to the development of the fruit. The shapes are based on Stern (1966 p. 318-319 Fig. 19 and p. 325 Fig. 21). The shape of the spikelet is affected by the number and size of the floral bracts, and by the stage of development of the rachilla, and thus restricts its usefulness.

#202. Female-fertile spikelets <whether laterally, dorsiventrally or not compressed>/
1. laterally compressed <Plates 24.2, 25.4>/
2. dorsiventrally compressed/
3. <more or less> terete <Plate 25.5>/

#203. Spikelet prophylls <of the female-fertile spikelets: whether present at base of spikelet>/
1. present <Plates 25.1, 25.2>/
2. absent/
   • Where both terminal and lateral female-fertile spikelets are present, the lateral spikelets are scored. When only terminal female-fertile spikelets are present, their prophylls (if present) are distant from the flowers and floral bracts, due to the interposition of lateral spikelets, and I have scored the spikelet prophyll ‘absent’.

#204. Spikelet prophylls <number per spikelet, when tubular scored as one>/
   • The number of spikelet prophylls directly reflects their position, so this character is the numerical equivalent of the following one.

#205. Spikelet prophylls <whether lateral or dorsiventral to the flowers, with respect to the floral axis>/
1. lateral <Plates 22.8–9>/
2. dorsiventral <Plates 24.2, 25.1–2, 31.1>/
   • When a single prophyll is present it is dorsiventrally placed with respect to the rachilla axis (some deviation from this being seen in Trilepis and its ‘relatives’). When two prophylls are present they are invariably laterally placed. This implies phylogenetic derivation of one state from the other: the result of two prophylls ‘fusing’, or ‘splitting’ of one into two. Haines (1966)
argued that the divided prophyll in the mapanioids represents a derived specialization, and its parallel occurrence in *Schoenoides* (nested amongst taxa with single dorsiventral prophylls), supports this contention.

#206. Spikelet prophylls <length: relative to the subtending bracts>/
1. longer than the subtending bracts <Plates 24.2, 25.2>/
2. <more or less> equalling the subtending bracts in length/
3. shorter than the subtending bracts <Plate 26.3>/
   - As the relative length of the spikelet prophylls to subtending bracts may vary throughout the inflorescence, this character is best assessed from lateral spikelets in the mid-third of the inflorescence

#207. Spikelet prophylls <whether subtending male flowers, bisexual flowers, female flowers or sterile>/
1. subtending male flowers <Plate 22.8>/
2. subtending bisexual flowers <Plate 25.2>/
3. subtending female flowers <Plates 26.1–2>/
4. sterile <Plates 24.2, 25.7>/

#208. Spikelet prophylls <whether bract-like or tubular>/
1. bract-like <the margins free to the base> <Plates 25.1, 25.7>/
2. tubular <at least proximally> <Plates 26.1–3>/
   - Spikelet prophylls require careful examination when young, to avoid overlooking barely tubular prophylls which may split with age and then appear bract-like.

#209. Spikelet prophylls <whether constituting perigynia>/
1. constituting perigynia <i.e. tubular and flask-shaped> <Plates 22.4, 26.1–3>/
2. not constituting perigynia <implicit>/
   - To avoid repeating attribute #207,3 I have taken a narrower definition of a perigynium than most authors. I do not consider bract-like female-fertile prophylls to constitute perigynia.

#210. Perigynia <whether containing a female flower, or a female flower and a male axis>/
1. containing only a female flower <Plates 26.1–3>/
2. containing a female flower and a male axis/
   - Here a 'male axis' is a rachilla with male-fertile floral bracts, as seen in *Kobresia* and *Schoenoxiphium*. 
#211. Perigynia <colour: whether milky-white/>
   1. milky-white <Cymophyllus>/
   2. not milky-white <implicit>/

#212. Spikelet prophylls <whether possessing an adaxial pulvinus>/
   1. adaxially pulvinate <Plate 31.1>/
   2. epulvinate <Plates 25.1–2, 25.7>/

#213. Spikelet prophylls <texture>/
   1. ‘hyaline’ <i.e. transparent> <Plate 25.7>/
   2. ‘membranous’ <i.e. translucent> <Plate 25.1>/
   3. ‘chartaceous’ <i.e. opaque>/

#214. The <spikelet prophyll> keels <whether indumented>/
   1. indumented <Plate 22.8>/
   2. glabrous/

#215. Margins <of the spikelet prophylls: whether indumented>/
   1. indumented/
   2. glabrous/

#216. Rachillae <female-fertile spikelets: whether vestigial, elongated or contracted>/
   1. vestigial <Plates 22.8, 26.2>/
   2. contracted <Plates 24.6, 24.8>/
   3. elongated <Plates 24.1, 25.1, 25.4, 26.9>/
   • The rachilla is ‘vestigial’ when it is not readily visible in the normal course of dissection under the stereomicroscope, or when it does not form a distinct portion between floral bracts or above the spikelet prophyll. ‘Contracted rachillae’ have visible internodes which are shorter than the nodes are wide. When the internodes are longer than the nodes are wide, the rachillae are ‘elongated’. The spikelet ‘peduncle’ is not included as part of the rachilla.

#217. Rachillae <female-fertile spikelets: whether of definite or indefinite growth>/
   1. of indefinite growth <Plates 24.4, 25.1>/
   2. of definite growth <Plates 24.5–6, 25.8>/
   • Some taxa have female-fertile spikelets which always seem to bear about the same number of fruits, on rachillae of about the same length, no matter what the resource availability. Such spikelets have rachillae of ‘definite growth’. Conversely, those taxa in which the rachillae continue to grow and bear more flowers (but not necessarily set more fruit) in response to favourable environmental conditions possess rachillae ‘of indefinite growth’. 
#218. Rachillae <female-fertile spikelets: whether falling or persistent>/
   1. deciduous <at maturity> <Plates 24.2, 26.5>/
   2. persistent <Plates 24.1, 24.6, 24.8, 25.1, 26.9>/

#219. Rachillae <female-fertile spikelets: whether disarticulating above the prophyll>/
   1. disarticulating above the prophyll <Plate 24.2>/
   2. disarticulating below prophyll <Plates 26.2, 26.3>/

#220. Rachillae <female-fertile spikelets: whether ‘shattering’>/
   1. ‘shattering’ <i.e. with points of abscission at the base of each fruit, breaking when mature into several pieces> <Plates 26.6>/
   2. not shattering <implicit>/

#221. Rachillae <female-fertile spikelets: prolongation>/
   1. <greatly> exceeding the flowers <Uncinia> <Plate 26.1>/
   2. not <greatly> exceeding the flowers <implicit>/

• This is a unique character identifying Uncinia, and should not be confused with the elongated rachillae of Kobresia and Schoenoxiphium, which distally bear fertile floral bracts.

#222. Rachillae <female-fertile spikelets: whether distally hooked or straight>/
   1. distally hooked <Uncinia> <Plate 26.1>/
   2. distally straight <implicit>/

• A unique feature of Uncinia.

#223. Rachillae <female-fertile spikelets: whether enlarged and spongy below the floral bracts>/
   1. ‘bulbous’ <spongy> below the floral bracts <Diplacrum – pro parte>/
   2. not bulbous <implicit>/

#224. Rachillae <female-fertile spikelets: whether enlarged and woody with age>/
   1. becoming enlarged and woody with age <Tylocarya> <Plate 24.7>/
   2. not becoming enlarged and woody with age <implicit>/

#225. Rachillae <female-fertile spikelets: whether developing deep pits in which the fruit are seated>/
   1. deeply pitted <Tylocarya> <Plate 24.7>/
   2. not deeply pitted <implicit>/

#226. Rachillae <female-fertile spikelets: whether with ‘wings’ – not to be confused with incompletely deciduous floral bracts>/
   1. with ‘wings’ adjacent to the flowers <Plates 25.1, 25.4>/
   2. ‘wingless’ <Plate 24.1>/
• The rachilla wings constitute flanges along the rachilla independent of the bases of the floral bracts (see also #236 below).

#227. The <rachillae> wings <whether deciduous>/
  1. deciduous <Plate 25.1>/
  2. persistent/

#228. <Rachilla> internodes <fertile and sterile, whether of equal length>/
  1. <more or less> equal in length <whether fertile or sterile> <Plates 24.6, 24.8>/
  2. of <markedly> different lengths <the fertile ones elongated> <Plate 26.9>/

#229. The fertile <rachilla> internodes <whether straight, zigzag or flexuose>/
  1. <more or less> 'straight' <Plates 24.1, 24.6, 24.8, 25.1 25.4>/
  2. zigzag <i.e. sharply angled>/
  3. flexuose <i.e. curved> <Plate 26.9>/

#230. The fertile <rachilla> internodes <whether thick and corky or undifferentiated at maturity>/
  1. thick and corky at maturity <Plate 26.5–6>/
  2. neither thick nor corky at maturity <implicit>/

#231. Floral bracts <female-fertile spikelets: whether present>/
  1. present/
  2. absent <Plate 26.2>/

• Floral bracts are fertile (subtending a flower) or sterile bracts (or glumes or scales) of the ultimate inflorescence axis (see Eiten 1976a), exclusive of any spikelet prophylls. By contrast, Tucker (1987 p. 409) described the rachilla of *Kylinga* with "the two lowest sterile scales of its spikelets being greatly reduced". These two sterile bracts are the subtending bract (which belongs to the next lower order axis and not the spikelet), and the sterile spikelet prophyll.

#232. Proximal sterile bracts <female-fertile spikelets: number>/
  • Only sterile ‘floral bracts’ proximal to the ‘fertile floral bracts’ are scored, and not ‘subtending bracts’ or spikelet prophylls.

#233. Fertile floral bracts <female-fertile spikelets: number>/
  • The fertile floral bracts are described irrespective of the sex of the flowers, but only in female-fertile spikelets.
#234. Floral bracts <female-fertile spikelets: whether pouch-like, sac-like, or open>/
1. pouch-like <Ascolepis> <Plate 26.8>/
2. sac-like <Bisboeckelera, Calyptrocarya> <Plates 23.8 26.7>/
3. open <implicit> <Plates 25.1, 25.4>/

- The sac-like floral bracts of Bisboeckelera are reminiscent of the perigynia of Carex, but are readily distinguished by their position. The sac-like floral bracts of Bisboeckelera terminate an inflorescence unit which has lateral male or sterile spikelets. Below this is a small, sterile, bract-like prophyll (homologous with the perigynium). The same arrangement occurs in Calyptrocarya, but here the floral bract may be mistaken for the fruit surface. Careful examination of the female will reveal the style protruding through a small orifice in the top of the sac-like bract, which is free from the fruit wall.

#235. Floral bracts <female-fertile spikelets: whether persistent or deciduous>/
1. persistent/
2. deciduous <Plates 24.1, 24.7, 25.1>/

- When the rachilla is deciduous but the floral bracts remain attached to it, the floral bracts are ‘persistent’.

#236. Floral bracts <female-fertile spikelets: whether completely deciduous>/
1. completely deciduous <implicit> <Plate 24.1>/
2. incompletely deciduous <the rachilla retaining the base of the floral bracts> <Plates 25.4, 25.6>/

- Incompletely deciduous floral bracts leave a flange of tissue, often triangular, on the rachilla. As some taxa have these flanges of tissue as well as rachilla wings (#226), these features are treated separately. However, in at least some cases (e.g. Fimbristylis) they may be different components of the same structure and so the two characters should be considered somewhat dubious.

#237. Floral bracts <of each female-fertile spikelet: whether deciduous individually or collectively>/
1. deciduous individually <implicit>/
2. deciduous collectively <Plate 25.3>/

- Actinoschoenus, Arthrostylis, Trichoschoenus, and Trachystylis have floral bracts which are deciduous collectively. However, I have found the last to be variable (Plate 24.8). It is necessary to examine the bases of the deciduous floral bracts to confirm that the rachilla is absent, to avoid overlooking deciduous rachillae (which fall with their floral bracts attached).
#238. Floral bracts <female-fertile spikelets: whether deciduous alone or with the fruits>/
1. falling with the enclasped fruit <Plates 26.8, 28.6>/
2. falling alone <not enclasping the fruit; implicit>/
   • State 1 is implicit in cases where the fruit is enclosed by the floral bract, but also occurs in some genera where the floral bracts are open. However, the character is usually variable (and perhaps more widespread than indicated) in species with open floral bracts, and may prove to be relatively unreliable.

#239. Floral bracts <female-fertile spikelets: disposition>/
1. spirally disposed/
2. distichous <comment if spirodistichous> <Plates 22.2, 24.1–2, 24.5–6, 25.1>/
3. tristichous <comment if spirotristichous> <Plates 23.6 25.5>/
   • I distinguish between tristichous floral bracts and ‘spiralled’ floral bracts, by contrast with Goetghhebeur (1986), who treated even obviously tristichous arrangements as spiralled. ‘Spiralled’ may be a ‘left-overs’ category, including obscurely spirotristichous (etc.) forms, but some attempt is needed to account for the obvious differences.

#240. Floral bracts <female-fertile spikelets: colour at maturity>/
1. pallid-brown <includes yellow-brown>/
2. green/
3. red-brown/
4. blackish <to purple> <Plates 23.6, 24.1>/

#241. Floral bracts <female-fertile spikelets: length, proximally to distally along the spikelet>/
1. decreasing in <absolute> length acropetally <Plate 31.5>/
2. similar in <absolute> length along the spikelet <Plates 24.1–2, 25.1>/
3. increasing in <absolute> length acropetally <Plates 24.6, 24.8, 28.8>/
   • Applied only to mature floral bracts. Subtle differences in length are almost always apparent within spikelets, but only gross differences are catered for here (e.g. state 1: Baeothryon; state 2: Cyperus; and state 3: Costularia).

#242. Floral bracts <female-fertile: shape of the apex>/
1. ‘rounded at the apex’ <includes emarginate>/
2. acute <Plates 24.6, 24.8>/
3. mucronate <Plate 28.8>/
4. ‘aristate’ <includes acuminate> <Plate 25.5>/
• The terms used are Stern’s (1966 p. 328 Fig. 23). No distinction has been made between the presence or absence of an awn, though this may be worthwhile in the future.

#243. Floral bracts <female-fertile spikelets: whether markedly recurved at their tips>/
1. markedly recurved at their tips <Plates 24.2, 25.5>/
2. with straight tips <implicit>/

• Goetghebeur (1986) linked Evandra with Caustis, partly on the grounds that both have floral bracts markedly recurved at their tips. However, the former is variable for this character, as are most of the genera with this feature (e.g. Mesomelaena).

#244. Floral bracts <female-fertile spikelets: texture>/
1. ‘hyaline’ <i.e. transparent>/
2. ‘membranous’ <i.e. translucent> <Plates 24.8, 25.4>/
3. ‘chartaceous’ <i.e. opaque> <Plates 23.6, 24.6>/

#245. Floral bracts <female-fertile spikelets: whether indumented>/
1. indumented/
2. glabrous <Plate 26.8>/

#246. <Floral-bract> indumentum <position>/
1. marginal/
2. on the keel/
3. dorsal <exclusive of the keel>/
4. ventral <Plate 23.6>/

#247. Floral-bracts <indumentum: form>/
1. ‘scabrous’ <Plates 23.8, 26.7>/
2. ‘puberulous’/
3. ‘pilose’/

• See #45 above.

#248. The lowest floral bract of the <female-fertile> spikelets <whether with a distinct tubular sheath>/
1. with a distinct tubular sheath <e.g. Egleria> <Plate 24.4>/
2. ‘open’ <implicit>/

#249. Each flower <female-fertile spikelets: whether enclosed directly by its subtending floral bract or by a distal floral bract>/
1. enclosed <directly> by its subtending floral bract <Plate 25.1>/
2. enclosed <directly> by a distal floral bract <Plate 26.9>/
• Haines (1966) pointed out that the flowers in *Rhynchospora*, *Schoenus* and their relatives are enwrapped by a distal floral bract. This feature, particularly when combined with flexuose rachillae, led many earlier authors to describe racemose spikelets as cymose.

#250. Terminal flower <female-fertile spikelets: whether present; after Goetghebeur 1986>/
1. present <Plate 23.8>/
2. absent/

• Flowers in the Cyperaceae are generally axillary, but in a few (namely the Hypolytreae and the Bisboeckelereae) there is no evidence that the most distal flowers are axillary (Raynal 1971; Eiten 1976a; Goetghebeur 1986). I have therefore interpreted these two groups of genera as possessing terminal flowers. This character should be used cautiously in identification, since some genera, e.g. *Carex* and *Lipocarpha*, have axillary flowers which superficially appear 'terminal'.

#251. Hermaphrodite flowers <female-fertile spikelets: number>/
per spikelet/
• Hermaphrodite flowers have seemingly functional-fertile male and female parts.

#252. Female-only flowers <female-fertile spikelets: number>/
per spikelet/
• Female-only and functionally female-fertile flowers (with aborted males) are scored as 'female-fertile flowers', e.g. *Carex* and *Lepidosperma* respectively.

MALE-ONLY SPIKELETS

#253. Floral bracts of male spikelets <whether distichous or spiralled>/
1. distichous/
2. tristichous <or spirotristichous>/
• 'Spiralled' includes spirotristichous.

#254. Functionally male-only flowers <male-fertile spikelets: number>/
per spikelet/
• Male-only and functionally male-fertile flowers (with aborted females) are scored as 'male-only flowers', e.g. in some Cariceae and *Abildgaardia* respectively.
PERIANTH

#255. Perianth <whether present>/
   1. present <Plates 27.1–7>/
   2. absent/
   • When present, the ‘perianth’ is located outside the stamens. By contrast, a ‘hypogynium’ occurs only between the stamens and the ovary. Goetghebeur (1986) interprets the floral bracts within the highly reduced spikelets of the mapanioids as "glumellae" equivalent to perianth segments. I interpret the cupular structure at the base of the fruit in Scleria and others as a perianth. A number of authors interpret this structure as a hypogynium, not homologous with the typical perianth (e.g. Franklin Hennessy 1965; Goetghebeur 1986; Tucker 1987), citing Blaser (1940, 1941) for support. For example, Tucker (1987 p. 421) stated that "the hypogynium is apparently derived from receptacular tissue, as is shown by its vascularization (Blaser 1940, 1941b)". In fact, Blaser (1941b p. 833) is equivocal: "the ‘hypogynium’ represents either receptacle or floral appendages and is not an expansion of the ovary wall." Given the lack of clear evidence for the origin of the cupular perianth in Scleria et al., I have opted to assess the situation by reinterpreting the structure for successive cladistic analyses (see Chapter 9).

#256. Perianth <segments or lobes: number>/

#257. Perianth <whether of ‘scales’, ‘bristles’, or ‘cupular’>/
   1. of ‘scales’ <Plates 27.1–2, 27.4, 27.7>/
   2. of ‘bristles’ <Plates 27.3, 28.3–4, 28.6>/
   3. ‘cupular’ <Plate 24.5>/
   • ‘Scales’ are generally much wider than thick. ‘Bristles’ are rounded in transection or linear in lateral view. ‘Cupular perianths’ are usually discoid, cartilaginous and occur only in unisexual flowers. These definitions are not absolute, and further work is required to establish more distinct character-state boundaries. To avoid mismatches due to developmental change of the perianth, this character should be applied to fruit rather than flowers.

#258. Perianth <texture: based on dried material>/
   1. cartilaginous <Plate 27.6>/
   2. brittle/
   3. scarious/
   4. spongy/
#259. Perianth members <whether persistent on the rachilla>/
   1. persistent on the rachilla <e.g. Oreobolus> <Plate 27.1>/
   2. deciduous <from the rachilla> with the fruit <implicit> <Plates 27.3–7>/

#260. Perianth members <after the fruit fall: whether persistent>/
   1. persistent at the base of the fruit <implicit> <Plate 28.6>/
   2. separating from the fruit/

#261. Perianth members <relative length in situ>/
   1. vestigial/
   2. shorter than the fruit <in situ> <Plates 27.1, 27.4>/
   3. equal to the fruit <in situ>/
   4. much exceeding the fruit <Plates 27.3, 28.6>/

#262. Perianth members <whether elongating at maturity>/
   1. elongating with maturing of the fruit <e.g. Eriophorum>/
   2. not elongating <markedly> with maturing of the fruit <implicit>/

#263. Perianth members <overall shape: whether tridentate>/
   1. tridentate <Trianoptiles> <Plates 27.7>/
   2. not tridentate <implicit>/

#264. Perianth members <whether like a fox-tail>/
   1. fox-tail like <Pleurostachys>/
   2. not fox-tail like <implicit>/

#265. Perianth members <whether indumented>/
   1. indumented <Plates 27.2, 27.4–5, 27.7>/
   2. glabrous <Plate 27.6>/

#266. Perianth members <indumentum: form>/
   1. barbate <Plates 27.3, 28.4>/
   2. plumose <Plate 27.5>/

• The perianth in the Trilepideae is described here as plumose. However, in at least some Coleochloa species the ‘indumentum’ bears some poorly developed barbs. Developmental or SEM studies are needed to confirm their status.

#267. <Perianth> indumentum <whether retrorse or antrorse>/
   1. retrorse <Plate 30.4>/
   2. antrorse <Plates 27.5, 27.7, 28.3>/

ANDROECIUM; POLLEN

#268. Stamens <hermaphrodite or male-only flowers: number>/
#269. Stamens <whether adhering to both the floral bracts and fruit by entanglement of the staminal filaments>/

1. adhering to the floral bracts <and the fruit at fruiting stage by entanglement of the staminal filaments> <Plate 29.7>/
2. free from the floral bracts <implicit>/

- Mature fruits in *Gahnia pro parte* and *Morelotia* are suspended in the air by their filaments, which become entangled in the floral bracts. The fruit thus is presented for bird dispersal. Benl (1937, 1940) showed variations in the mode of attachment, which indicate parallel development of this character.

#270. 'Staminal' meristems <whether present>/

1. present in the female-only flowers <Uncinia and Cymophyllus>/
2. absent <implicit>/

- I follow Goetghebeur (1986 pp. 1088 and 1060) in scoring the occurrence of "knobbsels" or 'staminal' meristems about the female, in *Cymophyllus* and *Uncinia*.

#271. Anthers <colour>/

1. yellow-green/
2. not yellow-green <includes white and yellow – implicit>/

- Yellow-green anthers are a feature shared by *Carpha* and *Trianoptiles*. Generally other genera possess yellow to almost white anthers, though they dry to grey in *Lepironia* and brick-red from greenish-yellow in *Caustis dioica*.

#272. Anthers length:breadth ratio/

- Anther lengths expressed here include any apiculus and/or basal appendages, and refer to mature but indehisced anthers.

#273. Anthers <whether sterile proximally>/

1. sterile proximally <Plates 28.1, 29.6>/
2. fully fertile <implicit> <Plates 29.3, 29.5>/

- For this purpose, the anther sac is defined with reference to the extent of the endothecial thickening. The endothecium is readily discernible when anthers are viewed between cross polarizers or phase contrast. The anthers are usually delimited from the filaments by an abscission zone. Proximally sterile anthers were also observed by Kern (1974) in some *Rhynchospora* species. *Syntrinema* clearly possesses proximally sterile anthers, corroborating its link with *Rhynchospora*. 
#274. Anthers <whether with ‘basal appendages’>/
1. with ‘basal appendages’ <Plates 29.3, 29.5, 29.8>/
2. basally unappendaged/
   • ‘Basal appendages’ are present if the epidermal cells at the base of loculae
   are more than one cell distant from the endothecial thickening.

#275. <Anther> ‘basal appendages’ <whether forming spongy lobes>/
1. forming prominent spongy lobes <e.g. Egleria> <Plates 29.3, 29.8>/
2. not comprising spongy lobes <implicit> <Plate 29.5>/
   • Eiten (1968) described the anther bases of Egleria as forming prominent
   spongy lobes. Such lobes appear to the unaided eye as distinct white bases to
   the anthers, and also occur (though less well developed) in Tylocarya.

#276. Anthers <whether ‘apiculate’ from the connective>/
1. ‘apiculate’ <Plates 29.1–3>/
2. not apiculate/
   • Anthers are ‘apiculate’ if the connective extends for more than one cell
   beyond the apex of the anther sac.

#277. <Anther> apiculus <length, as a percentage of the total anther length including
   the apiculus>/
percent of anther length/
   • Basal appendages and apiculi are included in anther length. This character
   may be a more objective way of addressing variation in apiculus as opposed to
   the subsequent character.

#278. <Anther> apiculus <form>/
1. ‘obtuse’ <Plates 29.1, 29.3>/
2. ‘acute’/
3. ‘acuminate’ <Plates 29.2>/
   • Truncate anther apiculi have generally been scored as ‘obtuse’. However,
   even if the apex is rounded, where the apiculus is more than twice as tall as it
   is wide, it is scored as ‘acuminate’. ‘Acute’ is applied to apiculi with pointed
   apices which are less than twice as tall as wide.

#279. <Anther> apiculus <dorsoventral view: whether as wide as thecae>/
1. as wide as the thecae <Plates 29.1–2>/
2. narrower than the thecae <as wide as the connective> <Plate 29.3>/
   • Many published illustrations of anthers depict apiculi inaccurately.
#280. <Anther> apiculus <whether indumented>/
1. indumented <Plates 29.2, 29.4>/
2. glabrous <Plate 29.1>/
#281. <Anther> apiculus <indumentum: form>/
1. papillose/
2. scabrous <Plates 29.2>/
#282. Filaments <whether connate>/
1. connate/
2. free <implicit>/
   • Eiten (1976b) described Syntrinema as possessing male flowers with filaments connate to the apex, but in some C₄ Rhynchospora species the apparently connate filaments, are an artifact of drying. Connate filaments are known in some Carex species (and the Juncaceae) where they are distally free.
#283. Filaments <whether markedly elongating after anthesis>/
1. markedly elongating <after anthesis> <Plate 31.7>/
2. desiccating <after anthesis; implicit>/
   • Extremely prominent filaments are an obvious feature of some cyperaceous inflorescences, which are described in the literature (e.g. Kern 1974 p. 501) as having "filaments strongly elongated after anthesis".
#284. Endothecial thickening <whether spiralled or forming a girdle>/
1. spiralled <Plate 29.9>/
2. girdling/
   • Dahlgren and Clifford (1982 p. 140; see also Kuhn 1908; Untawale and Bhasin, 1973) list Carex, Cladium, Cyperus, Kyllinga, Eleocharis, and Eriophorum as exhibiting 'girdling' endothecial thickening, while Cyperus, Eleocharis, Rhynchospora, and Scleria are listed under 'spiralled' thickening. I have examined representatives from thirty genera, including Cyperus, Eleocharis, and Schoenoplectus, using phase contrast and cross-polarizers, and in all cases observed the endothecial thickening to be spiralled. Care is needed, as spiralled endothecium can superficially appear to be girdling, so I consider all reports of girdling endothecium suspect. Sonication of anthers combined with scanning electron microscopy may be necessary to resolve the situation. Meanwhile, I have entered Dahlgren and Clifford’s data in the descriptions, but have omitted the characters from classificatory analyses.
#285. Pollen grains <whether few or many aperturate>/

1. few <1–6> aperturate/
2. many <more than 6> aperturate <Plate 27.9>/

- The discontinuities in the exine of sedge pollen grains have been referred to as apertures (Koyama 1956; Tucker 1987), poroid or tenuitate (Dahlgren and Clifford 1982) and porate (Guppy unpublished data). Dahlgren and Clifford (1982 p. 164) reported pollen grains of the Cyperaceae to be mostly ulcerate, "some with up to 3 additional lateral poroid or elongate tenuitates". However, I have recognized two states following Koyama (1956). Only Baumea, Machaerina and Tricostularia have many-aperturate pollen grains. Another 20 genera are recorded with few-aperturate pollen grains. Guppy (unpublished data) recorded uniaperturate pollen in the mapanioids Hypolytrum and Mapania. This suggests that 'uniaperturate' is usefully recognized as a separate state.

#286. Pollen grains <whether bicellular or tricellular>/

1. bicellular/
2. tricellular <Plate 27.8>/

- Bicellular and tricellular pollen grains (Knox 1984) were previously termed binucleate and trinucleate respectively (e.g. Brewbaker 1967; Dahlgren and Clifford 1982). My own observations cover most of the 23 genera recorded for this character, and some of them conflict with those reported in Dahlgren and Clifford (1982). They record Fimbristylis as bicellular, while I found both Fimbristylis and Abildgaardia to be tricellular; and I recorded bicellular pollen in Rhynchospora and Syntrinema, whereas Dahlgren and Clifford (1982) list Rhynchospora as tricellular. Further studies are needed to clarify whether the differences represent intrageneric variability or errors; meanwhile I have not included this character in classificatory analyses.

HYPOGYNIUM

#287. Hypogynium <between the stamens and ovary: whether present>/

1. present <e.g. Ficinia> <Plates 30.1, 30.6, 31.4>/
2. absent <implicit>/

- A hypogynium is defined as an outgrowth near the base of the gynoecium, differing from the latter in texture, but inserted above the stamens (cf. Arnold and Gordon-Gray 1982). It is often (e.g. in Ficinia) distally free from the gynoecium, and produced into three lobes. The presence in some
Mesomelaena species of both a hypogynium and a perianth of scales separated by stamens confirms that these structures are not homologous. In Scleria the presence of female-only flowers, i.e. without filaments, prevents interpretation of its cupular structure as a hypogynium as defined above.

GYNOECIUM

#288. Style <degree of division>/
1. divided nearly to base <Plate 30.2>/
2. divided for about half its length <Plate 30.3>/
3. divided for much less than half its length <Plate 30.6>/
4. merely notched <Plate 28.2>/

#289. Style <relative length>/
1. <much> longer than the fruit/
2. about as long as the fruit/
3. <much> shorter than the fruit/

#290. Style <whether terete>/
1. ‘terete’ <Plate 30.2>/
2. ‘flattened’ <or markedly angular> <Plates 30.1, 31.7>/
   • The distinction between terete and flattened styles is usually obvious. Those that are triangular in trans-section have been regarded for the present purpose as ‘flattened’, qualified with an appropriate comment. The extent of changes in shape on drying needs to be further assessed, for some terete styles may become triangular. It may prove preferable to lump ‘triangular’ styles with ‘terete’ or to establish a further state for them.

#291. Style <whether winged>/
1. winged <Plate 31.7>/
2. not winged <Plate 30.1>/
   • The styles are winged when the margins are thin, flat and hyaline, or membranous.

#292. Style <below the style branches and above the apex of the fruit, whether indumented>/
1. indumented <Plates 24.3, 25.6, 27.7>/
2. glabrous <Plate 30.3>/
#293. Style <indumentum: form>/
1. ‘papillose’ <includes scabrous> <Plate 25.6>/
2. ‘puberulous’/
3. ‘pilose’/
   • See #64 and #45 above.

#294. Style-base <whether continuous with the fruit apex>/
1. continuous with the fruit apex <Plates 26.2, 30.7, 30.3>/
2. sharply differentiated from the fruit apex <Plates 24.3, 25.6, 26.4, 27.7, 30.1–2>/
   • A discontinuity in size or texture may demarcate the style from the fruit, and is usually more obvious when the latter is immature.

#295. Style-base <shape>/
1. ‘enlarged-bulbous’ <Plates 24.3, 30.4, 31.2>/
2. ‘enlarged-pyramidal’ <or conical> <Plates 25.6, 28.3–4, 28.6, 30.1–2>/
3. ‘not enlarged’ <regardless of whether flattened, triangular in section or cylindrical> <Plates 26.2, 30.3, 30.7>/
   • The shape of the base of the style is assessed in relation to the shape as a whole. ‘Enlarged-bulbous’ has a convex or annular outline, and ‘enlarged-pyramidal’ has a concave or triangular outline.

#296. Style-base <whether persistent>/
1. persistent <Plates 25.6, 27.7, 30.2, 30.4>/
2. deciduous <Plate 30.1>/
   • Persistence of the style-base can be judged where the style-base is sharply differentiated from the fruit apex (see #294 above). In Rhynchospora rubra, the style-base is obvious, enlarged and persistent, yet above the style-base there is an abscission zone, delimiting the plane-shaped portion of the style. Similarly, abscission zones may be seen in gynoecia with unenlarged styles (e.g. in Cyperus: Plate 30.7) that are otherwise continuous with the fruit. The abscission zone provides the key to distinguish fruit from style, and further observations on it would probably lead to improved, properly comparative descriptive data.

#297. Stigmata <number>/

#298. Stigmatic surface <whether papillose>/
1. papillose <Plate 30.2>/
2. glabrous <Plates 28.2, 30.3, 30.7>/
   • See also #64 above.
#299. Stigmatic papillae <form/>

1. ‘long’ <Plate 30.9/>
2. ‘foot-like’ <Plate 30.8/>

- ‘Long’ stigmatic papillae are usually obvious to the unaided eye, and are far longer than the cells are long. By contrast, ‘foot-like’ stigmatic papillae are easily overlooked, and are shorter than the cells are long.

#300. Stigmatic papillae <whether zoned/>

1. ‘zoned’ <Plate 30.9/>
2. not zoned/

- Raynal (1973 p. 147) described ‘zoned’ papillae as a feature uniting members of his Fimbristylideae: "les papilles...annuelées". The zonation appears to result from an unevenness in the deposition of the wall, rather than from any obvious partitioning.

#301. Fruit <colour at maturity>/

1. white/
2. grey/
3. green/
4. brown/
5. red/
6. black/

#302. <Shape of the> fruit <in the broadest lateral view>/

1. ‘spherical’ <includes subspherical and lenticular>/
2. ovate <Plate 24.5>/
3. oblong <Plate 30.3>/
4. elliptical <Plate 24.8>/
5. obovate <Plates 27.3, 28.3, 31.5>/
6. lanceolate <Plate 27.4>/

- The shapes are from Stern (1966 pp. 318-319 Fig. 19 and p. 325 Fig. 21).

#303. Fruit <shape in> trans-section <whether circular, elliptical or triangular>/

1. circular <Plate 28.5>/
2. elliptical <Plate 28.4>/
3. triangular <includes depressed-ovate> <Plate 27.7>/

#304. Fruit <whether laterally, dorsiventrally or not compressed>/

1. laterally compressed <Plate 28.6>/
2. dorsiventrally compressed <Plate 31.5>/
3. not compressed <Plates 27.1, 27.5>/
#305. Fruit <whether ‘winged’>/
1. ‘winged’/
2. wingless <implicit>/
   • The wings may be fine and membranous as in *Fimbristylis pterosperma*, or massive and opaque as in *Chorizandra*. In either case they are composed of multicellular processes of the pericarp. Small ridges commonly associated with ribs or veins are ignored, as are simple ridges at the margins of rows of epidermals (e.g. see *Schoenoplectus*).

#306. Fruit <excluding a pedicel: whether ‘stalked’>/
1. ‘stalked’ <Plates 28.5, 31.8>/
2. sessile <Plate 31.5>/
   • This character describes whether the fruit is more or less abruptly constricted and prolonged into a ‘stalk’. As ‘stalked’ fruits occur widely in seemingly distantly related taxa, this character is included more as an aid to identification. ‘Fruit stalked’ may be equivalent to the term "gynophore" of some authors, but since that term is often used interchangeably with hypogynium (see Arnold and Gordon-Gray 1982), I have avoided it.

#307. <Fruit> stalk <as part of the fruit: whether hollow>/
1. hollow <*Capitularina>/
2. solid <implicit>/

#308. <Fruit> apex <whether formed into a beak>/
1. beaked <Plates 27.5, 28.5>/
2. beakless <Plates 24.5, 24.8>/
   • The beak forms an extension at the top of the fruit, and may originate from ‘pericarp’ or ‘style-base’ (i.e. formation of the beak may be homoplasious; see also the earlier comments on the definition of the style-base).

#309. <Fruit> beak <whether solid or hollow>/
1. solid <implicit>/
2. hollow/

#310. <Fruit> beak <length>/
1. ‘apiculate’ <Plates 31.5, 31.8>/
2. ‘acuminate’ <Plate 31.2>/
3. ‘subulate’/
   • Terms follow Stern (1966).
#311. Fruit <whether longitudinally 'ribbed', i.e. with more than three prominent ribs>/
1. <longitudinally> prominently 'ribbed’/
2. without prominent ribs <implicit>/
   • Ribs associated with the veins, two or three (or rarely four as in *Tetrariopsis*), are ignored, as are the raised junctions of vertical rows of epidermal cells.

#312. Fruit <whether 'rugose’>/
1. 'rugose’ <Plates 25.6, 28.9, 31.5>/
2. not rugose <implicit>/
   • 'Rugose’ fruits have horizontal folds or undulations which are usually associated with longitudinally elongated epidermal cells.

#313. <Fruit> epidermal cells <whether longitudinally or transversely elongated, or isodiametric>/
1. <markedly> longitudinally elongated <Plate 31.5>/
2. <markedly> transversely <to the axis of the fruit> elongated <Plate 31.8>/
3. <more or less> isodiametric <implicit> <Plate 31.4>/

#314. <Fruit> epidermal cells <whether 'cancellate', 'constituting hairs’ or 'smooth’>/
1. 'cancellate’ <Plate 31.8>/
2. 'constituting hairs’ <Plate 28.6>/
3. <relatively> 'smooth’ <Plate 31.2>/
   • 'Cancellate’ epidermal cells are more or less honeycomb shaped, and have markedly concave outer periclinal walls, such that the anticlinal walls appear raised and form a reticulum. Epidermal cells 'constituting hairs’ here include markedly convex or papillate epidermals (see #315,1 below) if they can be detected with up to 10x magnification.

#315. Fruit <indumentum: form>/
1. 'papillose’ <Plates 28.6, 32.2>/
2. 'scabrous’ <i.e. constituting prickle-hairs> <Plate 27.5>/
3. 'hispid’/
4. 'warty’/

#316. Mesocarp <whether spongy or fibrous>/
1. spongy <Plate 32.3>/
2. fibrous <Plates 32.1–2>/
   • The fruit of *Cyperaceae* is a one seeded and indehiscent nut, nutlet or achene. The pericarp is conventionally interpreted as comprising three layers
(Esau 1965): an exocarp comprising the outer epidermis, a mesocarp of fibres (state 2) or parenchyma (state one; the fruit being more or less drupaceous), and an endocarp (see #318 and #319). The pericarp vascular bundles are included in the mesocarp. Koyama’s interpretation of some sedge fruits as compound-walled structures is rejected here (see Haines and Lye 1973 for a reinterpretation of his illustrations). I interpret my own observations corroborating those of Shah (1968), Haines and Lye (1973) and Goetghebeur (1986).

#317. Mesocarp <whether oily>/
1. oily/
2. not oily <implicit>/
   • A special feature of Gahnia.

#318. Endocarp <whether sclerenchymatous or membranous>/
1. sclerenchymatous/
2. membranous/
   • The endocarp comprises either fibres and/or sclereids (state 1), or thin-walled cells, almost devoid of contents (often crushed at maturity), and elongated tangentially relative to the transverse axis (state 2). The endocarp is free from the testa. The testa, which also has vascular bundles encloses abundant endosperm and a basal embryo.

#319. Endocarp <whether ‘dark’ or ‘light’>/
1. ‘dark’/
2. ‘light’ <in colour; implicit>/
   • When the fruit is sectioned and examined with up to 10x magnification, the endocarp may appear either ‘dark’ or ‘light’ in colour. The cause of this optical effect is not apparent in thin sections viewed with a compound microscope.

#320. Endocarp <whether with internal transverse annular furrows>/
1. with transverse annular furrows (Gahnia pro parte) <Plate 31.3>/
2. ‘smooth’ <implicit>/

EMBRYO

#321. Embryo <type: mostly from Goetghebeur 1986>/
1. Carex-type <Plates 33.2–3, 33.5>/
2. Trilepis-type/
3. Schoenus-type/
4. Helothrix-type/
5. Fimbristylis-type <Plates 32.8, 33.6>/
6. Carpha-type <Plates 33.4>/
7. Tylocarya-type/
8. Bulbostylis-type <Plates 32.7>/
9. Abildgaardia-type/
10. Cyperus-type <Plate 33.8>/
11. Ficinia-type <Plate 33.9>/
12. Schoenoplectus-type/
13. Bolboschoenus-type/
14. Eleocharis-type/
15. Websteria-type/
16. Juncus-type/

• The embryo-types and data are mostly those compiled by Goetghebeur (1986) mainly from Van der Veken (1965), Juget (1970), Veberlen (1970), and Van der Linden (1971), with some modifications. I have recognized the Juncus-type as distinct from the Carex-type. Variation illustrated or noted by Goetghebeur, but not necessarily reflected in his embryo-type nomenclature has been incorporated, e.g. Cyperus subgenus Cyperus is scored as states 10 and 11 (cf. Goetghebeur 1986 pp. 86-87), and Erioscirpus is scored as states 5 and 10 (cf. Goetghebeur 1986 p. 308 Figs 8.3.2E-F). Similarly, for the following characters the apparent variation has been encoded rather than simply relying on the catch-all key and embryo-type descriptions given by Goetghebeur (1986: Chapter 3).

#322. Embryo <shape>/
1. turbinate <Plates 32.7, 32.8, 33.1>/
2. ellipsoid <Plates 33.8, 33.9>/
3. mushroom-shaped <fungiform> <Plate 32.4>/

#323. Cotyledon <whether ‘markedly widened’>/
1. ‘markedly widened’ <Plate 32.4>/
2. not markedly widened <Plate 32.7>/

• To avoid the linking of state 1 with mushroom-shaped embryos (#322), the embryos have been interpreted as ‘markedly widened’ when the cotyledon is more than twice as wide as the coleoptile/coleorhiza portion.
#324. Coleoptile <position>/
   1. lateral <Plates 33.2–3>/
   2. sublateral <Plate 32.7>/
   3. basal <Plates 32.4, 32.8, 33.4, 33.8>/

#325. First embryonic leaf primordium <whether detectable>/
   1. detectable <Plates 32.4, 32.8>/
   2. not detectable <Plate 33.1>/

#326. First embryonic leaf primordium <whether exerted beyond the coleoptile>/
   1. exerted beyond the coleoptile <Plate 32.4>/
   2. enclosed by the coleoptile <Plates 32.6, 32.8>/

#327. Germination pore <orientation with respect to the first embryonic leaf primordium>/
   1. perpendicular to the first embryonic leaf primordium/
   2. parallel with the first embryonic leaf primordium <Plate 32.5>/

#328. Second embryonic leaf primordium <whether detectable>/
   1. detectable <Plate 33.7>/
   2. not detectable <Plate 33.2>/

#329. Second embryonic leaf primordium <whether well developed>/
   1. ‘well developed’/
   2. ‘rudimentary’ <Plate 33.9>/
   • The second leaf is ‘well developed’ when it is at least half the size of the first leaf.

#330. Third embryonic leaf primordium <whether detectable>/
   1. detectable/
   2. not detectable <Plate 33.9>/

#331. Coleorhiza <position>/
   1. lateral <Plates 32.4, 32.8>/
   2. subbasal <Plate 33.4>/
   3. basal <Plate 32.7>/

#332. Embryo ‘constriction’ <position relative to the coleorhiza>/
   1. present, above the coleorhiza <Plates 33.7, 33.9>/
   2. present, below the coleorhiza/
   3. absent <Plates 33.2, 33.8>/

**CYTOLOGY**

#333. Chromosome base number/
HOST SPECIFICITY OF PATHOGENIC FUNGI

#334. <Susceptibility of genus to Puccinia sensu lato>/

1. susceptible to *Puccinia sensu lato*/
2. not recorded as susceptible to *Puccinia sensu lato* <implicit>/

- Broad base-line data for the occurrence rusts (and smuts: an exception being those of Cariceae) on sedges are not available in the literature (contrast with the Poaceae, see Watson and Dallwitz 1988). The scant data are mostly from Savile (1979) and my observations. This and the following two characters are at present unsatisfactory and they have been masked out of the descriptions pending authoritative mycological vetting.

#335. <Susceptibility of genus to Ustilaginales>/

1. susceptible to *Ustilaginales* <Plate 31.6>/
2. not recorded as susceptible to *Ustilaginales* <implicit>/

- Data mainly from Zundel (1953) and Savile (1979), with nomenclatural changes after Kukkonen (1983). A few additional sources, and some of my observations, are listed by way of comments. A recent treatment of the smut genera (Vánky 1987) gives little information on host taxa, especially of the Cyperaceae, and the generic limits of some of the smut genera are not clear, so that cross-referencing with previous accounts (e.g. Kukkonen, 1983) is limited. See #334 above.

#336. Infected by <susceptibility of genus to Ustilaginales genera>/

1. *Anthracoidea* <Plate 31.6>/
2. *Cintractia*/
3. *Cintractiella*/
4. *Entorrhiza*/
5. *Entyloma*/
6. *Farysia*/
7. *Schizonella*/
8. *Sorosporium*/
9. *Sphacelotheca*/
10. *Testicularia*/
11. *Thecaphora*/
12. *Tolyposporium*/
13. *Urocystis*/
14. *Ustilago*/

- See #334 above.
NUMBER OF SPECIES; DISTRIBUTION

#337. <Number of species>/

- The number of species usually represents an approximation. Most data are from Goetghebeur (1986) or relevant monographs and recent treatments of genera.

#338. <World distribution: this ‘character’ intended primarily for convenience in key-making>/

1. Western Eurasia, U.S.S.R. <includes Iran, Iraq, Turkey>/
2. Mediterranean/
3. Eastern Asia <Japan, China to India>/
4. Africa <and Saudi Arabia>/
5. Pacific <Malaysia, Indonesia, Australasia, Pacific Islands>/
7. South and Central America, West Indies/
8. Arctic/

#339. <Geographical distribution>/

- The ‘character’ is maintained to allow scoring of highly localized genera and some fine-scale distributions.

#340. Australasia distribution:

1. Tasmania/
2. New South Wales/
3. Australian Capital Territory/
4. Victoria/
5. Western Australia/
6. Queensland/
7. Northern Territory/
8. South Australia/
9. New Guinea/
10. New Zealand/
11. not known in Australasia <implicit>/

#341. Floristic kingdoms: <after Takhtajan 1969. Data for Takhtajan’s floristic regions (see below)>/

1. Holarctic/
2. Paleotropical/
3. Neotropical/
4. Cape/
5. Australian/
6. Antarctic/

- The data, for #341-356, especially those for some of the subregions, are as yet incomplete. These geographic ‘characters’ have been left unrecorded where the distribution of a genus remains uncertain.

#342. Holarctic subkingdoms: <after Takhtajan 1969>/
1. Boreal/
2. Tethyan <ancient Mediterranean>/
3. Madrean <Sonoran>/

#343. Paleotropical subkingdoms: <after Takhtajan 1969>/
1. African/
2. Madagascan/
3. Indomalesian/
4. Polynesian/
5. Neocaledonian/

#344. Boreal subkingdom regions: <after Takhtajan 1969>/
1. Arctic and subarctic/
2. Euro-Siberian/
3. Eastern Asian/
4. Atlantic North American/
5. Rocky Mountains/

#345. Tethyan subkingdom regions: <after Takhtajan 1969>/
1. Macaronesian/
2. Mediterranean/
3. Irano-Turanian/

#346. African subkingdom regions: <after Takhtajan 1969>/
1. Saharo-Sindian/
2. Sudano-Angolan/
3. West African Rainforest/
4. Namib-Karroo/
5. Ascension and St. Helena/

#347. Indomalesian subkingdom regions: <after Takhtajan 1969>/
1. Indian/
2. Indo-Chinese/
3. Malesian <Malayan> / 
4. Papuan / 

#348. Polynesian subkingdom regions: <after Takhtajan 1969> / 
1. Hawaiian / 
2. Polynesian / 
3. Fijian / 

#349. Neotropical regions: <after Takhtajan 1969> / 
1. Caribbean / 
2. Venezuela and Suriname / 
3. Amazon / 
4. Central Brazilian / 
5. Pampas / 
6. Andean / 
7. Fernandezian / 

#350. Australian regions: <after Takhtajan 1969> / 
1. North and East Australian / 
2. South-West Australian / 
3. Central Australian / 

#351. Antarctic regions: <after Takhtajan 1969> / 
1. New Zealand / 
2. Patagonian / 
3. Antarctic and subantarctic / 

#352. <Euro-Siberian subregions> / 
1. European <subregion> / 
2. Siberian <subregion> / 

#353. <Atlantic North American subregions> / 
1. Canadian-Appalachian <subregion> / 
2. Southern Atlantic North American <subregion> / 
3. Central Grasslands <subregion> / 

#354. <Sudano-Angolan subregions> / 
1. Sahelo-Sudanian <subregion> / 
2. Somalo-Ethiopian <subregion> / 
3. South Tropical African <subregion> / 
4. Kalaharian <subregion> /
#355. <North and East Australian subregions>  
1. Tropical North and East Australian <subregion>  
2. Temperate and South-Eastern Australian <subregion>  

#356. <Antarctic and subantarctic subregions>  
1. South Temperate Oceanic Islands <subregion>  
2. Antarctic <subregion>  

**TAXONOMY**  

#357. <Tribe: Goetghebeur 1986>  
1. Hypolytreae/  
2. Chrysitricheae/  
3. Schoeneae/  
4. Rhynchosporeae/  
5. Arthrostylideae/  
6. Dulichieae/  
7. Scirpeae/  
8. Abildgaardieae/  
9. Eleocharideae/  
10. Fuireneae/  
11. Ficinieae/  
12. Cypereae/  
13. Trilepideae/  
14. Cryptangieae/  
15. Sclerieae/  
16. Bisboeckelereae/  
17. Cariceae/  

#358. <Subfamily: Goetghebeur 1986>  
1. Mapanioideae/  
2. Cyperoideae/  
3. Sclerioideae/  
4. Caricoideae/  

#359. ‘Nearest neighbours’ <in ascending order of ‘distance’, according to the most recent DIST calculations using the descriptions applying to the classificatory analyses (Chapter 9). Note that these are safely interpretable as ‘closest taxonomic relatives’ only when reciprocal lists are in agreement.
The misleading appearance of the same large genera (Ficinia, etc.) in many lists probably reflects their internal variability.

**ECOLOGY**

#360. <Habitat light requirement>/
   1. shade species/
   2. open habitats/

#361. <Habitat water requirement>/
   1. hydrophytic/
   2. helophytic <i.e., in marshy places>/
   3. mesophytic/
   4. xerophytic/

#362. <Salt tolerance, etc.>/
   1. halophytic/
   2. glycophytic <= not halophytic>/

#363. <PH tolerance>/
   1. calcicole/
   2. calcifuge/

#364. <Whether weedy>/
   1. weedy/
   2. not weedy <implicit>/

**COMMENTS; LITERATURE CITED**

#365. <Comments>/

#366. <Relevant literature>/
   • Used to record non-comparative information (e.g. taxonomic and nomenclatural comments, and miscellaneous observational data)

**SAMPLES**

#367. General sample <species and collectors> –/
   • Identifies the herbarium sheets or vouchers examined and used for scoring of at least some characters.

#368. Anatomical sample <species and collectors> –/
   • Identifies the specimens examined for vegetative anatomy for which semi-permanent or permanent microscope slides are housed in the Taxonomy Laboratory at RSBS. This is often an underestimate of the material examined,
as temporary preparations from fresh material (for which vouchers also exist) are not listed here.

FAMILIAL CHARACTERS

#369. Fruit <whether indehiscent>/
   1. indehiscent <implicit>/
   2. dehiscent/
   • I have used the Juncaceae as the outgroup of the Cyperaceae (cf. Metcalfe 1971; Juget 1972; Savile 1979; Dahlgren and Clifford 1982; Goetghhebeur 1986) in cladistic analyses. The following characters have been included to unite the genera of the Cyperaceae and the genera of the Juncaceae, respectively, in these analyses (see Chapter 10).

#370. Placentae <whether uniovulate>/
   1. uniovulate <implicit>/
   2. multiovulate/

#371. Endosperm formation <whether nuclear or helobial, data from Dahlgren and Clifford 1982>/
   1. nuclear/
   2. helobial/

#372. Pollen <whether in pseudomonads, data from Dahlgren and Clifford 1982>/
   1. in pseudomonads <implicit>/
   2. in tetrads/

CURRENT CLASSIFICATION

#373. <Subfamilies: see Chapter 9>/
   1. Cyperoideae/
   2. Caricoideae/
   • The classification based on my analyses (Chapter 9), is conveniently appended here to maintain parity between the character numbers in the character list and those referred to throughout the thesis, particularly in the classificatory analyses (Chapter 9). The last two characters will be repositioned with the other taxonomic characters (#357-359) in a subsequent REORDER.

#374. <Tribes: see Chapter 9>/
   1. Cypereae/
   2. Scirpeae/
3. Abildgaardieae/
4. Arthrostyliideae/
5. Rhynchosporaeae/
6. Schoeneae/
7. Cryptangieae/
8. Trilepideae/
9. Cariceae/
10. Sclerieae/
11. Bisboeckelereae/
12. Hypolytreæe/

• See #373 above.
Plate 1


Plate 1.3: Habit long-stoloniferous. Leaves elaminate. Culms dimorphic: the fine sterile culms at the nodes appear here like roots and would be submerged. The fertile culms (arrow) are emergent and bear inflorescences which are always restricted to a solitary spikelet. *Egleria fluctuans*: A. Ducke 20 July 1912 (BRI).


Plate 1.5: Caespitose annual herbs. Their inflorescences are borne at ground level (but are not ‘basal spikelets’) and constitute the bulk of these small plants. *Volkiella disticha*: M. Mueller 493 (PRE).

Plate 1.6: Caespitose annual herb, with fine roots. Primary inflorescence bracts foliose, tristichous. *Courtoisina (Courtoisia assimilis)*: W. Giess 6676 (PRE).

Plate 1.7: Habit long-stoloniferous. Leaves elaminate. Culms dimorphic: the fine sterile culms at the nodes appear here like roots and would be submerged. The fertile culms (arrow) are emergent and bear inflorescences that are always restricted to a solitary spikelet (cf. *Egleria* above). *Websteria confervoides*: G.E. Gibbs Russell 1502 (PRE).

Plate 1.8: Perennial, with a fibrous matted ‘trunk’. Leaves laminate. Inflorescence comprising more than a solitary spikelet, elongated, and ‘conipaniculate’. The fascicled appearance of the inflorescence indicates ‘prophyllar’ branching. Lateral inflorescence branches elongated and ‘coniplaniculate’. *Everardia montana* ssp. *duidae*: J.A. Steyermark 93322 (K).

Plate 1.9: Annual herbs with radical leaves. Leaf sheaths ‘blackish’. Inflorescence anthelate, the lateral branch inflorescences capitate. Primary inflorescence bracts tristichous. *Monandrus (Cyperus hamulosus)*: B. de Winter 4929 (PRE).
Plate 2

Plates 2.1-9: Morphology of Cyperaceae. 2.1-8: Herbarium specimens; 2.9 fresh material.

Plate 2.1: Plants differentiated into separate sterile laminate (L, P, and S), and fertile elaminate (arrow) shoots. Culms ‘central’. ‘Petiolate’ leaves divided into lamina (L), ‘petiole’ (P), and sheath (S). Inflorescence ‘conipaniculate’, lateral branch inflorescences anthelate. Bisboeckelera microcephala: J. Florschuetz 1819 (U). Scale = 15 cm.

Plate 2.2: Plants differentiated into separate sterile laminate (L, P, and S), and fertile elaminate shoots (each bearing an inflorescence). ‘Petiolate’ leaves divided into lamina (L), ‘petiole’ (P), and sheath (S). Inflorescence capitate. Paramapanta simplex: L.J. Brass 13481 (BRI). Scale = 15 cm.

Plate 2.3: Base of plant. Perennial (previous years’ growth represented by the burnt stubble). Culms (C) ‘axillary’, as indicated by the presence of a prophyll (P) on the culm, at the base of the uppermost internode, adjacent to the leaves (L). The keeled abaxial surface of the prophyll is visible. Cyathocoma (Macrochaetium hexandrum): J.P.A. Acocks 23217 (PRE). Scale = 5 mm.

Plate 2.4: Part of plant showing a lateral shoot originating at the base of the uppermost culm internode. The shoot bears a prophyll (P). The culm is central to the leaves below (arrows), which are pseudopetiolate. The junction between the lamina and the ‘pseudopetiole’ is indicated by the arrows. The inflorescence comprises two spikelets. Oreobolus oxycarpus: R. Pullen 2469 (CANB). Scale = 2 mm.

Plate 2.5: Detail of 2.4 showing the prophyll (P) with two abaxial keels adjoining the culm (C), while its adaxial surface enwraps the lateral (vegetative) shoot (S). The long arrow indicates the junction of the base of the lamina and the apex of the ‘pseudopetiole’. The short arrows indicate the leaves of the central axis to which the culm belongs. One short arrow (right) also marks the junction of the ‘pseudopetiole’ and the leaf sheath. Oreobolus oxycarpus: R. Pullen 2469 (CANB). Scale = 4 mm.

Plate 2.6: Part of a lamina with a translucent and colourless margin, which is undulate in the plane parallel to the leaf surface. Cymophyllus fraseri: (MEL 1543850). Scale = 3 mm.

Plate 2.7: Base of plant showing leaf sheath breaking down into fibres. Both the aggregation of the leaf bases and slightly bulbous bases of the culm contribute to the swollen appearance of the bases of the plants (centre and right). Kyllingiella polyphylla: J.B. Gillett 12991 (EA). Scale = 3 mm.

Plate 2.8: An underground tuber (dried and shrivelled), attached to its mother plant via a rhizome (arrow). Cyperus esculentus: W.A.T. Harding 16 November 1976 (BRI). Scale = 3 mm.

Plates 4.1-9: Morphology of Cyperaceae. 4.1-6 and 8-9: Herbarium material; 4.7 fresh material.

Plate 4.1: Base of culm (centre) and its ‘split’ prophylls (long arrows), which indicate that the culm is ‘axillary’. The leaf bases (short arrows) that persist after the abscission of the laminae. Microdracoides squamosus: Morton K685 (K). Scale = 2 mm.

Plate 4.2: Base of plant showing distichous (to spirodistichous) phyllotaxis. Costularia brevicaulis: L.E. Moss 7612 (K). Scale = 5 mm.

Plate 4.3: Acute, chartaceous ligule. Cyathochaeta avenacea: A. Morrison 3 December 1903 (BRI). Scale = 2 mm.

Plate 4.4: Tubular leaf sheaths, with ‘truncate’ (upper) to slightly n-shaped (lower), indumented apices. Note that the leaf sheath fronts are similar in texture (i.e. cartilaginous) to the backs. Didymiandrum stellatum: G.T. Prance et al. 9789 (K). Scale = 2 mm.

Plate 4.5: Leaf sheath (right) with fronts differing in texture from the backs; i.e. hyaline to membranous (asterisk) and cartilaginous respectively. The sheath is prolonged into an indumented, membranous ligule with a free limb (arrow). Phylloscirpus (Scirpus nevadensis): M.E. Peck 15386 (K). Scale = 1 mm.

Plate 4.6: A cauline leaf with a tubular sheath, entire margins, n-shaped and glabrous apices. Leaf sheath front is similar in texture (cartilaginous) to the back. Dulichium arundinaceum: L.B. Smith 25 August 1946 (BRI). Scale = 2 mm.

Plate 4.7: An extravaginal vegetative shoot (arrow) of a cauline leaf sheath (in nature lies horizontally, oriented vertically to fit the page). Note the leaf sheath (uppermost) with overlapping margins and V-shaped apices. Cladium procerum: M.D. Crisp 6878 (CBG). Scale = 10 mm.

Plate 4.8: Leaf sheath with margins overlapping distally and indumented, V-shaped sheath apices. The fronts and backs of the sheaths are similar and cartilaginous. Costularia leucocarpa: J. Bossa 7773 (K). Scale = 1 mm.

Plate 4.9: Tubular leaf sheath with entire margins, and n-shaped (asterisk), indumented sheath apices. Both the apex of the leaf sheath and the front of the sheath are indumented. Everardia montana ssp. duidae: J.A. Steyermark 93322 (K). Scale = 2 mm.
Plate 5

Plates 5.1-8: Culm epidermes. Longitudinal axis of culms across the page.


Plate 5.3: Intercostal cells irregular, at least near the stomata. Mid-third of culm glabrous, subsidiaries mostly dome-shaped to triangular. *Lepidosperma effusum*: M.D. Crisp 5231 (CBG). Scale = 100 µm.

Plate 5.4: Epidermal zones absent. Stomata present, though sparse. *Diplasia karataefolia*: B. Croat 17547 (NSW). Scale = 100 µm.

Plate 5.5: Epidermal zones wider intercostally than costally. Epidermis glabrous, but stomata obscured by projections from the adjacent epidermal cells; the projections irregular. *Neesenbeckia punctoria*: E.R. Orchard 36 (K). Scale = 100 µm.

Plate 5.6: Epidermal zones wider intercostally than costally. Intercostal cells irregular. Epidermis glabrous, but stomata obscured by projections from the adjacent epidermal cells; the four projections rounded. *Lepironia articulata*: J.J. Bruhl 526 (CANB). Scale = 50 µm.


Plate 5.8: Costal and intercostal zones of equal width. Stomata not obscured. *Ficinia elongata*: C.H. Stirton 6382 (K). Scale = 100 µm.
Plate 6

Plates 6.1-8: Culm epidermes. Longitudinal axis of culms across the page.

Plate 6.1: Intercostal epidermal zones (the light fine bands) wider than the costal zones (the narrow dark bands; one cell wide). The relatively large cells at top left are underlying parenchymatous cells. Straight intercostal cell anticlinal walls, stomata absent. *Websteria confervoides*: P.A. Smith 1797 (PRE). Scale = 100 µm.

Plate 6.2: The costal zones are one cell wide (appearing straight walled in the plane of focus) and contain conical silica bodies (two rows of fine dark points). Sinuate intercostal cell anticlinal walls, triangular subsidiaries. *Eleocharis retroflexa* ssp. *subtilissima*: W. Ellery 15 (PRE). Scale = 50 µm.

Plate 6.3: The costal zones are one cell wide (the narrow, rectangular cells) and contain conical silica bodies (note the L/O effect: dark dots to ‘white’ dots, lower to upper planes of focus) Sinuate intercostal cell anticlinal walls and triangular subsidiaries. *Kyllinga polyphylla*: D.P. Darmawardhana 25 (CANB). Scale = 100 µm.

Plate 6.4: The ‘organic foot’ of the conical silica bodies (arrow) has stained. In some of these cases minor points surround the central dark-staining point, representing ‘satellite cones’. Prickle-hair adjacent to the numeral. *Tetramopsis octandra*: J. Seabrook 130 (CANB). Scale = 100 µm.

Plate 6.5: Intercostal cells regular and rectangular, the intercostal cell anticlinal walls markedly sinuate, and subsidiaries triangular to dome-shaped. *Fimbristylis dichotoma*: (CANB 293361). Scale = 100 µm.

Plate 6.6: Intercostal cells regular and rectangular. Silica bodies four per cell (the serial light dots in two of the costal cells). Epidermal tannin idioblasts apparent as black cells. *Trachystylis stradbroke*: S.T. Blake 22673 (BRI). Scale = 100 µm.

Plate 6.7: Intercostal epidermal zones (the central darker band) wider than the costal zones (the light bands). Intercostal cells regular and rectangular. *Lipocarpha microcephala*: J.J. Bruhl 287 (CANB). Scale = 100 µm.

Plate 6.8: Intercostal cell anticlinal walls sinuate. Silica bodies (the white dots) have ruptured the epidermis in places (arrows). *Fuirena squarrosa*: A.E. Radford 15859 (MEL). Scale = 100 µm.
Plate 7

Plates 7.1-8: Culm Epidermes. Longitudinal axis of culms across the page.

Plate 7.1: Epidermal zones absent, i.e. costal zones absent. Epidermis papillose (arrows). Stomata present, though sparse. Subsidiaries obviously paracytic, though one is bisected (the lower right), a common feature in the family. *Scirpodendron ghaeri*: P.F. Stevens LAE 58624 (NSW). Scale = 100 µm.

Plate 7.2: Intercostal cell anticlinal walls markedly sinuate. The ‘external’ silica bodies are located between the sini of the anticlinal walls (arrow). *Schoenoides oligocephalus*: J.J. Bruhl 628 (CANB). Scale = 50 µm.

Plate 7.3: Epidermal zones (at a lower plane of focus) wider costally (the light bands) than intercostally (the dark bands). The epidermis scabrous, with solid prickle-hairs (arrows) surmounted on multicellular dome-shaped trichomes. *Gahnia subaequiglumis*: S.M. Prober 161 (CANB). Scale = 50 µm.

Plate 7.4: Stomata raised above the epidermis. Subsidiaries triangular to dome-shaped. *Fuirena umbellata*: J.J. Bruhl 214 (CANB). Scale = 100 µm.

Plate 7.5: Epidermis scabrous to pilose, the former mostly costal and out of focus (the light band), and the latter intercostal (the darker band). *Schoenus ericetorum*: S.T. Blake 10782 (BRI). Scale = 100 µm.

Plate 7.6: Epidermal zones wider intercostally (dark bands) than costally (light bands). Stomata obscured by projection from the adjacent epidermal cells; the lobes irregular (cf. Plate 5.5). *Schoenus imberbis*: J.J. Bruhl Grose Rd. (CANB). Scale = 200 µm.


Plate 7.8: Intercostal cells markedly irregular. *Baumea rubiginosa*: J.J. Bruhl 518 (CANB). Scale = 100 µm.
Plate 8

Plates 8.1-8: Transverse sections of culms (mid-third of the uppermost internode below the inflorescence).

Plate 8.1: Epidermal cell outer walls moderately thickened; the outer walls of ‘silica cells’ characteristically thinner. Showing two obvious (and a third obscure) conical silica bodies with their bases on the proximal periclinal epidermal wall above the fibre strand. *Epischoenus complanatus*: E.E. Esterhuysen 17776 (PRE). Scale = 50 µm.

Plate 8.2: Epidermal cells isodiametric. The stomata hardly raised, the subsidiaries smaller than the adjacent epidermal cells and lacrymose. Palisade mesophyll present. *Epischoenus complanatus*: E.E. Esterhuysen 17776 (PRE). Scale = 50 µm.

Plate 8.3: Epidermal cells noticeably ‘radially elongated’. Mesophyll translucent tissue and air cavities absent. Sclerenchyma (the non-staining fibres) comprising strands (in contact with the epidermis but not the vascular bundles), girders (attached to the epidermis and vascular bundles), and caps (adaxial to the vascular bundles). *Pseudoschoenus inanus*: P. Muller 619 (K). Scale = 100 µm.

Plate 8.4: Epidermal cell outer walls moderately thick. Tannin idioblasts epidermal (cf. Plate 6.6), in the chlorenchyma, and in the vascular bundles. The fibre strands almost continuous, and the caps coalescing to form a ‘ring’. *Everardia montana* ssp. *duidae*: J.A. Steyermark 93322 (K). Scale = 200 µm.


Plate 8.6: Epidermal cell outer walls extremely thick; the cuticle darkly staining, the wall appearing white. Stomata sunken (small arrow), and obscured by projections (large arrow) from the adjacent epidermal cells. Prominent tannin idioblasts present in the chlorenchyma. *Chrysitrix junciformis*: H.C. Taylor 3888 (PRE). Scale = 200 µm.

Plate 8.7: Stomata distinctly raised. The subsidiaries lacrymose. Mesophyll air cavity present. The primary vascular bundle possesses a prominent protoxylem lacuna, and a parenchymatous bundle sheath of large colourless cells, lateral to the metaxylem vessels, in places more than one cell wide. *Fuirena umbellata*: J.J. Bruhl 214 (CANB). Scale = 100 µm.

Plate 8.8: Epidermal cell outer walls extremely thick; the walls darkly staining. Stomata, in the intercostal depression, raised (top centre). The palisade mesophyll radiating from the vascular bundles. *Schoenus ericetorum*: S.T. Blake 10782 (BRI). Scale = 100 µm.
Plate 9

Plates 9.1-8: Transverse sections of culms (mid-third of the uppermost internode below the inflorescence).

Plate 9.1: Intercostal zones differentiated into alternating narrow stomatal (the small epidermals) and wide astomatal zones (the large 'bulliform-like' epidermals) separated by narrow costal zones (cf. Pl. 5.2). 'External' silica bodies just visible above the wide astomatal zones. Culm not medullated, i.e. without pith; the central bundles coalesced. *Actinoschoenus filiformis*: M. Ramos September 1922 (NSW 181450). Scale = 200 µm.

Plate 9.2: Trans-section 'narrow elliptical'. Culm medullated (i.e. with pith). Tannin idioblasts present in the chlorenchyma. Spongy and palisade mesophyll present. 'Maximum cells-distant count' more than one. *Episcoenus complanatus*: E.E. Esterhuysen 17776 (PRE). Scale = 1 mm.

Plate 9.3: Fertile culm trans-section broadly elliptical. Culm 'reticulate' (with one complete partition visible) and therefore described as 'solid'. Not appreciably photosynthetic. Without pith translucent tissue but with pith air cavities. Hypodermis present. *Websteria confervoides*: P.A. Smith 1797 (PRE). Scale = 200 µm.


Plate 9.8: Trans-section triangular to broadly elliptical. Tannin idioblasts present in the chlorenchyma and pith. *Ficinia fascicularis*: Acocks 9090 (K). Scale = 200 µm.
Plate 10

Plates 10.1-9: Transverse sections of culms (mid-third of the uppermost internode below the inflorescence).

Plate 10.1: Pith (asterisks) and mesophyll translucent tissue (the two outer oval areas) present and breaking down to form air cavities. One ‘ring’ of vascular bundles (including the three outer bundles) partially embedded in chlorenchyma. Parenchymatous bundle sheath extensions present on the outer three bundles (the colourless cells extending to the epidermis). *Bolboschoenus fluviatilis*: M. Gray 3921 (CANB). Scale = 200 µm.


Plate 10.4: Hypodermis present. All vascular bundles contiguous with chlorenchyma. The outer two small secondary vascular bundles are completely embedded in chlorenchyma, while the two primary bundles are partially embedded in chlorenchyma. A partial parenchymatous bundle sheath is apparent on one of the secondary bundles (arrow). The primary bundles are not associated with sclerenchyma. ‘Maximum cells-distant count’ one. *Lipocarpha microcephala*: J.J. Bruhl 287 (CANB). Scale = 200 µm.

Plate 10.5: Subsidiaries larger than the adjacent epidermal cells, ‘vertical-rectangular’ (curved-rectangular). The hypodermis is interrupted only by the substomatal cavity. *Hypolytrum nemorum*: J.J. Bruhl 478 (CANB). Scale = 50 µm.


Plate 10.7: Stoma flush. Hypodermis present. All vascular bundles contiguous with chlorenchyma. The chlorenchyma mostly composed of brick-shaped cells. Only secondary bundles are shown. Internal to the small celled mestome sheath are the ‘large’, chlorenchymatous cells of the boundary layer cells. ‘Maximum cells-distant count’ one. *Cyperus laevigatus*: J.J. Bruhl 65 (CANB). Scale = 100 µm.


Plate 11

Plates 11.1-9: Transverse sections of culms (mid-third of the uppermost internode below the inflorescence).

Plate 11.1: Culm medullated, initially 'solid'. Not all vascular bundles contiguous with chlorenchyma. Cladium procerum: M.D. Crisp 6878 (CBG). Scale = 200 µm.

Plate 11.2: Epidermal zones absent. Hypodermis present. Pith with translucent tissue (the inner oval areas composed of colourless-cells), this breaking down to form air cavities. The culm photosynthetic only in the region of the outer air cavities. Diplasia karataefolia: B. Croat 17547 (NSW). Scale = 200 µm.

Plate 11.3: Epidermal cells markedly 'radially elongated'. Tylocarya cylindrostachya: A.F.G. Kerr 21294 (BM). Scale = 50 µm.

Plate 11.4: Subsidiaries larger than the adjacent epidermal cells, lacrymose. Sclerenchyma comprising a girder (outer fibres) and a cap (inner fibres). The non-chlorenchymatous parenchymatous bundle sheath (the four lateral colour cells outside the mestome sheath) is interrupted by fibres. Baeothryon caespitosum: C.C. Townsend 73/154 (PDA). Scale = 50 µm.


Plate 11.6: Sclerenchyma (non-staining) composed of strands (subepidermal), and inner and outer caps associated with the bundles. The caps coalescing to form a 'ring'. Spongy mesophyll present, palisade mesophyll absent. Microdracoides squamosus: Morton K685 (K). Scale = 50 µm.

Plate 11.7: Epidermal cell outer walls extremely thick. Stomata (centre and right) flush. Mesophyll translucent tissue and air cavities absent. Palisade mesophyll present. 'Maximum cells-distant count' more than one. Scirpoides holoschoenus: W.M. Caine June 1917 (NSW 181479). Scale = 100 µm.


Plate 11.9: The rounded thin-walled epidermal cells are silica cells. The epidermal zones wider costally than intercostally. Translucent tissue only poorly developed (asterisk). Afrotrilepis pilosa: R. Letouzey 13915 (NSW). Scale = 100 µm.
Plate 12

Plates 12.1-8: Transverse sections of culms (mid-third of the uppermost internode below the inflorescence).

Plate 12.1: Costal and intercostal zones of more or less equal width. Culm medullated (i.e. with pith). Mesophyll translucent tissue present, breaking down to form air cavities. *Carex rafflesioida*: J.J. Bruhl 551 (CANB). Scale = 100 µm.

Plate 12.2: Stomata flush. Sclerenchyma comprising a girder and caps. ‘Maximum cells-distant count’ more than one. *Scleria sphacelata*: J.J. Bruhl 515 (CANB). Scale = 100 µm.

Plate 12.3: Subsidiaries similar in size to the adjacent epidermal cells, lacrymose (arrow). Substomatal chambers without sclereids. Parenchymatous bundle sheath (the large non-chlorenchymatous cells) complete, despite the presence of some cap fibres. Ratio of sclerenchyma groups : vascular bundles greater than 1:1. *Schoenoplectus mucronatus*: J.J. Bruhl 538 (CANB). Scale = 200 µm.


Plate 12.6: Epidermal zones wider costally than intercostally. Parenchymatous bundle sheaths only adjacent mextaxylem vessels (the colourless, rounded cells lateral to the primary bundles). ‘Maximum cells-distant count’ one. *Sphaerocyperus erinaceus*: H.M. Richards 15066 (K). Scale = 200 µm.

Plate 12.7: Sclerenchyma comprising strands, girders and caps, in contact with all of the vascular bundles. Sclerenchyma groups to vascular bundles ratio greater than 1:1. *Mesomelaena tetragona*: E. Bailey (CANB 63655). Scale = 200 µm.

Plate 12.8: Pith with translucent tissue (right of scale), breaking down to form air cavities. Tannin idioblasts present in the chlorenchyma. *Cyathocoma (Macrochaetium hexandrum)*: S. Garside 10 October 1920 (K). Scale = 200 µm.
Plates 13.1-8: Leaf blade epidermes. Longitudinal axis of leaves across page. Scales = 100 µm


Plate 13.2: Abaxial epidermal cell anticlinal walls sinuate. Subsidiaries narrowly dome-shaped. Leaf blade indumented (two unicellular papillate trichomes are present in a different plane of focus, centre right). *Schoenus maschalinus*: J.J. Bruhl 7 October 1986 (CANB).

Plate 13.3: Abaxial leaf blade epidermal zones wider intercostally (darker zones) than costally (lighter bands). Abaxial epidermal cells irregular. The sunken stomata are in a different plane of focus. The organic feet of conical luminal silical bodies appear as circular, darker-staining regions within the costal zone cells. *Ptilanthelium deutsum*: S.M. Prober 356 (CANB).


Plate 13.5: Abaxial leaf blade epidermal zones absent. Epidermal cells irregular. Luminal silica bodies globular (an organic component of these darkly staining). Stomata clearly paracytic; the two subsidiaries per stoma thin-walled and triangular. *Scirpodendron ghaeri*: P.F. Stevens LAE 58624 (NSW).


Plate 14


Plate 14.4: Abaxial epidermal cell anticlinal walls irregular. Luminal silica bodies conical (represented by the irregularly-shaped and lightly stained areas within the costal cells) and globular (the non-staining areas at the ends of the stomata). Tannin idioblasts epidermal (the very dark-staining cells). *Machaerina insulare*: R.D. Hoogland 8807 (CANB). Scale = 100 µm.


Plates 14.7-8: Abaxial epidermis (Pl. 14.7: low focus; Pl. 14.8: high focus). Intercostal cells markedly irregular. Epidermis papillose, costal and intercostal. The four papillae adjacent to each stoma have a high irregular outline, and obscure the stomata. *Vesicarex collumanthus*: A.M. Cleef 5611 (U). Scale = 50 µm.
Plate 15

Plates 15.1-8: Leaf blade epidermes. Longitudinal axis of leaves across page. Scales = 100 µm.


Plate 15.2: Abaxial leaf blade epidermal zones of equal width. Stomata obscured by projections from the adjacent epidermal cells. *Cyathochaeta avenacea*: A. Morrison 3 December 1903 (BRI).

Plate 15.3: Adaxial epidermis scabrous (i.e. the prickle-hairs) to pilose, intercostally and costally. *Scleria sphacelata*: L.A. Craven 5599 (CANB).

Plate 15.4: Abaxial epidermis. Intercostal zones papillose. The associated crustaceous appearance is due to cuticular waxes, not silica. Stomata obscured by projections from the adjacent epidermal cells. *Chorizandra cymbaria*: S.M. Prober 243 (CANB).

Plate 15.5: Abaxial epidermis. Stomata not obscured by projections from the adjacent epidermal cells. Subsidiaries triangular to dome-shaped. *Fuirena umbellata*: J.J. Bruhl 214 (CANB).


Plate 15.8: Abaxial epidermis. Hairs unicellular, scabrous to pilose (the two shown are intermediate in length). The ‘organic foot’ of luminal conical silica bodies is deeply staining (e.g. above scale). *Sphaerocyperus erinaceus*: H.M. Richards 15066 (K).
Plate 16


Plate 16.1: Costal zone (dark-staining) one cell wide. Epidermal cells regular. Subsidiaries triangular. The relatively dark-staining points within the cells of the costal zone each represent the ‘organic foot’ of conical silica bodies. Monandrus (Cyperus squarrosus): E.S. Steele 6 August 1909 (BRI). Scale = 100 µm.


Plate 16.3: The truncated sini of the costal zone anticlinal cell walls are related to the occurrence of silica bodies ‘embedded in the outer periclinal wall’ (cf. Pl. 13.7: Scirpodendron). Subsidiaries mostly triangular, some dome-shaped. Thoracostachyum sumatranum: J.J. Bruhl 308 (CANB). Scale = 100 µm.

Plate 16.4: Subsidiaries mostly dome-shaped to rectangular. Kyllingiella microcephala: H. and H.E. Wanntorp 405 (PRE). Scale = 100 µm.

Plate 16.5: Epidermal zones wider costally (light bands) than intercostally (dark and stomatal bands) to of equal width. Microdracoides squamosus: Morton K685 (K). Scale = 100 µm.

Plate 16.6: Epidermal zones markedly wider intercostally (the irregular stomatal bands) than costally (two, single cell wide bands, composed of more regular cells). The ‘organic feet’ of the luminal conical silica cells are apparent in the costal cells (mostly two per cell). Tannin idioblasts (the dark-staining cells) epidermal. Didymiandrum stellatum: G.T. Prance et al. 9789 (K). Scale = 50 µm.

Plate 16.7: Subsidiaries triangular. Tylocarya cylindrostachya: A.F.G. Kerr 21294 (BM). Scale = 100 µm.

Plate 17

Plates 17.1-8: Transverse sections of the leaf blades (mid-third of lamina). Bifacial leaves with adaxial epidermis uppermost.


Plate 17.2: Luminal silica bodies conical (barely visible as a non-staining point above the adaxial fibre strand) and globular (arrows). Intervascular translucent tissue present (centre left), breaking down to form air cavities. Parenchymatous bundle sheaths (non-chlorenchymatous thin-walled cells surrounding the vascular bundles) with adaxial extensions. *Bolboschoenus fluviatilis*: M. Gray 3921 (CANB). Scale = 100 µm.

Plate 17.3: Intervascular translucent tissue (the cells barely visible) breaks down to form air cavities. Parenchymatous bundle sheath (large colourless cells) complete, without extensions. *Eleogiton fluitans*: M. Evans 2778 (CANB). Scale = 100 µm.

Plate 17.4: Abaxial epidermal cell outer walls thin. Stomata raised. Subsidiaries smaller than the adjacent epidermal cells. Mesophyll air cavities present. Parenchymatous bundle sheath complete (despite the inclusion of some cap fibres in the vascular bundle − right), adaxial extensions present. Sclerenchyma not in contact with all of the vascular bundles. *Cyperus tenellus*: J.J. Bruhl 301 (CANB). Scale = 200 µm.

Plate 17.5: Subsidiaries larger than the adjacent epidermal cells, ‘vertical-rectangular’ to lacrymose. *Blysmopsis rufra*: F.A. Stafleu 338 (NSW). Scale = 50 µm.

Plate 17.6: Epidermis papillose. Stomata sunken, obscured by projections from the adjacent epidermal cells. Translucent tissue absent. Sclerenchyma including a girder (lower right) and caps (abaxial to the small bundle and adaxial to the large bundle). Spongy (upper) and palisade (lower) mesophyll present. *Chorizandra cymbaria*: S.M. Prober 243 (CANB). Scale = 50 µm.

Plate 17.7: The stoma raised, not obscured. Subsidiaries much smaller than the adjacent epidermal cells, square. *Acriulus greigiiifolius*: R.W. Haines 129 (K). Scale = 50 µm.

Plate 17.8: Vascular bundle sheaths (primary bundles) three. Parenchymatous bundle sheath only adjacent a metaxylem vessel (arrows). The mestome sheath (between the parenchymatous bundle sheath and the metaxylem vessels) thick-walled and non-chlorenchymatous. The boundary layer cells ‘large’, chlorenchymatous (dark-staining) and interrupted by metaxylem. Sclerenchyma not in direct contact with the vascular bundles. ‘Maximum cells-distant’ count one. *Cyperus laevigatus*: J.J. Bruhl 65 (CANB). Scale = 50 µm.
Plate 18


Plate 18.3: Trans-section ‘thickly crescentiform’. Hypodermis adaxially ‘complete’ (i.e. the central portion). Vascular bundles ‘inverted’. Mesomelaena tetragona: E. Bailey (CANB 63655). Scale = 1 mm.


Plate 18.5: Multilayered hypodermis adaxially ‘complete’. Note that the translucent tissue (asterisks) is adaxial to the vascular bundles and contiguous with, but distinct from the hypodermis. Cyathocoma (Macrochaetium hexandrum): S. Garside 10 October 1920 (K). Scale = 200 µm.


Plate 18.8: Midrib (lower left) with a secondary bundle (arrow) abaxial to the primary bundle, anatomically symmetrical. Parenchymatous bundle sheaths absent. Sclerenchyma not in contact with the vascular bundles. Abaxial epidermal cell outer walls moderately thickened to thin. Stomata flush to raised. Kyllinga polyphylla: D.P. Darmawardhana 25 (CANB). Scale = 100 µm.
Plate 19


Plate 19.1: Major lateral rib (right) of a ‘flanged V-shaped’ leaf. Bulliform cells abaxially, only over the main lateral vein (arrow), and covering the adaxial surface. *Bisboeckelera microcephala*: J. Florschuetz 1819 (U). Scale = 200 µm.

Plate 19.2: Trans-section ‘thickly crescentiform’. Translucent tissue more or less adaxial to vascular bundles, breaks down to form air cavities. *Blysmopsis rufra*: F.A. Stafleu 338 (NSW). Scale = 200 µm.


Plate 20.1: Lateral portion of lamina. Hypodermis abaxially ‘complete’, particularly well developed in association with the primary vascular bundles (there are a number of small secondary bundles close to the adaxial surface between the primaries) but otherwise patchy. Bulliform cells present. Translucent tissue present, aerenchymatous, more or less abaxial to the vascular bundles. Torulinium odoratum: P.J. Darbyshire 708 (CANB). Scale = 200 µm.


Plate 20.3: Midrib (lower right) and lateral portion of lamina. Hypodermis abaxially ‘complete’, though not apparent in the vicinity of the midrib. Hypodermal cells distinctly larger than the adjacent epidermal cells (the epidermals barely visible). Bulliform cells adaxially, median only. Vascular bundles ‘zig-zagged’. Cephalocarpus rigidus: B. Maguire 32831 (U). Scale = 200 µm.


Plate 20.5: Midrib (lower right) and portion of lamina. Mesophyll air cavities absent. Vascular bundles in one row. Parenchymatous bundle sheaths interrupted by fibres. Exocarya sclerioides: S.M. Prober 346 (CANB). Scale = 200 µm.

Plate 20.6: Midrib region. Stoma (lower left) raised. Midrib without a secondary bundle abaxial to the primary bundle, anatomically symmetrical. ‘Maximum cells-distant count’ more than one. Exocarya sclerioides: S.M. Prober 346 (CANB). Scale = 100 µm.

Plate 20.7: Midrib region. Hypodermis adaxially median only, multitiered. Hypodermal cells distinctly larger than the adjacent epidermal cells. Bulliforms absent (the large colourless cells all belong to the hypodermis). The midrib markedly asymmetrical. Cladium procerum: M.D. Crisp 6878 (CBG). Scale = 200 µm.

Plate 20.8: Midrib portion of lamina. Leaf blade with a markedly keeled midrib. Hypodermis adaxially median only. Hypodermal cells not larger than the adjacent epidermal cells. Midrib anatomically symmetrical. Bolboschoenus fluviatilis: M. Gray 3921 (CANB). Scale = 200 µm.

Plate 21.1: Abaxial epidermal cell outer walls moderately thickened. Large lateral metaxylem vessel elements of the primary bundle interrupt the small boundary layer cells. The thick-walled non-chlorenchymatous bundle sheath is contiguous with a cap adaxially (C) and a girder abaxially (cut by the scale). The parenchymatous bundle sheath is interrupted by fibres, and has adaxial and abaxial extensions (asterisks). *Scirpus polystachyus*: M.P. Austin 86 (CANB). Scale = 100 µm.

Plate 21.2: Primary vascular bundle with parenchymatous bundle sheath extensions. The boundary layer cells internal to the thick-walled mestome sheath are generally small relative to the other bundle parenchyma. Note the conical silica bodies in the parenchymatous bundle sheath, with their bases toward the fibre girder (arrow) in addition to the more usual epidermal location (above left end of scale.). *Cladium procerum*: M.D. Crisp 6878 (CBG). Scale = 50 µm.

Plate 21.3: Two multicellular 'spines', basally continuous; the lower broken (asterisk) and the upper complete except for its silica prickle-hair, the location of which is indicated by the arrow. *Reedia spathacea*: B.R. Maslin 1682c (CANB). Scale = 100 µm.

Plate 21.4: Primary vein with adaxial and abaxial girders (G). Luminal conical silica bodies are visible in the epidermis above the girder fibres. The artifactual separation of the adaxial silica body (SI) shows the extent of its ‘organic foot’. *Erioscirpus comosus*: R.C. Singh 189 (NSW). Scale = 50 µm.

Plate 21.5: Primary vein with adaxial and abaxial girders. The ‘non-chlorenchymatous’ parenchymatous bundle sheaths only adjacent metaxylem vessels (arrows). *Sphaerocyperus erinaceus*: H.M. Richards 15066 (K). Scale = 50 µm.

Plate 21.6: Midrib with adaxial bulliform cells (contrast *Gahnia*: Pl. 18.2). Hypodermis adaxial median only. Stoma (lower left) flush. *Morelotia affinis*: G. Bagnall 56270 (NSW). Scale = 100 µm.

Plate 21.7: Silica bodies ‘external’ (i.e. forming cones seated on the epidermis; arrows). Stomata flush (adaxial surface), their subsidiaries lacrymose. Sclerenchyma comprising adaxial and abaxial girders. Parenchymatous bundle sheaths (asterisks) interrupted by fibres. Mestome sheaths ‘non-chlorenchymatous’ (comprising unusually large cells). The boundary layer cells internal to the mestome sheath are relatively large, but ‘non-chlorenchymatous’. Spongy mesophyll present, palisade mesophyll absent. *Schoenoides oligocephalus*: J.J. Bruhl 628 (CANB). Scale = 100 µm.


Plate 22

Plate 22.1-9: Inflorescence and floral morphology.

Plate 22.1: Base of plant showing sessile female basal spikelets (asterisks — marking the site of the fruit). Extremely long styles largely contained by the associated bract (arrows). The fruit are borne just below ground level. *Trianoptiles stipitata*: M. Levyns 7641 (PRE). Scale = 10 mm.

Plate 22.2: Inflorescences restricted to solitary spikelets. These bisexual (anthers and curled style branches of the spikelet, centre right). Floral bracts distichous (to spirodistichous). *Eleocharis caespitosissima*: J.J. Bruhl 356 (CANB). Scale = 5 mm.

Plate 22.3: Base of plant showing subterranean (ground level indicated by dotted line) basal spikelets (arrows) borne on positively geotropic culms. Immature aerial spikelet top left. *Eleocharis caespitosissima*: J.J. Bruhl 356 (CANB). Scale = 10 mm.

Plate 22.4: Androgynous terminal capitate inflorescence (the distal dark region composed of filaments and some anthers). The proximal female-only spikelets are composed of solitary female-only flowers enclosed by perigynia (asterisks). Primary inflorescence bracts scale-like. *Cymophyllus fraseri*: (MEL 1543855). Scale = 10 mm.

Plate 22.5: Pseudoaxillary capitate inflorescence. Primary inflorescence bracts foliose (and culm-like; appearing as a continuation of the culm). Subtending bracts ('blackish') imbricate and enclosing 'synanthena' (not visible, cf. Pl. 22.8). *Lepironia articulata*: J.J. Bruhl 526 (CANB). Scale = 5 mm.

Plate 22.6: Inflorescence primary axis (arrow) elongated. Lateral inflorescence branch (L) elongated. The lateral inflorescence branch base enclosed by the sheathing bases of its subtending bract — removed here (the arrowheads indicate the point of severance) to reveal the epulvinate tubular inflorescence prophyll (P). *Cladium procerum*: M.D. Crisp 6878 (CBG). Scale = 4 mm.

Plate 22.7: Inflorescence 'conipaniculate'. Lateral branch inflorescences 'planipaniculate' (the arrows indicate one such corymbose branch). Primary inflorescence bracts foliose. *Becquerella cymosa* ssp. *cymosa*: R.M. Harley 20171 (K). Scale = 15 mm.

Plate 22.8: A 'synanthena' (centre) showing subtending bracts (S; imbricate but teased apart, cf. Pl. 22.5); two lateral spikelet prophylls (P), each subtending a male-only flower; male-only flowers subtended by floral bracts (F), and terminal gynoecium (G). The male-only flowers (more than three) are represented by solitary stamens (A; i.e. the filaments). Rachilla vestigial. *Thoracostachyum sumatranum*: L.J. Brass 29376 (CANB). Scale = 1 mm.

Plate 22.9: Incomplete inflorescence, after the primary inflorescence bracts have fallen, revealing two lateral spikelet prophylls (cf. Seberg, 1986). *Schoenoides oligocephalus*: A. Mosca! 11881 (HO). Scale = 4 mm.
Plates 23.1-8: Inflorescence and floral morphology.

Plate 23.1: Inflorescence (from above) contracted, capitate, with the sexes mixed. Primary inflorescence bracts foliose, graded in length and tristichous (spirotristichous). *Kyllinga polyphylla*: D.P. Darmawardhana 25 (CANB). Scale = 5 mm.


Plate 23.3: Pendulous proliferous inflorescence, at the ‘apex’ of a culm (C), bearing spikelets (S) with distichous floral bracts, and tristichous vegetative shoots (arrows) with pseudopetioles. The arrows indicate the junction of the lamina and pseudopetiole. *Cyperus gracilis*: J.J. Bruhl 165 (CANB). Scale = 5 mm.


Plate 23.7: Capitate lateral branch inflorescence, showing subtending bracts (arrow) and female-only and male-only spikelets. The smooth, shiny fruits (asterisks) are revealed as a result of damage to their enclosing sac-like floral bracts (cf. Pl. 23.8). *Bisboeckeleria microcephala*: J. Lanjouw 2211 (U). Scale = 2 mm.

Plate 23.8: Three spikelets; a terminal female-only spikelet (F), and two lateral male-only spikelets with their subtending bracts (S). Floral bract of the female-fertile spikelet sac-like, scabrous. The male-only spikelets are lateral to the female-fertile spikelet as indicated by the presence of a prophyll (P2; with two keels barely visible). The prophyll on the same axis as the female-fertile spikelet (P1) is separated from it by the lateral male-only spikelets, subtending bracts and prophylls. *Bisboeckeleria microcephala*: J. Lanjouw 2211 (U). Scale = 1 mm.
Plate 24


Plate 24.1: Female-fertile spikelets. Rachillae persistent, elongated (arrow), wingless, straight. Floral bracts completely deciduous, distichous, similar in length along the spikelet. *Ficinia angustifolia*: E.E. Esterhuysen 90877 (K). Scale = 2 mm.

Plate 24.2: Female-fertile spikelets laterally compressed. Spikelet prophylls (P) longer than the subtending bracts (S), sterile, dorsiventral. Rachillae deciduous, disarticulating above the prophyll. Floral bracts (F) distichous, similar in length along the spikelet. *Queenslandiella hyalina*: A. Bogdan 5353 (K). Scale = 2 mm.

Plate 24.3: Lateral inflorescence branch bases enclosed by sheathing base of bract (asterisk). Style base (arrow) sharply differentiated from fruit apex, persistent, indumented. Leaf blades pilose. *Cephalocarpus rigidus*: J.A. Steyermark 109441 (U). Scale = 3 mm.


Plate 24.5: Inflorescence prophyll (P) proximal to a female-fertile spikelet, bearing a single female-only flower (centre right), and a male-only spikelet (centre left). Rachilla of female-fertile spikelet of definite growth. Floral bracts distichous. Perianth (arrow) ‘cupular’. Fruit apex beakless. *Scleria boivinii*: F.R. Irvine 5056 (K). Scale = 2 mm.

Plate 24.6: Two spikelets. Rachilla (arrow) contracted, of definite growth, persistent, wingless, straight, floral bracts completely deciduous. The sterile and fertile rachilla internodes more or less equal in length. Floral bracts (lower right) distichous, decreasing in absolute length acropetally, acute. *Costularia leucocarpa*: J. Bossa 7773 (K). Scale = 2 mm.


Plate 24.8: Two female-fertile spikelets. Rachillae contracted, persistent, straight. The sterile and fertile rachilla internodes more or less equal in length. Floral bracts incompletely deciduous (arrowheads), glabrous. Two of the floral bracts have not yet fallen; the upper large and fertile, the lower small and sterile. Fruit beakless. *Trachystylis stradbrokensis*: S.T. Blake 22673 (BRI). Scale = 1 mm.

Plate 25


Plate 25.1: Two incomplete female-fertile spikelets. Spikelet prophyll (P) bract-like, epulvinate, membranous, dorsiventral to the subtending bract (SB). Rachillae (RA) elongated, persistent, with wings (RW) adjacent to the flowers. The fertile internodes ‘straight’. Floral bracts open, deciduous, distichous, similar in absolute length acropetally. Each flower enclosed by its subtending floral bract. *Cyperus papyrus*: S.T. Blake 19195 (BRI). Scale = 1 mm.

Plate 25.2: Female-fertile spikelets. Rachis (lower left) not ‘widened’. Spikelets linear. Spikelet prophylls (P) dorsiventral, longer than the subtending bracts (SB), subtending bisexual flowers (the style apparent at the apex of the prophyll), epulvinate. *Dulichium arundinaceum*: L.B. Smith 25 August 1946 (K). Scale = 3 mm.


Plate 25.4: Two incomplete laterally compressed female-fertile spikelets. Rachillae elongated, with wings adjacent to the flowers (asterisk, and base of white arrow). The fertile rachilla internodes ‘straight’. Floral bracts open, distichous, incompletely deciduous (arrows), membranous. *Pycreus albomarginatus*: S.T. Blake 17575 (CANB). Scale = 1 mm.

Plate 25.5: Part of a lateral branch inflorescence with female-only flowers. Female-fertile spikelets more or less terete. Floral bracts tristichous, similar in length acropetally, ‘aristate’ (arrows), at least some with markedly recurved tips. *Lagenocarpus verticillatus*: J.A. Steyermark 89702 (BRI). Scale = 1 mm.

Plate 25.6: Floral bracts incompletely deciduous (arrowhead). Style-base sharply differentiated from the fruit apex, enlarged-pyramidal, persistent, papillose. Fruit ‘rugose’. *Rhynchospora rugosa*: E.P. Heringer 6294 (K). Scale = 1 mm.

Plate 25.7: Subtending bract (SB) and spikelet prophyll (P) of a female-fertile spikelet (Pl. 25.8). Spikelet prophyll sterile, bract-like, epulvinate, hyaline. *Ascopholis gamblei*: B.H.M. Nijalingapp 20 August 1975 (NSW). Scale = 1 mm.

Plate 25.8: Rachilla vestigial, of definite growth, deciduous. Floral bract pouch-like (the extent of the fused bract indicated by the arrow), persistent. *Ascopholis gamblei*: B.H.M. Nijalingapp 20 August 1975 (NSW). Scale = 1 mm.
Plate 26


Plate 26.1: Female-only spikelets and subtending bracts (S). Spikelet prophylls (P) subtending female flowers, tubular (the splitting of the upper and lower prophylls is an artifact), constituting perigynia. Rachillae (R) greatly exceeding the flowers, distally hooked. *Uncinia compacta*: C. Totterdell 307 (CANB). Scale = 2 mm.

Plate 26.2: Sagittal section of a perigynium showing the fruit of the subtended female flower. The rachilla is vestigial and disarticulates below the prophyll. Floral bracts absent. Style base continuous with the fruit apex, not enlarged. Fruit beaked. *Vesicarex collumanthus*: A.M. Cleef 5611 (U). Scale = 2 mm.

Plate 26.3: Female-only spikelets. Spikelet prophylls (P) shorter that the subtending bracts (S). Spikelet prophylls constituting perigynia. Rachillae (not visible) disarticulating below the prophylls. *Carex fascicularis*: J.J. Bruhl 12 (CANB). Scale = 2 mm.

Plate 26.4: Female-fertile spikelet (centre left) androgynous. Spikelet prophyll (P) equalling the subtending bract (S) in length. Rachilla (R) with an extremely long internode between the female (arrow) and a putatively male-fertile floral bract (F). Style base sharply differentiated from the fruit apex (arrow). Stigmata three. *Schoenoxiphium lanceum*: Ecklon 851 (MEL). Scale = 2 mm.

Plate 26.5: Sagittal section of a spikelet. The fertile rachilla internode thick and corno (R), encloses the dark linear fruit, and bears a distal floral bract (arrow). *Remirea maritima*: M. Lazarides 563 (CANB). Scale = 1 mm.


Plate 26.7: Sac-like, scabrous floral bract. Note the orifice (arrow) though which the style emerged. Stigmata two. *Calyptrocarya glomerulata*: T.P. Harris 438 (K). Scale = 0.5 mm.

Plate 26.8: Floral bracts pouch-like (adaxial view left, abaxial view right; arrow indicates apex of pouch), glabrous, enclosing bisexual flowers (note the two stamens and two stigmata, left). *Ascolepis capensis*: J. Cooper March 1873 (MEL 1543822). Scale = 1 mm.

Plate 26.9: Rachillae elongated, persistent, flexuose. Rachilla internodes of markedly different lengths; fertile elongated (FI), sterile contracted (SI). Each flower (N, nut) enclosed by a distal floral bract (arrows). The fascicled spikelets indicate a ‘prophyllar branching’ pattern. *Schoenus brevifolius*: G. Goodrick 302 (CANB). Scale = 3 mm.
Plates 27.1-7: Floral morphology; 8-9: Pollen.

Plate 27.1: Perianth of six 'scales', persistent on the rachilla, shorter than the fruit. Fruit not compressed. *Oreobolus oxycarpus*: D.A. Ratkowsky 1 February 1974 (HO). Scale = 1 mm.

Plate 27.2: Perianth of indumented 'scales'. *Fuirena umbellata*: J.J. Bruhl 214 (CANB). Scale = 0.2 mm.

Plate 27.3: Perianth of many 'bristles'. Perianth members deciduous from the rachilla with the fruit, much exceeding the fruit. Fruit obovate. *Eriophoropsis virginica*: L. Griscom 10 September 1916 (NSW). Scale = 0.5 mm.

Plate 27.4: Perianth of three indumented 'scales'. Note the fused bases of the plumose antrorse indumentum components, which form the scale in view (cf. Pl. 27.5). Fruit lanceolate. *Colechloa setifera*: K.J. Bloem 135 (PRE). Scale = 1 mm.

Plate 27.5: Perianth of three indumented 'scales' (one arrowed; the absence of the perianth from the right fruit is an artifact of damage). Perianth members pilose, the hairs antrorse. Fruit not compressed, beaked, scabrous (at least distally). *Everardia montana* ssp. *duidae*: J.A. Steyermark 93322 (K). Scale = 1 mm.

Plate 27.6: Perianth of three glabrous, more or less vestigial 'scales' (arrow). Fruit stalked, not compressed. *Lagenocarpus verticillatus*: J.A. Steyermark 89702 (BRI). Scale = 0.5 mm.

Plate 27.7: Perianth of three tridentate indumented 'scales'. Perianth barbate (distally) to plumose (proximally). Style-base indumented, sharply differentiated from the fruit apex, persistent. Fruit triangular in trans-section. *Trianoptiles stipitata*: E. Esterhuysen 34682 (PRE). Scale = 2 mm.


Plate 27.9: A multi-aperture pollen grain. Five apertures are visible in this plane of focus; four apertures indicated by arrows, and one apparent as a black line across the centre of the grain. *Tricostularia paludosa*: N.T. Burbidge 4 April, 1948 (CANB). Scale = 50 µm.

Plate 28.1: Base of male-only flower; two bristles (B), and three adhering stamens (one marked with an asterisk). The anthers sterile proximally (arrows), as distinct from the filaments (F). *Syntrinema brasiliense*: Luetzelburg 1223 (M). Scale = 0.5 mm.

Plate 28.2: Apex of a female-fertile flower; two filaments (F) and style (S). The style merely notched. Stigmatic surface glabrous. *Syntrinema brasiliense*: Luetzelburg 1223 (M). Scale = 0.5 mm.

Plate 28.3: Obovate fruit with enlarged style-base (SB) sharply differentiated from the fruit apex. Perianth of bristles (B) proximal to the filament (F). Perianth members persistent at the base of the fruit, barbate, the barbs antorse. *Rhynchospora cyperoides*: Eggers July 1881 (BRI). Scale = 1 mm.


Plate 28.5: Beaked and stalked fruit, circular in trans-section. *Paramapania simplex*: L.J. Brass 13481 (BRI). Scale = 2 mm.

Plate 28.6: Perianth of barbate ‘bristles’ (B), persistent at the base of the fruit. Perianth members much exceeding the fruit. The floral bracts (FB) inconsistently fall with the encased fruit. Style-base (SB) sharply differentiated from the fruit apex, enlarged-pyramidal, persistent. Fruit papillose, laterally compressed. *Rhynchospora wightiana*: J.J. Bruhl 404 (CANB). Scale = 3 mm.

Plate 28.7: Unisexual spikelets. Stigmatic surface papillose (S), the papillae ‘long’. *Scleria levis*: J.J. Bruhl 522 (CANB). Scale = 4 mm.

Plate 28.8: Unisexual spikelets. Female-fertile spikelet with mucronate floral bracts, decreasing in length acropetally. Fruit (G) beakless. *Scleria levis*: J.J. Bruhl 522 (CANB). Scale = 2 mm.

Plate 28.9: Perianth of ‘bristles’ (B). Style-base (SB) sharply differentiated from the fruit apex, enlarged, persistent. Fruit ‘rugose’. *Costularia brevicaulis*: L.E. Moss 7612 (K). Scale = 0.5 mm.
Plate 29

Plates 29.1-9: Androecium.


Plate 29.5: Base of anther showing poorly developed ‘basal appendages’. *Tricostularia undulatum*: J.J. Bruhl 325 (CANB). Scale = 100 µm.

Plate 29.6: Junction between apex of filament and base of anther indicated by arrowhead. Anther sterile proximally (i.e. from the arrow to the arrowhead). *Rhynchospora rubra*: J.J. Bruhl 573 (CANB). Scale = 200 µm.

Plate 29.7: Stamens adhering to the floral bracts (F) and the fruit by attachment of the staminal filaments; i.e. the fruit suspended by the filaments. *Morelotia gahniiformis*: St. John 26779 (NSW). Scale = 3 mm.

Plate 29.8: Anthers apiculate and with basal appendages. The ‘basal appendages’ forming prominent spongy lobes; these probably acting as buoys in the water, with the pollen held above water level. *Egleria fluctuans*: A. Ducke 20 July 1912 (BRI). Scale = 0.5 mm.

Plate 29.9: Spiralled endothecial thickening; best seen where the thickening stretched (arrow). *Vesicarel collumanthus*: A.M. Cleef 5611 (U). Scale = 50 µm.
Plate 30

Plates 30.1-9: Floral morphology; gynoecium.

Plate 30.1: Hypogynium present above the stamens (arrows indicate the base of the filaments; arrowheads indicate the apex of the hypogynium). Style-base ‘flattened’ (i.e. pronouncedly angular), sharply differentiated from the fruit apex, enlarged-pyramidal, deciduous. Actinoschoenus filiformis: P.K. Latz 7764 (CANB). Scale = 1 mm.

Plate 30.2: The spikelet prophyll, a perigynium (P) opened to reveal the gynoecium (centre) and rachilla (in a different plane of focus, arrow). Stigmata three, stigmatic surface papillose. Style-base terete, sharply differentiated from the fruit apex, enlarged-pyramidal, persistent. Uncinia tenella: N.T. Burbidge 2998 (CANB). Scale = 0.5 mm.


Plate 30.4: Aborted gynoecium with perianth of bristles (B). Style-base (S) sharply differentiated from the fruit apex (arrow), enlarged-bulbous, persistent. Eleocharis geniculata: J.J. Bruhl 317 (CANB). Scale = 200 µm.

Plate 30.5: Aborted gynoecium, with perianth of bristles (B; not to be confused with filaments, F). Style-base (S) sharply differentiated from the fruit apex (arrow), enlarged-pyramidal, persistent. Gymnoschoenus sphaerocephalus: J.J. Bruhl 635 (CANB). Scale = 200 µm.

Plate 30.6: Bisexual flower. Three stamens (at base) spread apart to reveal hypogynium (dark region proximal to the ovary, apex indicated by arrowhead). Style-base sharply differentiated from the fruit apex (arrow), enlarged-pyramidal. Two stigmata. Fimbristylis sp.: J.J. Bruhl 494 (CANB). Scale = 200 µm.

Plate 30.7: Style divided for about half its length, glabrous. Style-base continuous with the fruit apex (but with an abscission zone, arrowhead). Stigmatic surface glabrous (the irregularities due to pollen grains). Cyperus tenuispica: D.P. Darmawardhana 12 (CANB). Scale = 200 µm.


Plate 31


Plate 31.1: Rachis (R) with female-fertile spikelets (FF). Spikelet prophylls (P) dorsiventral to the subtending bracts (S), adaxially pulvinate (arrows). *Mariscus lucidus*: M. Gray 3914 (CANB). Scale = 4 mm.


Plate 31.3: Sagittal section of fruit showing internal transverse angular furrows. The mesocarp (MC) is thick and fibrous, and endocarp (EC) membranous. Endosperm (EN) shrunken (an artifact of drying) accentuating the space (top) between the testa and pericarp. *Gahnia sieberiana*: (CANB 22768). Scale = 1 mm.

Plate 31.4: Fruit (N) with filament (F) and turgid hypogynium (HY). *Ficinia angustifolia*: E.E. Esterhuysen 90877 (K). Scale = 1 mm.

Plate 31.5: Beaked, obovate fruit with perianth of ‘bristles’ (arrows). Beak apiculate (A), ‘rugose’ (characteristic of markedly longitudinally elongated epidermal cells). *Schoenoplectus dissachanthus*: R. Perry 242 (CANB). Scale = 1 mm.


Plate 31.7: Markedly elongated filaments (F) and a suspended fruit. Style ‘flattened’, winged, glabrous (WS). Style-base sharply differentiated from the fruit apex (arrows), enlarged, persistent. *Androtrichum trigynum*: Rosengurttx B3904 (U). Scale = 1 mm.


Plate 31.9: Base of fruit (ST) with fungal infection (Fl). Hyphae (arrows) may be mistaken for indumentum (cf. Clarke 1908 Tab. 110.9-10). *Gymnoschoenus sphaerocephalus*: J.J. Bruhl 635 (CANB). Scale = 200 µm.
Plates 32. 1-3: Fruit anatomy. 4-8: Embryo morphology; whole mounts.

Plate 32.1: Transverse section of fruit (stained with Melzer’s reagent). Epidermis (EP) constitutes the epicarp. Pericarp vascular bundle (V1) located in the fibrous mesocarp. Endocarp (EC) composed of thin-walled cells elongated in the transverse plane. Testa vascular bundle (V2). The contents of the outer layer of the endosperm (asterisk) are non-staining, the remainder (EN) is heavily stained, indicating amyloids. *Mariscus scaber*: J.J. Bruhl 497 (CANB). Scale = 50 µm.

Plate 32.2: Transverse section of fruit (stained with Melzer’s reagent). The papillate epidermis constitutes the epicarp. Pericarp vascular bundle (V) located in the fibrous mesocarp. Endocarp (asterisk) composed of thin-walled cells elongated in the transverse plane. *Hellmuthia membranacea*: T. Arnold 705 (PRE). Scale = 200 µm.

Plate 32.3: Transverse section of fruit (stained with Melzer’s reagent). Epidermis composed of darker-staining cells constitutes the epicarp (EP). The pericarp vascular bundle (V) located in the parenchymatous mesocarp (the air-liquid interfaces appear black). The endocarp (EC) is composed of sclereids. The testa (T) is contiguous with the endosperm (asterisk). *Thoracostachyum sumatranum*: P. van Royen 4065 (CANB). Scale = 200 µm.


Plate 32.5: Basal view (high focus). Cotyledon (CO) markedly widened. Germination pore (arrow; at a lower plane of focus cf. Pl. 32.6) perpendicular to the first embryonic leaf primordium (asterisk, L1). *Fuirena incrassata*: J.J. Bruhl 445 (CANB). Scale = 50 µm.


Plate 32.7: Optical sagittal section (vertical axis inclined left to right). Embryo turbinate. Cotyledon not markedly widened. Coleoptile (right) and coleorhiza (CR) basal. First embryonic leaf primordium (asterisk) present. *Bulbostylis barbata*: D.P. Darmawardhana 7 (CANB). Scale = 100 µm.

Plate 33

Plates 33.1-9: Embryo morphology; whole mounts.


Plate 33.4: Optical sagittal section (vertical axis in line with left arrow). Coleoptile basal. Coleorhiza (CR) subbasal. First leaf primordium present (L1). *Carpha nivicola*: J.J. Bruhl 143 (CANB). Scale = 200 µm.


Plate 33.7: Optical sagittal section (enlargement of part of Pl. 32.4). First embryonic leaf primordium (L1) well developed and exerted beyond the germination pore (GP). Second embryonic leaf primordium present (small arrows). Embryo ‘constriction’ present above the coleorhiza (large arrow). *Eleocharis caespitosissima*: J.J. Bruhl 356 (CANB). Scale = 100 µm.


Chapter 4

A Comparative Developmental Study of Some Taxonomically Critical Floral/Inflorescence Features in Cyperaceae

Abstract

Morphology at different developmental stages was investigated by dissection and by SEM in five sedges: *Eleocharis* (3 species) and *Schoenoplectus* (both Cyperoideae, Scirpeae), and *Lepidosperma* (Caricoideae, Schoeneae). In each case all the perianth segments (scales or bristles) were positioned outside the staminal primordia or stamens, consistent with classical interpretations of flowers. Putative exceptions and previous alternative interpretations of floral morphology in the Cyperaceae are discussed. SEM developmental studies of the Hypolytreae are needed for further clarification of interpretative floral/inflorescence morphology in the family.

Introduction

Controversial questions of inflorescence and floral morphology are of considerable taxonomic interest in the Cyperaceae, because alternative interpretations have led to different classificatory solutions. For example, Schultze-Motel (1964) and Kern (1974) interpreted the 'flowers' as synanthia and therefore included the Hypolytreae in the same subfamily as the Cypereae; by contrast Koyama (1961, 1971), accepted them as conventional flowers, and so separated these two tribes at subfamily level. Three monotypic tribes, viz. Dulichieae (Schultze-Motel 1959b), Syntrinieae and Micropapyreae (Eiten 1976b), were established to cope with seemingly aberrant floral morphologies. At the heart of the problem is the fact that the basic question, "What is a flower?", poses peculiar difficulties in this group. Advocates of the euanthium theory (e.g. Pfeiffer 1927; Hutchinson 1934, 1973; Kubitzki 1966; Shah 1967; Dahlgren and Rasmussen 1983; Dahlgren et al. 1985; Seberg 1986, 1988a-b) accept the trimerous floral arrangement within the spikelets of the Cyperaceae, exemplified by *Schoenoplectus*, as collectively representing a conventional flower: i.e. with a gynoecium surrounded by anthers, and often these in turn surrounded by a 'perianth' of bristles or scales. On the other hand, Mattfeld (1935, 1938), Holttum (1948), Schultze-Motel (1959, 1971), Kern (1962, 1974), and Clifford (1987) interpret such a 'hermaphrodite flower' as a "pseudanthium" (or "synanthium"): i.e. a composite floral
structure, representing or derived from a number of 'flowers'. A third interpretation by Meeuse (1975), Meert and Goetghebeur (1979), and Goetghebeur (1985, 1986), derives the 'hermaphrodite flower' or "anthoid" from a "gonoclad" comprising a number of "monandra" (meromonandrial glumellae each subtending a meromonandrial anther, i.e. a stamen plus a bract) and a central "monogyna" (or female). The difference between the pseudanthial and anthoid interpretations reflects different theories regarding the origins of the angiosperm flower, but in practice seems to be largely semantic. Both seek to derive hermaphrodite flowers in the Cyperaceae from the floral units of the Hypolytreae (sensu Chapter 9 = Mapanioideae of Goetghebeur 1986; termed 'the mapanioids' in the present discussion).

Seberg (1988a p. 130 and 1988b pp. 187-188) stated that the conflicting arguments in favour of the pseudanthial and anthoid theories are all "vague" or "aprioristic" and "eclectic", and "largely unfounded". Goetghebeur (1986), however, presented numerous floral diagrams which portray stamens on the same level as or even outside some of the scales or bristles, consistent with the pseudanthial/anthoid interpretations he favours. These are reminiscent of Clarke's (1909) diagrams, but the latter clearly favoured a pentacyclic interpretation of cyperaceous flowers.

Esau (1965 p. 567) advocated comparative developmental studies of dissected material to understand floral development, and Barnard (1957 p. 117, and Plate 1 Figs 4.1-3) studied the floral development in *Schoenoplectus validus* via light microscopy. However, the latter's comments on and illustrations of the relative position of stamens and bristles are ambiguous, in that he described the inner perianth bristles as arising between stamens, without reference to whether they were on the same level. His illustration of floral primordia (Plate 1, Fig. 1) seems to show the stamens and inner perianth segments on the same level, whilst those of later developmental stages (Plate 1, Figs 4.2-3) show the perianth at a lower level than the stamens. Barnard (1957) concluded that the flowers in *S. validus* are of the "liliaceous type", yet later he reinterpreted this work in support of pseudanthial/anthoid interpretations of such flowers (Barnard 1961) as did Goetghebeur (1986). The SEM studies of *Eleocharis*, *Lepidosperma*, *Schoenoplectus* reported here support the conventional interpretation of the *Schoenoplectus*-type flower, and characters #168-268 (Chapter 3; Appendix 1) have been interpreted accordingly.
Methods and Materials

Plants were sampled directly from the field (Sullivans Creek, Canberra) or from field-collected material grown under natural light in glasshouses. Identities were checked using appropriate literature. Vouchers will be lodged at CANB: *Eleocharis acuta* R. Br., JJB125; *E. dietrichiana* Boeck., JJB303; *E. geniculata* (L.) R. and S., JJB317; *Lepidosperma laterale* R. Br. var. *majus*, JJB516; *Schoenoplectus validus* (Vahl) Löve and Löve, JJB Sullivans Creek (i.e. the same locality as Barnard’s 1957 material).

For the examination of floral development, fresh material was dissected in 50 mM sodium phosphate buffer at pH 7, under a M5 Wild microscope, fixed in 2.5% glutaraldehyde in buffer for 2 h, washed twice in buffer over 1 h, post-fixed in 1% OsO₄ for 2 h at room temperature, washed in water, dehydrated in a graded ethanol series (15%, 30%, 50%, 70%, 90%, 95% twice, 100% twice, for 15 mins each), mounted on a 1:1 mixture of acetate:silver dag on aluminium stubs, coated with 100 Å of gold in a Dynavac 12/14 C evaporative coater, and examined and photographed using a Cambridge Stereoscan 360.

Other specimens (including *Syntrinema brasiliense* Radk. and Pfeiffer: Luetzelburg 1223, M) were examined with a Wild M5 stereo microscope, or with either a Leitz Orthoplan or a Wild M11 compound microscope.

Results

At the primordial (Fig. 4.1A), early pre-anthesis (Fig. 4.1B), late pre-anthesis (Figs 4.2A-D), and mature fruit (Figs 4.1C-D) stages all the ‘flowers’ examined possess ‘perianth’ segments (bristles or scales), androecium and gynoecium in acropetal sequence. In every case, all the perianth segments were observed to be positioned outside the stamina! primordia or stamens, although differences in the levels of insertion sometimes amounted to only a few cells.

In *Schoenoplectus validus* (Figs 4.1A and 4.2C) and *Eleocharis geniculata* (Figs 4.1B and D) the perianth segments are in two ‘whorls’. The inner ‘whorl’ of perianth segments is outside the stamens, and its members alternate with them. The segments of the outer ‘whorl’ alternate with those of the inner whorl, and are opposite the stamens. In *Eleocharis dietrichiana* (Fig. 4.1C), *E. acuta* (Figs 4.2A-B), and *Lepidosperma laterale* (Fig. 4.2D), the perianth segments are proximally connate and apparently
constitute one 'whorl'. Indeed, the micrographs of *E. acuta* (Fig. 4.2A) and *L. laterale* (Fig. 4.2D) show two separate but adjacent segments with common extended basal-tissue, indicating that their late development is from a common meristem.

The flowers and fruits of various other species, examined using stereomicroscopy/light microscopy during the course of a broader study of the Cyperaceae (see Appendix 1), followed the same positional patterns, with the perianth members exterior and proximal to the stamens. This was seen to be the case irrespective of whether the perianth is symmetrical with respect to the gynoecium as in *E. dietrichiana* (Fig. 4.1C), or asymmetrical as in *E. acuta* (Figs 4.2A-B).

**Discussion**

The evidence presented above is consistent with interpreting the floral structures (gynoecium, androecium, and perianth) of these Cyperaceae in accordance with classical ranalean ideas, or with the euanthium theory (cf. Kubitzki 1987; Seberg 1986, 1988a), in so far as the bristles or scales constitute a 'perianth' outside the stamens (by contrast with the floral bracts in the mapanioids, Fig. 4.3A-C). Two perianth whorls usually presented as 3+3 segments (e.g. Clarke 1909: sepal + petal homologues; or Goetghebeur 1986: meramonandrial glumellae) are frequently not apparent. In *Schoenoplectus validus* and *Eleocharis geniculata*, the bristles can reasonably be interpreted as constituting two whorls (Figs 4.1A-B and 4.1D, 2C), but in the other species investigated by scanning electron microscopy (Figs 4.1C, 4.2A-B and 4.2D) there is no alternative to interpreting the perianth segments as a single whorl. The latter arrangement highlights the independence of the perianth from the stamens. By contrast, Barnard (1957 p. 117) stated that in *S. validus* each of the outer perianth members "subtends one of the three stamens". This is correct only in the sense that outer perianth segments are opposite the stamens, but not in the sense of each segment being an organ "whose axil gives rise to a bud" (Jackson 1928 p. 370). Indeed, in *S. validus* where the perianth is two-whorled, the stamens are one whorl removed from the opposing perianth segments, rather than in their axils (Fig. 4.2C).

*Fuirena* (Nees 1835; Kern 1962), *Micropapyrus* and *Syntrinema* (Suessenguth 1943; Eiten 1976a-b) have been claimed as exceptions to the ranalean pattern described above. In each case, the perianth members were said to be internal to the stamens, implying a synanthial origin for their 'flowers' (e.g. Fig. 4.3D). However, Blaser (1941a) and Haines (1966 p. 55) found that the stamens in these species were attached
"at most on a level with the perianth segments and not outside them." Primordial material may be usefully employed to reveal the initial relative position of the stamens and the perianth, and whether any shift in position occurs during development. My own observations on a young flower of *Syntrinema brasiliense* showed the filaments surrounded by the perianth segments in the conventional manner (cf. Goetghebeur 1986). Goetghebeur (1986) suggested that the elevated position of the bristles relative to the stamens in *Micropapyrus viviparoides* is due to the fusion of the bristles with the stalk of the fruit, masking the basal point of attachment of the bristles below the stamens. More collections of these rare sedges are needed to clarify the matter via detailed developmental studies. Meanwhile, the evidence available for these genera is consistent with the conventional interpretation of their floral units as 'flowers' (cf. Chapter 3).

Synanthial and anthoid interpretations of hermaphrodite flowers in sedges are based largely on the complex floral structures of *Scirpodendron* and some of the other mapanioids. A *Scirpodendron* 'spikelet' consists of a terminal female with or without floral bracts (cf. Kern 1962; Goetghebeur 1986), a number of spirally disposed stamens each with its own floral bract, and two further stamens laterally placed and each subtended by a keeled bract (Fig. 4.3A). At the base of other mapanioid 'spikelets' there are also two laterally disposed keeled bracts, or a single dorsiventrally compressed bract-like or tubular organ (Fig. 4.3B-C). These may be fertile, and subtend two laterally disposed stamens, or be sterile. They are generally accepted as being prophylls rather than floral bracts (e.g. Holttum 1948; Haines 1966; Seberg 1986). Meert and Goetghebeur (1979) and Goetghebeur (1986) accept these distinct structures not as prophylls, but as "glumellae", homologous with both the distal non-keeled bracts within mapanioid spikelets, and the perianth segments of other taxa, e.g. of *Schoenoplectus*. Whilst detailed developmental studies of the prophylls in the mapanioids are needed to clarify whether they fundamentally comprise one bract or two, it seems reasonable to regard the mapanioid prophyll as homologous with the spikelet prophylls in other sedges. It is plausible that prophylls of different branching levels are homologous (they constitute the first organ of axes and are morphologically distinct, see also Blaser 1944 and Haines 1967), but it seems unlikely that prophylls are homologous with perianth segments, particularly as the perianth segments surround the anthers, and sometimes constitute a discrete whorl. The lack of homology of the prophylls with perianth members is obvious in *Dulichium* (Fig. 4.3E), where these two very distinct appressed structures belong to different axes. It has conventional *Cyperus*-like spikelets, with a proximal prophyll and distichous floral bracts along an elongated rachilla. The prophyll
is fertile and subtends a bisexual flower with a bristle-like perianth (cf. Eiten 1976a; Goetghebeur 1986). Yet application of the anthoid interpretation here would lead to the conclusion that the prophyll is homologous with the bristles.

The floral units of *Scirpodendron* and other mapanioids, interpreted in the euanthium and synanthial theories as spikelets, are interpreted in the anthoid theory as anthoids, or (more loosely) as ‘flowers’. However, the interposition of bracts between the gynoecium and stamens, and between the stamens themselves (Fig. 4.3A-C), is justification for interpreting these floral units as spikelets (or synanthia) rather than as ‘flowers’. Developmental SEM studies of the floral structures of mapanioids, using fresh material, are needed to corroborate this positional interpretation, which has been based on mature living or herbarium material. The proponents of the synanthial and anthoid theories propose a ‘reduction series’ within the mapanioids from complex floral units in *Scirpodendron* through *Mapania* to other mapanioids, e.g. *Principina* and some *Hypolytrum* species, with an apparently bisexual flower surrounded by only a prophyll (Fig. 4.3C). The synanthial theory applied to the Cyperaceae as a whole is based upon the notion that the mapanioids are ancestral in the family, and that *Scirpodendron* is the ‘archetypal’ sedge (the fact that it inhabits tropical rainforest being cited as ecological evidence of primitivity: e.g. Kern 1962).

Supporters of both the synanthial and the anthoid theories envisage a phylogenetic sequence from *Scirpodendron* and the other mapanioids, through *Schoenoplectus* and its relatives (with hermaphrodite flowers surrounded by a perianth), to *Cyperus* and its relatives (without a perianth). If the *Schoenoplectus* flower represents a highly reduced mapanioid synanthium or spikelet, one might expect the supposedly homologous perianth members to be interposed between the anthers, as Goetghebeur (1986; Fig. 4.3F) so often depicts them. However, the evidence presented above (Figs 4.1A-D and 4.2A-D) shows no support for this. Instead, the perianth members are all outside the anthers.

The occurrence of mapanioids, such as *Principina* and some *Hypolytrum* species, with apparently bisexual flowers subtended by only a prophyll, makes application of the synanthial theory to all hermaphrodite sedges appealing. On the other hand, the perianth in *Schoenoplectus* would then have to represent at least a secondary appearance, and its absence in *Cyperus* at least a secondary loss. Another explanation would be that the mapanioids are part of a different phyletic line from *Schoenoplectus*, *Cyperus* and their relatives, and that the occurrence of seemingly bisexual flowers across the family involves homoplasy. There is evidence to support this from my classificatory analyses (Chapter 9), in that *Principina* and *Hypolytrum* always grouped with *Scirpodendron* and
the other mapanioids (though *Hellmuthia* hardly ever did), and Goetghebeur (1986) recognizes the mapanioids as constituting a distinct subfamily.

If the *Scirpodendron*-type floral structure is ‘primitive’ within the Cyperaceae, one might reasonably expect to see a similar pattern in its sister group, generally accepted to be the Juncaceae (Juget 1972; Savile 1979; Haines and Lye 1983; Dahlgren *et al.* 1985; Goetghebeur 1986; Seberg 1988a). On the contrary, however, the floral units of the Juncaceae are readily and reasonably interpreted as conventional trimerous flowers, typical of monocotyledons in general (Dahlgren *et al.* 1985; see also Kubitzki 1987). Indeed, with notable exceptions (e.g. in Centrolepidaceae) angiosperm floral units in general seem reasonably interpretable as true flowers rather than as anthoids (see Dahlgren 1983; Doyle and Donoghue 1987; Kubitzki 1987).

Application of SEM developmental studies to the mapanioids may help further clarify interpretation of floral morphology in the Cyperaceae. However, to be convincing in these difficult circumstances, it is probable that any solutions derived from comparative morphology will require independent corroboration, for example via vegetative morphology, anatomy, nucleic acid sequencing, etc., and in the light of continuing taxonomic consideration.
Figures 4.1A-D: Scanning electron micrographs illustrating floral development of some sedges (F = filament; G = gynoecium; P = perianth segment; PI = inner perianth segment; PO = outer perianth segment; S = stamen).

Figure 4.1A: *Schoenoplectus validus*: a flower at the primordial stage showing the acropetal position of the two stigmatic branches (G), stamens, and perianth segments (cf. Fig. 4.2C). Scale = 50 µm.

Figure 4.1B: *Eleocharis geniculata*: the base of a flower at early pre-anthesis. Note the position of the perianth segments in inner and outer planes and that they are all external to the stamens (cf. Fig. 4.1D). Scale = 50 µm.

Figure 4.1C: *Eleocharis dietrichiana*: the base of a ‘flower’ at maturity showing the insertion of the staminal filaments between the gynoecium and perianth segments. Note that the perianth segments constitute one ‘whorl’. Scale = 200 µm.

Figure 4.1D: *Eleocharis geniculata*: the base of a ‘flower’ at maturity showing the insertion of the staminal filaments between the gynoecium and perianth segments. Note that the perianth segments constitute two ‘whorls’. Scale = 200 µm.
Figures 4.2A-D: Scanning electron micrographs illustrating floral development of some sedges (G = gynoecium; P = perianth segment; PI = inner perianth segment; PO = outer perianth segment; S = stamen; asterisk = shared base of adjacent perianth segments). Scales = 100 µm.

Figure 4.2A: *Eleocharis acuta*: abaxial view of the base of a flower at late pre-anthesis showing a stamen between the gynoecium and perianth segments. Note the common extended basal-tissue of two of the perianth segments.

Figure 4.2B: *Eleocharis acuta*: adaxial view of the base of a flower from the same individual as in Figure 4.2A at a later pre-anthesis stage showing the asymmetry of the perianth whose segments constitute one 'whorl'. Note that consideration of the relative positions of the floral parts in transverse section at the level marked "G" would lead to the spurious interpretation that the perianth segment is inserted between the gynoecium and stamen.

Figure 4.2C: *Schoenoplectus validus*: the base of a flower at late pre-anthesis showing the perianth segments in two 'whorls', both external to the stamens.

Figure 4.2D: *Lepidosperma laterale*: the base of a flower at late pre-anthesis showing a stamen between the gynoecium and a perianth segment. Note the common extended basal-tissue of two of the perianth segments (asterisk).
Figures 4.3A-F: Floral and spikelet diagrams of some sedges discussed in the text. The dotted lines in Figures 3A, 3C and 3E represent morphological variability. (X = stamens, hollow in 3D; solid triangles = perianth segments; ovals, hollow and hatched triangles = gynoecia; notched bracts, 3A-C, and two keeled bract, 3E = spikelet prophylls). Floral and spikelet axes: top of the page. Not to scale.

Figure 4.3A: *Scirpodendron ghaeri*: spikelet with subtending bract (bottom) and male-fertile spikelet prophylls, and male-only flowers with floral bracts, and central female. (Goetghebeur 1986 p.224 Fig. 8.1.11).

Figure 4.3B: *Mapania paradoxa*: spikelet with three male-only flowers, one with a floral bract, and central female with associated floral bracts. (Goetghebeur 1986 p.252 Fig. 8.1.6B).

Figure 4.3C: *Hypolytrum*: a problematically ‘flower-like’ spikelet. (Goetghebeur 1986 p.238 Fig. 8.1.4A).

Figure 4.3D: *Fuirena*: flower with floral bract. Note that the stamens are portrayed between the two whorls of perianth segments, but see text. (Kern 1962 p.143 Fig. 11).

Figure 4.3E: *Dulichium arundinaceum*: spikelet with subtending bract (bottom) and fertile adaxial spikelet prophyll, flowers with floral bracts, and sterile floral bracts. (Goetghebeur 1986 p.636 Fig. 8.9.1B).

Figure 4.3F: *Hymenochaeta grossa*: flower with floral bract. Note that the stamens are portrayed between the whorls of the perianth segments, but see text. (Goetghebeur 1986 p.358 Fig. 8.4.3B).
Chapter 5

The C₃ and C₄ Photosynthetic Pathways in the Cyperaceae

Abstract

The genera of the Cyperaceae have been surveyed by original observation and from the literature in order to assess the distribution of C₃ and C₄ photosynthetic pathways in the family. 119 of the 122 genera are included in the current sample, with 94 genera (77% of total, and 3369 species 67% of total) assigned as C₃, and 22 genera (18% of total, and 840 or 17% of total) as C₄. The genera Abildgaardia (2 C₃ species/15 C₄ species), Cyperus (subgenus Pycnostachys solidly C₃: 150 species; subgenus Cyperus solidly C₄: 300), Eleocharis (200 C₃ species/4 C₄ species) and Rhynchospora (200 C₃ species/21 C₄ species), are indisputably variable for this trait. Some data suggesting further infrageneric variation in photosynthetic pathways have been discussed. The 'one cell distant criterion' accurately predicts C₄ pathway in sedges, except in Eleocharis. Distribution and variability of photosynthetic pathways in Eleocharis are discussed. The distribution of photosynthetic pathways in relation to a new classification of the Cyperaceae is provided. Photosynthetic pathway is a useful taxonomic marker in the Cyperaceae, despite variability in this trait at all taxonomic levels and the apparently multiple origin of C₄ photosynthesis within the family. A checklist of C₃ and C₄ sedges is presented.

Introduction

Two distinct patterns of vegetative anatomy in sedges have long been recognized (Haberlandt 1884 p.281). One, with "radiate" chlorenchyma and a green sheath situated within the vascular bundles ('Kranz' anatomy), "is seen in certain species of Cyperus" (Haberlandt 1884 p.284). The other, exemplified by Carex and many other Cyperus species, involves non-radiate chlorenchyma and vascular bundles enclosed by a "sheath of large colourless cells". Botanists were quick to incorporate these discontinuities into the taxonomic framework of the Cyperaceae (e.g. "Chlorocyperaceen" and "Eucyperaceen" of Rikli 1895 p.560; see also Clarke 1908). More recent authors (e.g., Druyts-Voets 1970; see also Metcalfe 1971), in extending these anatomical studies and recognizing further variants (e.g. Sharma & Mehra 1972; Carolin et al. 1977; Gilliland
and Gordon-Gray 1978), have extended the taxonomic utility of vegetative anatomy in this family.

Subsequent to the discovery of $C_4$ photosynthesis, the correlations between chlorocyperoid (Kranz) anatomy and $C_4$ photosynthesis, and eucyperoid anatomy and $C_3$ (Calvin cycle) photosynthesis became apparent. Further correlations were detected within the Cyperaceae as with other families, of photosynthetic pathways with characteristic $\delta^{13}C$ value ranges (Bender 1971), with $CO_2$ compensation point values (Krenzer et al. 1975), and with geographical distributions, there being a concentration of $C_4$ sedge species and genera in the tropics and $C_3$ taxa in the temperate regions (Raynal 1972). Use of these correlates, particularly anatomical and $\delta^{13}C$ values, has allowed extensive prediction of $C_3$ and $C_4$ photosynthetic pathways in sedges (see Appendix 2), and has led to a reassessment, along structural/functional and evolutionary lines, of earlier taxonomic decisions based on purely anatomical discontinuities. Thus Raynal (1973) positioned his predominantly $C_4$ Cypereae and Fimbristylideae as terminal assemblages in a scheme of phylogenetic relationships of the Cyperoideae, with the $C_4$ genera uppermost indicating their assumed derived states.

There is need for some caution when using anatomical observations or $\delta^{13}C$ values alone as predictors of photosynthetic pathway, as $C_3$-$C_4$ intermediates may be overlooked (Hattersley 1987). The ‘maximum cells-distant count’ (Hattersley & Watson 1975) has proved to be a very reliable anatomical criterion in relation to grasses (Hattersley 1987). This explicit anatomical criterion for $C_3/C_4$ assignment, though seemingly applicable to sedges (Hattersley et al. 1977), has not previously been tested on them on a large scale. Instead, the relatively vague concepts of ‘radiate’ chlorenchyma and ‘Kranz’ anatomy have continued in use (e.g. Ueno and Koyama 1987; see also Chapter 6).

Cyperaceae have been covered in a number of surveys of photosynthetic pathway variation (e.g. Black 1976 and references therein; Raghavendra & Das 1978; Takeda et al. 1985; see Appendix 2 for more references), and various taxonomic conclusions regarding the family have been drawn (Lerman and Raynal 1972; Raynal 1973; Takeda et al. 1985). Major contributions to $C_3/C_4$ assessments, in terms of the numbers of species and genera sampled, have been made by Lerman and Raynal (1972; see below) and Takeda et al. (1985). A few genera, however, including some which are taxonomically controversial, remain totally unknown in this respect, and there is conflicting information about the photosynthetic pathways of others.

I have set out to obtain additional data, in order to examine critically the levels of correlation between physiological, biochemical and anatomical data pertaining to
photosynthetic pathways, and to fill significant gaps in the taxonomic coverage, to locate new variation within genera, and to identify taxa where C₃-C₄ intermediates may occur. In what follows, those new observations are presented and current knowledge of C₃/C₄ photosynthetic pathway variation in the Cyperaceae is summarized. A microfiche appendix (1) contains the first extensive, up to date compilation of photosynthetic pathway determinations for the Cyperaceae, with sources, and presents, also for the first time the valuable, original raw data of Lerman and Raynal (1972). The compilation is believed to be comprehensive with respect to the physiological and biochemical data. On the other hand, although anatomical evidence has been diligently sought in the literature, this is an operation which could be continued more or less indefinitely, and interpretation of published illustrations, particularly those which predate the discovery of C₄ photosynthesis, is often problematical.

Methods and Materials

Plant material

Plants were grown under half-shade in glasshouses maintained between 35°C (day maximum) and 15°C (night minimum), and regularly fertilized with Ruakura nutrient solution (Smith et al. 1983). Identities were conscientiously checked and vouchers will be lodged at CANB. Where samples were taken from herbarium material, voucher labels were attached to the sheets.

Anatomy and 'one cell distant criterion'

Selection and preparation of plant material were conducted as stated in Bruhl et al. (1987) and Chapters 6 and 7. Hand-cut sections of rehydrated herbarium material or fresh material, temporarily mounted, are generally adequate for ascertaining the maximum cells-distant count and applying the one cell distant criterion. The latter states that "in C₄ species no chlorenchymatous mesophyll cell is separated from the nearest PBS cell by more than one other chlorenchymatous mesophyll cell" (Hattersley and Watson 1975 p.325). In the Cyperaceae, application of this criterion involves counting the numbers of 'primary carbon assimilation' (PCA) cells distant from the PCR cells, ignoring non-PCR mestome sheath cells, parenchymatous bundle sheath (PBS) cells and any non-chlorenchymatous cells.

CO₂ compensation point analyses

A pulse flow system for CO₂ compensation point analysis was employed. Fresh healthy leaves or culms (photosynthetic material only) of glasshouse grown plants were...
placed in a 50 ml clear glass syringe. The syringe was fitted with a needle and the needle tip sealed with a rubber plug. The plunger was made airtight by lubrication with liquid paraffin. The sealed loaded syringe was placed in a growth cabinet under a photosynthetic photon flux density of 500 mmol photon m$^{-2}$s$^{-1}$ at 30°C, and were incubated for at least 20 minutes. A 30 ml gas sample from the syringe was then passed through a calcium chloride H$_2$O trap, to an infrared CO$_2$ gas analyzer (model ZAR, Fuji Electric, Japan). High grade nitrogen, at a flow rate of 4 l min$^{-1}$, was used as a carrier gas. The output from the analyser was recorded on an RDK Rikadenki chart recorder. The system was calibrated with 1, 2, and 3 ml samples of pure CO$_2$ (delivered with an SGE microlitre syringe) equivalent to 33.3, 66.6 and 100 ppm of CO$_2$ in 30 ml volumes respectively. The CO$_2$ concentration of the sample gas was calculated from the peak height of the CO$_2$ pulse. Controls were used to ensure that the sole source of CO$_2$ was that derived from the sample, and constituted the delivery of 30 mls of CO$_2$-free air, which resulted in no pen movement beyond the base line. The $\Gamma$ values presented in Table 5.2 represent means based on four replicates, except for the controls, where there were two replicates.

$\delta^{13}C$ values

For $\delta^{13}C$ value determinations, mature healthy leaf or culm samples from cultivated plants oven-dried at 70°C, or from herbarium specimens, were ground finely in liquid nitrogen with a mortar and pestle, or chopped finely with a razor. Samples of 0.2 to 3 mg were combusted using a modification of the classical Dumar method in a Carlo Erba 1106 Elemental Analyzer. The CO$_2$ produced was trapped automatically at liquid nitrogen temperature, then distilled from the cold finger and passed to a VG Isogas Sira-24 mass spectrometer for analysis. Standards used were the laboratory internal CO$_2$ standard gas and a standardized sucrose calibrated against international carbonate standards. The $^{13}C/^{12}C$ ratios are reported as $\delta^{13}C$ values in $\%$.

Evaluation of literature; nomenclature

Photosynthetic pathway determinations were collated from original publications, rather than from reviews, and anatomical data from publications preceding the discovery of C$_4$ photosynthesis have been used only where they seem to permit unambiguous interpretation. Nomenclature and generic and subgeneric circumscriptions used here correspond with the generic database (Appendix 1; see also Chapters 2 and 9), except for certain taxa provided with separate descriptions in order to allow taxonomic assessment of photosynthetic pathway variants or to cope with morphological variation. Thus, Costularia breviculmis was included in Costularia rather than being treated
separately, and the $C_3$-$C_4$ groups in *Abildgaardia, Eleocharis*, and *Rhynchospora* (including both the rhynchosporoid and chlorocyperoid $C_4$ groups), described separately in Appendix 1, have each been treated as single genera. The subgenera of *Carex* and *Ficinia* have not been employed here, but the subgenera *Pycnostachys* and *Cyperus* of *Cyperus* have been listed separately.

**Results and Discussion**

Appendix 2 shows that of the 122 genera and about 5100 species of Cyperaceae, 98 genera and 585 species have been investigated for photosynthetic pathway physiologically (98 genera/567 species) and/or biochemically (18 genera/59 species). The compilation includes new $\delta^{13}$C value determinations for 16 genera and 33 species (Table 5.1), and new $\Gamma$ values for 7 genera and 20 species (Table 5.2) obtained in this study. The determination of photosynthetic pathways, particularly at the generic level, is very comprehensive for this reasonably large family, and affords a reasonably sound basis from which to generalize about the likelihood of finding further variation, predict the photosynthetic pathway of the unassessed taxa, and discuss taxonomic implications of the available data. All but two genera (*Oreobolopsis* and *Rhynchocladium*) of the Cyperaceae can be assigned to a photosynthetic pathway (Table 5.4) with confidence on the basis of biochemical, physiological, and anatomical evidence (Tables 5.1-3; Chapter 7; Appendices 1 & 2). The present state of knowledge shows *Abildgaardia, Cyperus sens. lat.*, *Eleocharis* and *Rhynchospora* are variable, comprising both $C_3$ and $C_4$ species, while the remaining genera are consistently either $C_3$ or $C_4$.

The total anatomical sample covers all the genera except for two monotypics, *Oreobolopsis* and *Rhynchocladium*. Both are from relatively high altitudes (Koyama 1972, 1978), so they are probably $C_3$ (cf. Körner et al. 1988), but the relevant vegetative anatomy has been described only imprecisely for the former, and not at all for the latter (Koyama 1972, 1978). The anatomical sample is rather patchy at the species level, in that most of the smaller genera, along with some large ones (e.g. *Cyperus* subgenus *Pycnostachys* and *Rhynchospora* subgenus *Haplostylis*) have been thoroughly sampled, while other large genera such as *Lagenocarpus* and *Pleurostachys* have been examined for only one or two species. Nonetheless, the samples compare favourably with those

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1. *Koyamaea* (Thomas and Davidse 1989) is not included in the discussion or the counts, as it has only very recently been described. It is $C_3$. 
of many other micromorphological or anatomical features. For example, recent taxonomic treatments of the Cyperaceae have placed a great deal of reliance on embryo morphology (see Raynal 1973; Goetghebeur 1986), where the available data are less comprehensive.

'One cell distant criterion'

Cross-referencing between the different kinds of evidence presented in Appendix 2 shows excellent correspondence, and that all the photosynthetic pathways are correctly predicted using anatomical criteria, the few conflicting data are considered below. The data tabulated in Appendix 2 allow evaluation of the 'maximum cells-distant count' as a predictor of photosynthetic pathway in the Cyperaceae. Of the 113 genera and 243 species investigated anatomically for this criterion by me, 78 genera and 132 species have also been analysed for their δ13C values, 12 genera and 28 species for Γ, and eight genera and 33 species for both δ13C value and Γ. The photosynthetic pathway of 15 of the genera including 32 species has been determined biochemically. Congruence of the data shows, with the exception of Eleocharis, that the 'one cell distant criterion' (Hattersley & Watson 1975) is an accurate predictor of C4 in the Cyperaceae, while counts of greater than one accurately predict C3 (Appendix 2; see also Appendix 1). Given the simplicity and ease with which anatomical preparations can be made to determine photosynthetic pathway type, it is reasonable to suggest that such determinations should accompany the descriptions of new species and genera as a matter of routine.

In Eleocharis, the unequivocally C4 taxa (Tables 5.1-2; Bruhl et al. 1987) yield counts of one to four (i.e. often exceeding a count of one, even if the chlorophyllous layer of cells adjacent to the mestome sheath is considered to constitute a PBS and ignored, see Chapter 6). However, the chloroplast abundance in the PCA (C4 mesophyll) cells is relatively low and the more distant cells are equivocally chlorophyllous. Even where the criterion can be applied with confidence, the PBS may be chlorophyllous or more-or-less non-chlorophyllous (e.g. in Fimbristylis), with variation apparent within and between species. The stoichiometric and physiological significance of such variation is not clear, and warrants further investigation.

The C4 Eleocharis species are NAD-ME type, the only occurrence of this biochemical type in the Cyperaceae, and so variation in biochemical type coincides with breakdown of the C4 anatomical predictor; whereas C4 sedges are generally NADP-ME (Ueno et al. 1986; Bruhl et al. 1987; Chapter 6). The breakdown does not seriously impair use of the 'one cell distant' criterion in predicting photosynthetic pathway,
because of the apparent rarity of the NAD-ME type in this family. Although C_4
Eleocharis species would be incorrectly assigned to photosynthetic pathway using this
criterion, they are accurately predicted by ultrastructural features (see Chapter 7).

Conflicts in the data

Conflicting reports exist regarding the photosynthetic pathway status of Cyperus
papyrus (Table 5.3), with both C_3 and C_4 determinations obtained from more than one
labatory. My own anatomical observations on one accession support the C_4 status of
this species (Appendix 1-2), in agreement with Lerman and Raynal (Appendix 2) and
Jones and Milburn (1987), and I wonder whether the C_3 determinations were made on
the morphologically similar Cyperus alternifolius.

Similarly conflicting data have been presented in the literature for Cyperus
eragrostis (Cyperus subgenus Pycnostachys; Table 5.3; note that the C_4 values were
obtained from one laboratory). I therefore included C. eragrostis in my analyses, and
sampled one Australian and two New Zealand accessions, paying careful attention to
the identity of the material. All three proved to be C_3, with C_3 anatomy (Appendix 1),
very low or undetectable levels of C_4 acid decarboxylating enzymes (Chapter 6; Bruhl
et al. 1987) and with Γ (Table 5.2) and δ^{13}C values (Table 5.1) typical of C_3 species. It
seems more likely, therefore, that C. eragrostis is C_3.

In a further five cases of intra-specific and/or intra-generic variation in
photosynthetic pathway, it is also likely that the atypical report is erroneous. Saxena
and Ramakrishnan (1984) reported Pycreus globosus as anatomically C_3. By contrast,
all other evidence (including ultrastructural, physiological, biochemical, and further
anatomical characteristics) reported for this species (Table 5.3), and the genus in general
(Appendix 2), indicate C_4. The C_4 record for Cyperus pulchellus of Lerman and Raynal
(Appendix 2) is at odds with C_3 δ^{13}C values obtained for this species by Hesla et al.
(1982) and Takeda et al. (1985), and with all other data for the subgenus (see also Haines
and Lye 1983). Smith and Epstein’s (1971) C_4 δ^{13}C value for an unnamed Carex species
is at variance with all other available data for that genus, including one biochemically
typed species, δ^{13}C value determinations for 34 species, and Γ values for seven species.
Variation in photosynthetic pathway has also been reported for Scleria lithosperma
(Table 5.3), but "these discrepancies ... may have resulted from identificatory error of
plant materials" (Takeda et al. 1985 p.405) with regard to the C_4 values. Another twenty-
three species of Scleria appear in the literature as C_3 (Appendix 2), and my anatomical
observations (Appendix 1) and Γ values (Table 5.2) for Scleria also support the
contention that the genus is wholly C_3. Also Hofstra et al.’s (1972) listing of
Schoenoplectus (Scirpus) lateriflorus as C₄ based on C₄ anatomy and a low \( \Gamma \) value conflicts with other observations for this species (Table 5.3), and for the genus as a whole. My anatomical observations do not indicate even remotely C₄-like anatomy for S. lateriflorus. The \( \Gamma \) values presented by Takeda et al. (1980) for 17 Rhynchospora species include values that are higher than classic C₄ values (for species with rhynchosporoid anatomy, e.g. R. rubra: 10 µl l\(^{-1}\)), and that are lower than typical C₃ values (e.g. R. rugosa ssp. brownii: 32 µl l\(^{-1}\)). Such values are usually indicative of C₃-C₄ intermediates (cf. Hattersley et al. 1986; Table 5.2: cf. Eleocharis pusilla). Indeed the two values fall outside the range of values they obtained for control species: i.e. "less than 10 µl l\(^{-1}\) (for C₄ species) and ... more than 40 µl l\(^{-1}\) for C₃ species, though they did not query these results. More recent anatomical and biochemical investigations of R. rubra have, however, corroborated its C₄ status (Ueno et al. 1987; Bruhl et al. 1987).

The \(^{13}\)C values (Table 5.1), and C₄ anatomy (Appendix 1) for Rhynchospora armerioides and R. barbata (Table 5.1) confirm that Rhynchospora species with chlorocyperoid anatomy are also consistently C₄, as Ueno and Koyama (1987) initially reported (see also Chapter 6, Appendix 1).

Import of photosynthetic pathways on taxonomic problems

Two contrasting and independent examples indicate the value of photosynthetic pathway data in solving and posing taxonomic problems. Firstly, the monotypic Syntrinema is variously recognized, largely on the basis of floral morphology, as belonging to Rhynchospora (Ballard 1934; Goetghebeur 1986) or as a genus belonging to a separate tribe (Eiten 1976b). It is C₄ (Table 5.1; Appendix 1), and its vegetative anatomy (Ueno and Koyama 1987; Chapter 6) is typical of the C₄ Rhynchospora species with rhynchosporoid anatomy (Chapter 6). Rhynchosporoid anatomy is found only in these two genera, and therefore strongly supports the former taxonomic affiliation.

Secondly, Abildgaardia and Fimbristylis, two closely related and often synonymized genera (see Chapter 3), have previously been considered to be exclusively C₄ (cf. Table 5.3 & Appendix 2). Indeed, Raynal (1973) and Goetghebeur (1986) place these genera in a tribe in part characterized by C₄ photosynthesis and fimbristyloid anatomy (see Chapter 6). Anatomical observations (Appendix 1) and \(^{13}\)C value data (Table 5.1), however, indicate that Abildgaardia hygrophila and A. variegata, are C₃. Furthermore, Gordon-Gray’s (1971 p.562) observations for A. variegata (under Fimbristylis; "even the smaller bundles of the outer ring lie, not within the mesophyll but merely in contact with its inner margin ... The mesophyll in this species is especially well organized, the cells being palisade- like"), considered in retrospect, also hint at C₃
anatomy. Metcalfe's (1971 p.276) description of the chlorenchyma in A. hygrophila (also treated under Fimbristylis; "up to 6 layers of palisade cells") clearly indicates C\textsubscript{3} anatomy. Photosynthetic pathway and vegetative anatomy are valuable in substantiating a relatively close relationship between Syntrinema and Rhynchospora. Photosynthetic pathway is clearly a valuable taxonomic criterion (as seen by its consistency within most genera), but the Abildgaardia example illustrates the need for caution when generalizing from small samples of species.

Eleocharis

Rikli's (1895) "Chlorocyperaceen" genera have generally been found to be C\textsubscript{4} (Lerman and Raynal 1972: Ascolepis, Cyperus subgenus Cyperus, Fimbristylis, Hemicarpha, Kyllinga, Lipocarpha, and Monandrus). Rikli’s (1895) suggested division of Eleocharis (as Heleocharis) into two genera, Eleocharis with 'eucyperoid' anatomy, and Chlorocharis with 'chlorocyperoid' anatomy (i.e. with an inner chlorophyllous parenchyma sheath, or boundary layer cells; Table 5.5) seemed to be misleading in the context of photosynthetic pathways, in that subsequent literature on Eleocharis anatomy and photosynthetic pathway indicated a solidly C\textsubscript{3} genus (Table 5.3), i.e. including some of his "Chlorocharis" species (Table 5.5).

More recently it has been shown that at least some Eleocharis species (including one "Chlorocharis" species) are C\textsubscript{4} (Bruhl et al. 1987; Tables 5.1-2, see also Chapter 7; Ueno et al. 1988). Of Rikli’s (1895) "Chlorocharis" (Table 5.5), terrestrial forms of Eleocharis vivipara have recently been found to be C\textsubscript{4} (and NAD-ME; Ueno et al. 1988; cf. Bruhl et al. 1987). $\delta^{13}$C values for E. palustris, and E. tuberculosa, however, are typical of C\textsubscript{3} species (Appendix 2). Rikli (1895) listed five other species with only an "inner parenchymatous sheath" (i.e. possessing prominent chlorophyllous border parenchyma), implying that a typical PBS is absent, but, one of these, Eleocharis geniculata, has been examined in the present study, and it possesses an obvious 'non-chlorenchymatous' C\textsubscript{3}-like PBS outside the mestome sheath (Appendix 1; see also Chapter 6); $\delta^{13}$C and $\Gamma$ values (Tables 5.1-3), and biochemical assays (Bruhl et al. 1987) all confirm its C\textsubscript{3} status. This is despite the border parenchyma cells being somewhat more prominent and chlorophyllous than in most other C\textsubscript{3} species (cf. Chapter 7).

The essentially terrestrial species E. filiculmis, E. pellucida and E. quinquangularis have yet to be re-examined critically. They are members of the series Sulcatae and Multicaules (with spirally disposed bracts; Svenson 1939; Table 5.5), and are not closely related to the C\textsubscript{4} species which constitute part of the series Tenuissimae possessing distichous floral bracts (Svenson 1937). These three species therefore will probably
prove to be $C_3$. Only *E. tuberculosa* and *E. vivipara* were assigned to series *Tenuissimae* by Svenson (1937); the former appears to be $C_3$ (Table 5.3), while the dimorphic *E. vivipara* can be $C_4$. Ueno *et al.* (1988) provided convincing evidence in the form of $\delta^{13}C$ values, pulse-chase experiments and $C_4$ acid decarboxylation enzyme assays that the terrestrial form of *E. vivipara* is $C_4$ and the submerged aquatic form is $C_3$. Whilst they state that the anatomy changes (in subsequent growth) upon submersion of the terrestrial form from $C_4$ to $C_3$, and vise versa, their illustrations of these anatomical differences are inadequate for thorough evaluation, and they have not shown that an individual of the species is biochemically or physiologically variable. Nonetheless, the apparent intraspecific variability of photosynthetic pathways in *E. vivipara* (Ueno *et al.* 1988) is interesting in the context of the mechanism of development of $C_4$ photosynthesis. The variability correlates with the breakdown in the ‘one cell distant criterion’ amongst the previously known $C_4$ sedges (see above; Bruhl *et al.* 1987) and this suggests that these variabilities may have a common basis; both the $C_4$ form of *E. vivipara* and the apparently consistently $C_4$ *Eleocharis* species are NAD-ME type and members of series *Tenuissimae*. Their findings further highlight *Eleocharis* in general and specifically series *Tenuissimae* (particularly *E. vivipara*, as singularly appropriate species to study the evolution and expression of the $C_4$ syndrome. Such studies could be extended to grow the essentially submerged aquatic, and broadly related monotypes, *Egleria* and *Websteria* under terrestrial conditions to test the stability of their $C_3$ status (Appendix 2).

*Eleocharis* is home to further photosynthetic pathway variation. On the basis of intermediate anatomy (Chapter 7), low or undetectable $C_4$ enzyme values (Bruhl *et al.* 1987), $C_3$ $\delta^{13}C$ values (Table 5.1) and intermediate $\Gamma$ values (Table 5.2), supported by some ultrastructural evidence (Chapter 7), *E. pusilla* is interpretable as a $C_3$-like $C_3$-$C_4$ intermediate. A more thorough examination of Rikli’s (1895) ‘*Chlorocharis*’ and an extended survey may reveal more $C_3$-like $C_3$-$C_4$ intermediates, additional to *E. pusilla*, and further $C_4$ species. The known $C_4$ *Eleocharis* species share combinations of attributes including diminutive habit, distichous floral bracts, cancellate fruit, proliferating inflorescences, and amphicarpy. The search for new $C_4$ *Eleocharis* species might most profitably focus on species sharing these features, such as *E. brainnii*, *E. minima*, and *E. subfoliata*. 
Conclusions

The taxonomic sample for photosynthetic pathways in the Cyperaceae in general is particularly broad, with only a few outstanding gaps represented by some recently described monotypics and some large genera which remain poorly sampled. On the other hand, more biochemical typing is necessary across the family, particularly with regard to C₄ anatomical variation in *Rhynchospora* and *Eleocharis*. The most promising and interesting area for discovery of further C₄ species or further intrageneric variation is the predominantly C₃ Scirpeae, within and around *Eleocharis*. Information on photosynthetic pathway variation, especially with regard to anatomical aspects, has had a significant impact on taxonomy particularly at the species and generic levels (see Raynal 1973; Haines and Lye 1983). The taxonomic distribution of C₃ and C₄ types and of the photosynthetic pathway related anatomical suites of characters among the C₄ species at suprageneric level (Table 5.6) suggests multiple origins for them (i.e. for the biochemical types and the associated character suites) within the family (Chapter 6). The helophytic habit of many C₄ sedges, particularly the C₄ *Eleocharis* species, offers an attractive model to investigate the functional significance of C₄ photosynthesis in terms of nitrogen-use efficiency (rather than in terms of the traditional, but seemingly inappropriate, hypothesis which relates C₄ photosynthesis to water-use efficiency). Future investigations of the mechanisms of C₄ photosynthesis regulation in sedges should also address questions of particular agronomic interest (e.g. control of the "world's most troublesome weeds" Willis 1987, the C₄ *Cyperus rotundus* and *C. esculentus*) as well as broaching fundamental questions of differentiation and development.
Table 5.1. New $\delta^{13}$C values for Cyperaceae
PP = photosynthetic pathway implied from these values, (C$_3$) = C$_3$-C$_4$ intermediate deduced from other evidence. Taxa and vouchers cross-reference with Appendix 1.

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<th>$\delta^{13}$C value</th>
<th>PP</th>
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<td>-10.0</td>
<td>C$_4$</td>
</tr>
<tr>
<td>R. barbata</td>
<td>King</td>
<td>-10.4</td>
<td>C$_4$</td>
</tr>
<tr>
<td>R. barbata</td>
<td>King</td>
<td>-10.8</td>
<td>C$_4$</td>
</tr>
<tr>
<td>R. cephalantha var. pleiocephala</td>
<td>Smith</td>
<td>-26.5</td>
<td>C$_3$</td>
</tr>
<tr>
<td>R. cephalotes</td>
<td>McKee</td>
<td>-26.9</td>
<td>C$_3$</td>
</tr>
<tr>
<td>R. cephalotes</td>
<td>McKee</td>
<td>-27.5</td>
<td>C$_3$</td>
</tr>
<tr>
<td>R. cyperoides</td>
<td>Eggers</td>
<td>-25.5</td>
<td>C$_4$</td>
</tr>
<tr>
<td>R. longibracteata</td>
<td>McKee</td>
<td>-24.0</td>
<td>C$_3$</td>
</tr>
<tr>
<td>R. setifera</td>
<td>Montes 1173(NSW)</td>
<td>-27.6</td>
<td>C$_3$</td>
</tr>
<tr>
<td>R. setifera</td>
<td>Montes 1173(NSW)</td>
<td>-27.8</td>
<td>C$_3$</td>
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<tr>
<td>Rhychospora sp.</td>
<td>McKee</td>
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<td>C$_3$</td>
</tr>
<tr>
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<td>McKee</td>
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<td>C$_3$</td>
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<td>Smook</td>
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<td>C$_3$</td>
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<td>Syntrinema brasiliense</td>
<td>Loetzellburg</td>
<td>-10.0</td>
<td>C$_4$</td>
</tr>
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<td>Trachystylis stradbrokensis</td>
<td>Clarkson</td>
<td>-29.8</td>
<td>C$_3$</td>
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Table 5.2. New CO$_2$ Compensation Point Analyses of Sedges

$\Gamma =$ CO$_2$ compensation point in ppm, SE = standard error, PP = photosynthetic pathway implied from these values, C$_3$/C$_4$ = C$_3$/C$_4$ intermediate, * = no voucher. Taxa and vouchers cross-reference with Appendix 1.

<table>
<thead>
<tr>
<th>Species</th>
<th>Voucher</th>
<th>$\Gamma$</th>
<th>±SE</th>
<th>PP</th>
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<tr>
<td><em>C. eragrostis</em></td>
<td>JJB658</td>
<td>42</td>
<td>0.3</td>
<td>C$_3$</td>
</tr>
<tr>
<td><em>C. eragrostis</em></td>
<td>JJB658</td>
<td>46</td>
<td>0.5</td>
<td>C$_3$</td>
</tr>
<tr>
<td><em>C. gracilis</em></td>
<td>JJB519</td>
<td>40</td>
<td>0.9</td>
<td>C$_3$</td>
</tr>
<tr>
<td><em>Cyperus</em> subgen. <em>Cyperus</em></td>
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</tr>
<tr>
<td><em>C. rotundus</em></td>
<td>*</td>
<td>0</td>
<td>0.0</td>
<td>C$_4$</td>
</tr>
<tr>
<td><em>Eleocharis</em></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><em>E. acuta</em></td>
<td>JJB74</td>
<td>44</td>
<td>1.8</td>
<td>C$_3$</td>
</tr>
<tr>
<td><em>E. acuta</em></td>
<td>JJB33</td>
<td>47</td>
<td>1.5</td>
<td>C$_3$</td>
</tr>
<tr>
<td><em>E. acuta</em></td>
<td>JJB125</td>
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<tr>
<td><em>E. caespitosissima</em></td>
<td>JJB375</td>
<td>1</td>
<td>0.1</td>
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<tr>
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<td>JJB375</td>
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<tr>
<td><em>E. dulcis</em></td>
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<td>49</td>
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<tr>
<td><em>E. geniculata</em></td>
<td>JJB231</td>
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<td>C$_3$</td>
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<tr>
<td><em>E. minuta</em></td>
<td>JJB201</td>
<td>47</td>
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<tr>
<td><em>E. ochrostachys</em></td>
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<td><em>E. pallerens</em></td>
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<td>2.0</td>
<td>C$_3$</td>
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<tr>
<td><em>E. pusilla</em></td>
<td>JJB179</td>
<td>29</td>
<td>1.3</td>
<td>C$_3$/C$_4$</td>
</tr>
<tr>
<td><em>E. pusilla</em></td>
<td>JJB682</td>
<td>31</td>
<td>1.2</td>
<td>C$_3$/C$_4$</td>
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<tr>
<td><em>E. pusilla</em></td>
<td>JJB682</td>
<td>30</td>
<td>0.0</td>
<td>C$_3$/C$_4$</td>
</tr>
<tr>
<td><em>E. pusilla</em></td>
<td>JJB682</td>
<td>29</td>
<td>1.0</td>
<td>C$_3$/C$_4$</td>
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<td><em>E. sphacelata</em></td>
<td>JJB124</td>
<td>42</td>
<td>1.3</td>
<td>C$_3$</td>
</tr>
<tr>
<td><em>E. sphacelata</em></td>
<td>JJB579</td>
<td>51</td>
<td>1.6</td>
<td>C$_3$</td>
</tr>
<tr>
<td><em>E. tetraquetra</em></td>
<td>JJB672</td>
<td>41</td>
<td>2.0</td>
<td>C$_3$</td>
</tr>
<tr>
<td><em>Fuirena</em></td>
<td></td>
<td></td>
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<tr>
<td><em>F. umbellata</em></td>
<td>JJB214</td>
<td>43</td>
<td>1.2</td>
<td>C$_3$</td>
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<tr>
<td><em>Rhynchospora</em></td>
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<tr>
<td><em>R. corymbosa</em></td>
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<tr>
<td><em>R. wightiana</em></td>
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<td>C$_4$</td>
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<tr>
<td><em>Schoenoplectus</em></td>
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<tr>
<td><em>S. littoralis</em></td>
<td>JJB538</td>
<td>46</td>
<td>0.6</td>
<td>C$_3$</td>
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<tr>
<td><em>Isolepis</em></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><em>Isolepis prolifera</em></td>
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<tr>
<td><em>Scleria</em></td>
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<tr>
<td><em>S. ciliaris</em></td>
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<td>1.6</td>
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<tr>
<td><em>S. ciliaris</em></td>
<td>JJB505</td>
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<td>C$_3$</td>
</tr>
<tr>
<td><em>S. levis</em></td>
<td>JJB227</td>
<td>45</td>
<td>2.0</td>
<td>C$_3$</td>
</tr>
</tbody>
</table>

Controls: *Arachis hypogaea* 52 ±0.3, *Triticum aestivum* 51 ±1.5
Table 5.3. Conflicting Photosynthetic Pathway Determinations in the Cyperaceae

For each taxon, where multiple photosynthetic pathway determinations on different specimens have been listed in publications, the determinations are listed as separate entries. **A** = anatomy, (A) = anatomy deduced from literature, **B** = biochemistry, **Γ** = carbon dioxide compensation point (µl/l CO₂ or ppm), **H** = high Γ (40-52 ppm), **L** = low Γ (0-1 ppm), δ¹³C = δ¹³C values in %oo, **NADP** = NADP-ME, and **PHOS** = sugar phosphates as the initial products of photosynthesis, and **US** = ultrastructure. Generic concepts follow Chapter 9; where combinations are not available species have been listed under an appropriate synonym. "(Lerman and Raynal 1972)" refers to raw unpublished data which are referred to, in particular, in Lerman and Raynal (1972, see also Raynal 1973). "Bruhl" refers to unpublished data from the present study. See text for discussion.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Type</th>
<th>Method</th>
<th>Data</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. bildegardia ovata</em></td>
<td>C₄</td>
<td>δ¹³C</td>
<td>-11.3</td>
<td>(Lerman and Raynal 1972)</td>
</tr>
<tr>
<td><em>A. ovata</em></td>
<td>C₄</td>
<td>US</td>
<td>-11.8</td>
<td>Caroline et al. 1977</td>
</tr>
<tr>
<td><em>A. ovata</em></td>
<td>C₄</td>
<td>δ¹³C</td>
<td>-12.0</td>
<td>(Lerman and Raynal 1972)</td>
</tr>
<tr>
<td><em>A. triflora</em></td>
<td>C₄</td>
<td>δ¹³C</td>
<td>-12.6</td>
<td>Hesla et al. 1982</td>
</tr>
<tr>
<td><em>Fimbristylis monostachya</em></td>
<td>C₄</td>
<td>A/Γ</td>
<td>0</td>
<td>Raghavendra and Das 1976</td>
</tr>
<tr>
<td><em>F. macrantha</em></td>
<td>C₄</td>
<td>A</td>
<td></td>
<td>Takeda et al. 1985</td>
</tr>
<tr>
<td><em>F. oxytaxis</em></td>
<td>C₄</td>
<td>A</td>
<td></td>
<td>Takeda et al. 1985</td>
</tr>
<tr>
<td><em>Cyperus subg. Pycnostachys</em></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>C. eragrostis</em></td>
<td>C₄</td>
<td>Γ</td>
<td>L</td>
<td>Downton and Tregunna 1968</td>
</tr>
<tr>
<td><em>C. eragrostis</em></td>
<td>C₃</td>
<td>δ¹³C</td>
<td>-27.6</td>
<td>(Lerman and Raynal 1972)</td>
</tr>
<tr>
<td><em>C. eragrostis</em></td>
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<td>δ¹³C</td>
<td>-26.8</td>
<td>(Lerman and Raynal 1972)</td>
</tr>
<tr>
<td><em>C. eragrostis</em></td>
<td>C₃</td>
<td>δ¹³C</td>
<td>-12.8</td>
<td>Troughton et al. 1974</td>
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<tr>
<td><em>E. acicularis</em></td>
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<td>A</td>
<td>&gt;50</td>
<td>Haberlandt 1884</td>
</tr>
<tr>
<td><em>E. acutangula</em></td>
<td>C₃</td>
<td>A</td>
<td></td>
<td>Moss et al. 1969</td>
</tr>
<tr>
<td><em>E. acutangula</em></td>
<td>C₃</td>
<td>A</td>
<td></td>
<td>Druyts-Voets 1970</td>
</tr>
<tr>
<td><em>E. acutangula</em></td>
<td>C₃</td>
<td>A/Γ</td>
<td>5</td>
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<tr>
<td><em>E. brassii</em></td>
<td>C₃</td>
<td>A</td>
<td></td>
<td>(Lerman and Raynal 1972)</td>
</tr>
<tr>
<td><em>E. dulcis</em></td>
<td>C₃</td>
<td>A</td>
<td></td>
<td>Hesla et al. 1982</td>
</tr>
<tr>
<td><em>E. euvirgata</em></td>
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<td>A</td>
<td></td>
<td>Takeda et al. 1985</td>
</tr>
<tr>
<td><em>E. euvirgata</em></td>
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<td>A</td>
<td></td>
<td>Hesla et al. 1982</td>
</tr>
<tr>
<td><em>E. interstincta</em></td>
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<td>A</td>
<td></td>
<td>Takeda et al. 1985</td>
</tr>
<tr>
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<td>A</td>
<td></td>
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</tr>
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<td>A</td>
<td></td>
<td>Hesla et al. 1982</td>
</tr>
<tr>
<td><em>E. mucronata</em></td>
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<td>A</td>
<td></td>
<td>(Lerman and Raynal 1972)</td>
</tr>
<tr>
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<td>C₃</td>
<td>A</td>
<td></td>
<td>Hesla et al. 1982</td>
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Table 5.3. (continued)

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<th>Source</th>
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<td>Takeda et al. 1985</td>
</tr>
<tr>
<td>E. palustris</td>
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<td>(Lerman and Raynal 1972)</td>
</tr>
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<td>(Lerman and Raynal 1972)</td>
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<td>26.1</td>
<td>Bender 1971</td>
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<tr>
<td>E. sphacelata</td>
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<td>A/δ13C</td>
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<td>Takeda et al. 1985</td>
</tr>
<tr>
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<td>P. globosus</td>
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<td>NADP</td>
<td>Ueno et al. 1986</td>
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<td>P. globosus</td>
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<td>A/T</td>
<td>L</td>
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<td>A</td>
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<td>A/δ13C</td>
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Table 5.4. Summary of the distribution of the C<sub>3</sub> and C<sub>4</sub> photosynthetic pathway types in the genera of the Cyperaceae from the data in Appendix 2
Total numbers of species per genus in parentheses. Genera variable for photosynthetic pathway are underlined, and some subgenera are included. For comments on circumscription of the taxa, see Chapter 2.

<table>
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<tr>
<th>C&lt;sub&gt;3&lt;/sub&gt; Genera</th>
<th>C&lt;sub&gt;4&lt;/sub&gt; Genera</th>
<th>Unassigned Genera (see text)</th>
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<tbody>
<tr>
<td>Abildgaardia (2), Acriulus (1), Actinoschoenus (3), Afrotrilepis (2), Androtrichum (1), Anosporum (3), Arthrostyles (1), Baethryon (10), Baumea (30), Becquerelia (5), Bisboecklera (4), Blysmopsis (1), Blysmus (3), Bolboschoenus (16), Calyptrocarya (6), Capitularina (1), Carex subgen. (2000), Carpha (13), Caustis (10), Cephalocarpus (5), Chorizandra (4), Chrysitrix (4), Cladium (4), Coleochloa (7), Costularia (13), Courtoisina (2), Cyathochaeta (3), Cyathocoma (3), Cymophyllus (1), Cyprus subgen. Pycnostachys (150), Desmoschoenus (1), Didymandra (1), Diplocarpum (7), Diplasia (1), Dulichium (1), Egleria (1), Eleocharis (200), Eleogiton (5), Epischoenus (10), Eriophoropsis (1), Eriophorum (20), Eriocircus (2), Evandra (2), Everardia (15), Exocarya (1), Exochogyne (1), Ficinia (61), Fuirena (40), Gahnia (30), Gymnoschoenus (2), Hellmuthia (1), Hyponechaeta (1), Hypolytrum (50), Isoeleocharis (60), Kobresia (40), Kyllingiella (5), Lagencarpus (70), Lepidosperma (50), Lepironia (1), Lophoschoenus (8), Machaerina (15), Mapania (80), Mapaniopsis (2), Mesomelaena (5), Microdracoides (1), Micropapyrus (1), Morelotia (2), Neesenbeckia (1), Oreobolus (14), Oxyccymum (1), Paramapania (7), Phyllosticrpus (5), Pleurostachys (50), Principina (1), Pseudoschoenus (1), Pitlanthelium (1), Reedia (1), Rhynchosporia (200), Schoenoplectus (50), Schoenoxiphium (12), Schonoides (1), Schoenus (100), Scirpocharpa (22), Mariscus (200), Monandra (5), Nemum (10), Nelmesia (1), Pycreus (100), Queenslandiella (1), Remirea (1), Rhynchospora (21), Rikiella (4), Sphaerocyperus (1), Syntrinema (1), Torulinium (6), Tylocarya (1), Volkia (1).</td>
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| Oreobolopsis (1), Rhynchocladium (1). |

Oreobolopsis (1), Rhynchocladium (1).
Table 5.5. *Eleocharis* listed by Rikli (1895) as "Chlorocharis"
"Inner parenchymatous sheath" = prominent border parenchyma cells,
"Outer parenchymatous sheath" = parenchymatous bundle sheath. Series
according to Svenson (1929, 1937, 1939).

<table>
<thead>
<tr>
<th>Anatomical type/Species</th>
<th>Series</th>
</tr>
</thead>
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<td>&quot;Only inner parenchymatous sheath&quot;</td>
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</tr>
<tr>
<td><em>E. filiculmis</em></td>
<td><em>Sulcatae</em></td>
</tr>
<tr>
<td>(as <em>C. balansaeana</em>)</td>
<td></td>
</tr>
<tr>
<td><em>E. quinquangularis</em></td>
<td><em>Sulcatae</em></td>
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<tr>
<td>(as <em>C. emarginata</em>)</td>
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<tr>
<td><em>E. geniculata</em></td>
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<tr>
<td>(as <em>C. capitata</em> and <em>E. geniculata</em>)</td>
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<tr>
<td><em>E. pellucida</em></td>
<td><em>Multicaules</em></td>
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<tr>
<td>(as <em>C. subprolifera</em>)</td>
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<tr>
<td>&quot;Inner and outer parenchymatous sheath&quot;</td>
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<td><em>Pulustriformes</em></td>
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<tr>
<td><em>E. tuberculosa</em></td>
<td><em>Tenuissimae</em></td>
</tr>
<tr>
<td><em>E. vivipara</em></td>
<td><em>Tenuissimae</em></td>
</tr>
</tbody>
</table>

* Originally described by Svenson (1937) under "miscellaneous species of North America and the West Indies"
Table 5.6. Distribution of the C\textsubscript{3} and C\textsubscript{4} photosynthetic pathway types in relation to the proposed classification of the Cyperaceae

Genera with solid underlining are C\textsubscript{4}, genera variable for photosynthetic pathway are broken-underlined, genera not underlined are C\textsubscript{3}. For discussion of classification see Chapter 9.

**CYPEROIDEAE C\textsubscript{3} + C\textsubscript{4}**

*Cyperae C\textsubscript{3} + C\textsubscript{4}*

- Alnula, Ascolepis, Ascolophis, Courtoisina, Cyperus subgen. Pycnostachys, Cyperus subgen. Cyperus, Hemicarpha, Kyllinga, Lipocarpha, Mariscus, Monandrus, Pycreus, Queenslandiella, Remirea, Rikiella, Sphaerocyperus, Torulinium, Volkiella

**Scirpeae C\textsubscript{3} + C\textsubscript{4}**


**Abildgaardieae C\textsubscript{3} + C\textsubscript{4}**

- Abildgaardia, Bulbostylis, Crosslandia, Fimbristyris, Nemum, Nelmesia, Tylocarya

**Arthrostyleae C\textsubscript{3}**

- Actinoschoenus, Arthrostyleis, Trachystylis, Trichoschoenus

**CARICOIDEAE C\textsubscript{3} + C\textsubscript{4}**

*Rhynchosporeae C\textsubscript{3} + C\textsubscript{4}*

- Micropapyrus, Pleurostachys, Rhynchospora, Sytrinema

**Schoeneae C\textsubscript{3}**

- Baumea, Carpha, Caustis, Cladium, Costularia, Cyathochaeta, Cyathocoma, Epischoenus, Evandra, Gahnia, Gymnoschoenus, Lepidosperma, Lophoschoenus, Machaerina, Mesomelaena, Morelothia, Neesenbeckia, Oreobolus, Pttilanthelium, Reedia, Rhynchocladium*, Schoenoides, Schoenus, Tetraria, Tetrapiropsis, Trianoptiles, Tricostularia

**Cryptangieae C\textsubscript{3}**

- Cephalocarpus, Didymiandrum, Everardia, Exochogyne, Lagenocarpus

**Trilepideae C\textsubscript{3}**

- Afrotrilepis, Coleochloa, Microdracoides, Trilepis

**Cariceae C\textsubscript{3}**


**Sclerieae C\textsubscript{3}**

- Acriurus, Scleria

**Bisboeckelereae C\textsubscript{3}**

- Becquerelia, Bisboecklera, Calyptocarya, Diplacrum

**Hypolytreae C\textsubscript{3}**

- Capitularina, Chorisandra, Chrysix, Dinapia, Exocarya, Hellmuthia, Hypolytrum, Lepironia, Mapania, Mapaniopsis, Paramapania, Principina, Scirpodendron, Thoracostachyum

* presumed photosynthetic pathway, see text for discussion.
Chapter 6

Photosynthetic Pathways in the Cyperaceae: C4-Types, Anatomy and Biochemistry

Abstract

Activities of the C4 acid decarboxylation enzymes (NAD-malic enzyme, NADP-malic enzyme and phosphoenolpyruvate carboxykinase), and the anatomy of photosynthetic organs (leaves, culms, bracts) were investigated in 30 species from 12 C3, C4, and mixed (C3+C4) genera of sedges. The sample incorporated representatives of the three previously known C4 anatomical types in the family (fimbristyloid, chlorocyperoid, and rhynchosporoid), and of six genera previously uninvestigated biochemically, including Eleocharis (six species). Eleocharis is variable for photosynthetic pathway: three species proved to be C3, two C4 (E. caespitosissima and E. retroflexa), and one (E. pusilla) may be a C3-C4 intermediate. The C4 Eleocharis species exhibit a C4 anatomy ('eleocharoid') hitherto undescribed, and are NAD-ME type, by contrast with species of the other three C4 anatomical types examined in this and previous studies, which are all NADP-ME type. The PCK type remains unknown in the family. Anatomical anomalies and application to sedges of C4-type predictors useful for grasses are discussed.

Introduction

The existence of both C3 and C4 species within the Cyperaceae has been known since soon after the discovery of C4 photosynthesis itself (Johnson and Hatch 1968). A recent survey of photosynthetic pathway variation in the family (Appendix 2) shows 718 species to have been examined anatomically, 508 for δ13C value, and 58 for CO2 compensation point (T) value (see also Hofstra et al. 1972; Carolin et al. 1977; Takeda et al. 1980, 1985; Hesla et al. 1982). Anatomical variation among C4 sedges is also well known in terms of suites of features comprising the so-called 'fimbristyloid' and 'chlorocyperoid' types (e.g. Raynal 1973; Brown 1975; Takeda et al. 1985; Fig. 6.1) and the more recently discovered 'rhynchosporoid' type (Takeda et al. 1980; Fig. 6.1).

These C4 anatomical variations in the Cyperaceae have not been matched with discovery of variation in C4 acid decarboxylation enzymes (viz. NADP-malic enzyme, NAD-malic enzyme, or PEP carboxykinase type), by contrast with the situation in
Poaceae (e.g. Gutierrez et al. 1974; Hatch et al. 1975; and references in Hattersley 1987; but see Ohsugi and Murata 1980, 1981; Prendergast et al. 1986, 1987). Indeed, application to sedges of the kind of reasoning applied by Brown (1975) to grass bundle sheath configurations would point to all C₄ sedges being of the NADP-ME type; and all the information available up to now has been consistent with this expectation. Johnson and Hatch (1968) showed malate to be a major initial product of photosynthetic ¹⁴CO₂ fixation in Cyperus rotundus, Mariscus bowmannii (as C. bowmannii), Kyllinga brevifolia (as K. monocephala), and Pycreus polystachyos (as C. polystachyos), as had Jones et al. (1981) for C. longus; and Chen et al. (1974) found C. rotundus to be NADP-ME type. Recently Ueno et al. (1986) found 26 other C₄ sedges to be biochemically NADP-ME type (ten with fimbristyloid, 15 with chlorocyperoid, and one with rhynchosporoid type C₄ anatomy), and supposed all C₄ sedges to be NADP-ME type.

Here, Eleocharis (previously thought to be exclusively C₃; see Chapter 7) is shown to contain C₄ species characterized by a fourth type of C₄ anatomy, and that they are not NADP-ME type but NAD-ME. Some anatomical peculiarities of C₄ sedges revealed here are discussed in relation to the application of C₄-type predictors employed for the Poaceae.

Materials and Methods

Plants were grown from field collected material or seed, under half shade in glasshouses maintained between 35°C (day maximum) and 15°C (night minimum), and regularly fertilized with Ruakura nutrient solution (Smith et al. 1983). Identities of both original accessions and experimental plants were checked using appropriate floras and keys. Vouchers will be lodged at CANB.

Fresh material of photosynthetic organs (leaves and/or culms and/or inflorescence bracts) was hand-sectioned and temporary or semi-permanent mounts were examined with a Leitz Orthoplan compound microscope using bright field illumination or polarized light. Material of six species was also prepared as for electron microscopy (Fig. 6.1), prior to sectioning at 1-2 µm with glass knives, staining with 0.05% Toluidine Blue O in acetate buffer (Feder and O’Brien 1968), and photomicrography using a Leitz Orthomat system. To reduce starch content of the chloroplasts, material was first placed in the dark for 22 h (at 20°C). Tissue was fixed as described by Hattersley and Perry (1984), dehydrated in acetone and embedded in LR White (London Resin Company). Enzyme assays were performed as described by Prendergast et al. (1986), except that
the pH of the extraction buffer was 7.5. These procedures are based on the methods of Hatch (1973) and Hatch and Mau (1977a) (PCK), and Edwards et al. (1982), Hatch et al. (1982), and Ku et al. (1983) (NADP-ME and NAD-ME), with the PCK assay further modified by using 0.5 mM MnCl₂ instead of 2 mM, and 0.3 mM oxaloacetic acid instead of 0.6 mM. Chlorophyll determination followed Arnon (1949). Assays for species were done on single accessions, except as shown in Table 6.1. Extracts from four control species (NADP-ME, NAD-ME, PCK, and C₃ types) were assayed in each experiment. NADP-ME controls: Hyparrhenia hirta (11.28 µmol mg⁻¹ Chl min⁻¹) in the first experiment, and newly typed NADP-ME sedges in subsequent assays; NAD-ME controls: Eleusine coracana (2.02), Cynodon dactylon (1.96), or Panicum miliaceum (3.46, 3.97) in early experiments, and NAD-ME Eleocharis caespitosissima in later ones; and PCK controls: Brachiaria decumbens (7.65), Chloris gayana (3.77, 5.92, 7.01, 15.21, 17.89) or Sporobolus africanus (8.48, 10.74) (see checklist: Hattersley 1987). Anatomically typed C₃ sedges were used as C₃ controls (Table 6.1).

Results and Discussion

Enzyme Assays

Anatomical and enzyme assay results are presented in Table 6.1. With the major exception of Eleocharis (see below) they generally corroborate the findings of earlier work, especially that of Ueno et al. (1986). All of the Abildgaardia (2 species) and Fimbristylis (6 species) species sampled are NADP-ME type and have fimbristyloid C₄ anatomy (Fig. 6.1A). Abildgaardia and four of the Fimbristylis species are assayed for the first time here. Nearly all species in this sample with chlorocyperoid and rhynchosporoid C₄ anatomy (2 Cyperus species; 2 Mariscus species; 1 Pycreus species, Fig. 6.1B; 1 Lipocarpha species; and 3 Rhynchospora species, Fig. 6.1C) also exhibited significant or substantial NADP-ME activity, as expected. Some NADP-ME species exhibited NAD-ME activity above 1 µmol mg⁻¹ Chl min⁻¹ (Table 6.1), perhaps reflecting a secondary reaction of chloroplast NADP-ME rather than mitochondrial NAD-ME activity alone (Hatch and Mau 1977b; Hatch et al. 1982).

Kyllinga brevifolia and K. polyphylla showed NADP-ME activities below 2.46 µmol mg⁻¹ Chl min⁻¹ (Table 6.1), despite their unexceptional chlorocyperoid C₄ anatomy. Activities around this level have been found in the C₃-C₄ intermediate Flaveria ramosissima (Ku et al. 1983; cf. Neurachne minor: Hattersley et al. 1986), but ¹³C
value determinations confirm that *K. brevifolia* and *K. polyphylla* are C_4 (δ^{13}C = -10.4 and -10.8%_oo and -11.1 and -11.2%_oo respectively; see Chapter 7).

### C_4 Anatomical Types in Cyperaceae

The comparative anatomical data (Table 6.1) also generally confirm earlier work, to the extent that the chlorocyperoid, fimbristyloid, and rhynchosporoid C_4 anatomical types were found to occur in genera already known for these types (cf. Sharma and Mehra 1972; Raynal 1973; Carolin et al. 1977; Takeda 1980, Ueno and Koyama 1987; see also Appendix 1). However, novel C_4 anatomy in *Eleocharis* was found, and it is also necessary to reconsider the chlorocyperoid-type.

C_4 sedges of the chlorocyperoid type exhibit a previously undescribed anatomical characteristic: viz., a partial outer parenchymatous bundle sheath (PBS: usually very limited in extent), in nearly all of the primary vascular bundles (Fig. 6.1B; and apparent in Fig. 6.3 of Takeda *et al.* 1985, and in Fig. 6.2 of Ueno *et al.* 1986). The partial sheath consists usually of one or two, but sometimes of as many as five cells external and lateral to the mestome sheath on at least one side of the vein. These cells are elongated parallel to the vein axes in all species examined so far (Appendix 1: *Kyllinga brevifolia*, *K. polyphylla*, *Mariscus gunnii*, *M. scaber*, and *Pycreus polystachyos* in this study, and also *Remirea maritima*: JJB496, and cf. Fig 2, Takeda *et al.* 1980).

Rikli (1895) illustrated a primary bundle of *Mariscus tovari* (as *Cyperus incompletus*) which clearly shows such a partial PBS (labelled "d = chlorophyllose Durchlasszellen"), as distinct from the photosynthetic carbon reduction (PCR, or 'Kranz') tissue (labelled "a = äussere Parenchym scheide"). Later authors (e.g. Druyts-Voets 1970; Metcalfe 1971, Goetghebeur 1986) also have shown partial parenchymatous bundle sheaths, without commenting upon their presence as such. For example, Metcalfe (1971 p.375) considered the vascular bundles in *Mariscus* to have inner parenchymatous and outer fibrous sheaths (i.e., the boundary layer cells and mestome sheath respectively). Yet he (1971 p.376 Fig. 52) illustrated a number of chlorocyperoid species with an obvious partial PBS outside the mestome sheath, and even labelled one of the constituent cells as a "translucent cell". The general occurrence of a partial PBS in chlorocyperoid sedges seems to have been overlooked, the statement that chlorocyperoid anatomy constitutes two sheaths, an inner 'parenchymatous bundle sheath' (or Kranz-sheath) and an outer mestome sheath having become dogma (see Raynal 1973; Ueno and Koyama 1987). Ueno and Koyama (1987 p.72) even considered some *C_4 Rhynchospora* species to have anatomy "intermediate between the Fimbristyloid and Chlorocyperoid types because the outermost parenchyma sheath cells are retained
ambiguously". However, these *Rhynchospora* species simply possess conventional chlorocyperoid anatomy, with a partial PBS (see also Appendix 1). *Rhynchospora subplumosa* is anomalous, exhibiting a PBS about the mestome sheath on the phloem side of the vascular bundles, and should be included in future studies of the development of bundle sheaths in the Cyperaceae (cf. Dengler et al. 1985, 1986). I have been unable to detect a PBS in the leaves of *Alinula*, and *Hemicarpha*, or in the culms of *Alinula* (or in those of some *Eleocharis* species, see below), while the leaves of *Ascolepis*, *Kyllinga*, *Pycreus* and *Volkiella* are variable for this feature (Appendix 1). The available data, nevertheless, indicate that chlorocyperoid C₄ taxa without a PBS represent a minority of genera and species of this anatomical type (Appendix 1).

**Eleocharis**

Anatomical observations on fresh material of *Eleocharis caespitosissima* confirmed suspicions, aroused when contemplating Miller's (1982) illustration, that this species would prove to be C₄ (contrast Fig. 6.1E with Fig. 6.1D, showing C₃ *Eleocharis* anatomy). A search among a further 14 *Eleocharis* species revealed four more C₄ representatives: *E. retroflexa* subspecies *chaetaria*, *retroflexa*, and *subtilissima* (the identity of the last being based on immature material: W. Ellery 15 (PRE)), and *E. subcancellata* (Table 6.1; see also Chapter 7).

Negligible NADP-ME activity and no PCK activity could be detected in either *E. caespitosissima* or *E. retroflexa*. On the other hand, NAD-ME activity was substantial, making these two species the first known NAD-ME sedges. The NAD-ME C₄ type is now known not only in the Poaceae, Amaranthaceae, Chenopodiaceae and Portulacaceae (Gutierrez et al. 1974; Hatch et al. 1975) but also in the Cyperaceae. This discovery further highlights questions of considerable phylogenetic interest concerning photosynthetic pathway homologies across these diverse plant families (cf. Watson et al. 1985; Hattersley 1987). Of particular interest in the context of cell development and genetic expression is the recent report by Ueno et al. (1988) of a further NAD-ME sedge *Eleocharis vivipara* which exhibits intraspecific photosynthetic pathway variation (see Chapters 5 and 7). These C₄ species seem to be satisfactorily placed in *Eleocharis* taxonomically, possessing cladorious culms with leaves reduced to sheaths, inflorescences typical of the genus, a style with a dilated base that is persistent on the nut, and six retrorsely hispid hypogynous bristles; and in that context they appear to be closely related, all having been referred to series *Tenuissimae* by Svenson (1937). The series is, however, morphologically heterogeneous (see Chapter 7), and not all its members are C₄.
The C₄ Eleocharis species exhibit a peculiar form of C₄ anatomy, not previously reported in the Cyperaceae or in any other plant family. The PCR tissue layer in all primary vascular bundles examined occupies the "boundary layer" position internal to a mestome sheath (cf. Brown 1975), as in the fimbristyloid or chlorocyperoid types (Fig. 6.1E cf. Figs. 6.1A and 6.1B). Unlike in those types, however, PCR cells here usually occur between metaxylem vessel elements and laterally adjacent mestome sheath cells. Further, the C₄ Eleocharis species possess scattered PCR cell chloroplasts (Fig. 6.1E), by contrast with their centrifugal/peripheral position in the other C₄ anatomical types (e.g. Fig. 6.1C). This fourth type of C₄ anatomy in the sedges is conveniently designated the "eleocharoid" type.

The PCR cells always occur between the metaxylem vessel elements and the laterally adjacent mestome sheath cells in E. caespitosissima, E. retroflexa subspecies chaetaria, and E. subcancellata. However, in E. retroflexa subspecies retroflexa and subtilissima, the metaxylem vessel elements interrupt the PCR cells on one or both sides of the larger primary bundles. There are a few examples elsewhere in the family which show some overlap with the eleocharoid type. Raynal (1973 p.147 Fig. 6.1B) illustrated a primary vascular bundle of the culm of Nemum equitans (given by Raynal as an example of fimbristyloid C₄ anatomy: i.e. with a complete PBS) with the PCR cells between one of the metaxylem vessel elements and the mestome sheath, and some of my preparations of the leaves of Ascolepis capensis and leaves and culm of Bulbostylis paradoxa show most primary bundles having the PCR cells interrupted on one or both sides by the metaxylem vessel elements. Rikli’s (1895) drawing of a primary bundle of Mariscus tovari shows very small cells between one of the metaxylem vessels and the mestome sheath, although the boundary layer cells are still interrupted somewhat adaxial to the vessel element. However, it is probably not valid to interpret his drawing to this level of detail, and all the specimens of Mariscus examined in the present study have the boundary layer interrupted by the metaxylem vessel elements.

Although a PBS is clearly evident in C₃ Eleocharis species, its presence in the C₄ species is questionable. Although some or all of the cells adjacent to the outer wall of the mestome sheath are as rounded as are typical PBS cells, some or all the undisputed primary carbon assimilation (PCA: C₄ mesophyll) cells are equally rounded. Also, in the material examined so far (viz. E. caespitosissima and E. retroflexa subspecies retroflexa), these cells are no more elongated in the longitudinal axis than are any of the other mesophyll cells, and are therefore at best dubiously interpretable as PBS cells. Of the C₄ species other than C₄ Eleocharis that do not have the boundary layer cells interrupted by the metaxylem vessels elements, Bulbostylis paradoxa and Nemum
equitans have fimbristyloid-like anatomy with a complete PBS surround their bundles, while Ascolepis capensis has chlorocyperoid-like anatomy with at least some primary bundles possessing a partial PBS. None of these exceptional taxa has been investigated biochemically or ultrastructurally, so that full comparison of them with the C₄ Eleocharis species is not yet possible. Such studies, together with more detailed developmental studies in C₄ Eleocharis species, are needed to confirm these preliminary conclusions, and to elucidate structural homologies and the taxonomic implications (see Chapter 10).

The temperate Eleocharis pusilla has anatomy (Fig. 6.1F) which approaches that of a C₄ sedge, with boundary layer cells containing numerous chloroplasts internal to the mestome sheath (chloroplasts in boundary layer cells of C₃ sedges are less frequent: Fig. 6.1D). Intriguingly, the anatomy of E. pusilla is more like the C₄ fimbristyloid type (or more typical of the C₃ Eleocharis species) than the C₄ eleocharoid type, in that an outer parenchymatous bundle sheath is present, and the chlorophyllous boundary layer is interrupted laterally by metaxylem vessels (Fig. 6.1F). Despite its C₄-like anatomy, the activities of C₄ acid decarboxylases in E. pusilla are negligible (NAD-ME), non-detectable (PCK) and, in the case of NADP-ME, lower than levels for all the NADP-ME species in our sample (Table 6.1). This species exhibits C₃ $^{13}$C values (-26.7 and -28.7‰; for the two accessions in this study), but $\Gamma$ determinations have revealed values intermediate between those of C₃ and C₄ sedges; i.e. 29-31ppm, compared with ranges of 40-52ppm for C₃ species and 0-3ppm for C₄ species. These results are consistent with the hypothesis, for which there is ultrastructural support (Chapter 9), that E. pusilla is a C₃-like C₃-C₄ intermediate.

Comparisons with the Poaceae

Table 6.2 reveals little of taxonomic interest above the generic level other than that the C₄ genera of a tribe exhibit only one C₄ biochemical type, though, with the exception of Eleocharis, not exclusively so (cf. Chapter 9). However, only 43 C₄ species from eleven genera of Cyperaceae have yet been biochemically typed (Table 6.2), by contrast with 154 species from 50 genera for the Poaceae (checklist: Hattersley 1987). Extending the taxonomic sample seems likely to reveal further variation in the taxonomic pattern at the generic and tribal level in the Cyperaceae, from which neither PCK nor C₄-like C₃-C₄ intermediate species (review: Monson et al. 1984) are yet known. Not all the putative C₄ Eleocharis species have been investigated biochemically or for $\Gamma$ values, and as these are exceptional in combining C₄ $^{13}$C values with C₃-C₄ (Chapter 8) maximum cells-distant counts, they may be C₄-like C₃-C₄ intermediates.
As the PCR tissue in sedges is always contiguous with the metaxylem vessels (regardless of whether the PCR comprises boundary layer cells or mestome sheath), the XyMS structural criterion\(^1\), which very reliably distinguishes NADP-ME from NAD-ME and PCK 'classical' types in the Poaceae, is invalid for them. On this basis, all C\(_4\) sedges, including the known NAD-ME species, would be classed as XyMS- and predicted to be NADP-ME. NADP-ME grasses (Hattersley 1987; Prendergast et al. 1987) and sedges generally possess centrifugal/peripheral PCR chloroplasts. In NAD-ME grasses the PCR chloroplasts are typically centripetal (but see Prendergast et al. 1987 for exceptional structural/biochemical associations), while in the NAD-ME sedges they are scattered to somewhat centrifugal (Chapter 9). It seems more reasonable to expect that other NAD-ME sedges will have scattered PCR chloroplasts, than to view the known cases as exceptions by inference from knowledge of the Poaceae. In speculating about the possibility of finding PCK sedges, it seems worth noting that PCK grasses (the only family in which this biochemical type is known, see Hattersley 1987) always possess a PBS (as do all NAD-ME grasses), which, with the exception of Alloteropsis semialata, serves as the PCR site (Prendergast et al. 1987). No equivalent has been found in the Cyperaceae. Although both fimbristyloid and rhynchosporoid (NADP-ME) species possess a well developed PBS which is often chlorenchymatous, this layer has been shown for the fimbristyloid type to be functionally PCA (Hattersley et al. 1977). Recently Burnell and Hatch (1988) showed that the PCK species utilize a dual system of decarboxylation involving not only PEP carboxykinase, but also NAD-malic enzyme. Burnell (oral comm. 1988) has suggested that the biochemical evidence points towards the PCK type being derived from the NAD-ME type. If this is correct, the best place to extend the search for PCK sedges would be among the nearest taxonomic relatives of the known NAD-ME species, namely among the closest relatives of Eleocharis caespitosa and E. retroflexa in the series Tenuissimae (see Chapter 5).

\(^1\) Hattersley and Watson 1976 p.299: "presence (Xym+) or absence (XyMS-) of cells between the metaxylem vessel elements and laterally adjacent chlorenchymatous bundle sheath cells in the primary lateral vascular bundles".
Table 6.1. Activities of C4 Acid Decarboxylating Enzymes in the Cyperaceae

F = fimbristyloid C4 anatomy, C = chlorocyperoid C4 anatomy, R = rynchosporoid C4 anatomy, E = eleocharoid C4 anatomy, C3 = C3 anatomy; C3-C4 = C3-C4 intermediate. Enzyme activity measured in µmol mg−1 Chl min−1, ND = not detectable. NADP, NADP-malic enzyme; NAD, NAD-malic enzyme; PCK, phosphoenolpyruvate carboxykinase. For controls, see Materials and Methods. C4 type based on enzyme activities. c = use of culm material in assays; l = leaves; b = inflorescence bracts; mixtures of organs sometimes used. The classification follows Chapter 9.

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Subfamily CARICOIDEAE

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* Found to be NADP-ME also by Ueno et al. (1986).
Table 6.2. Number of species biochemically typed for photosynthetic pathway in the Cyperaceae
Compiled from data of Chen et al. 1974; Ueno et al. 1986, 1988; and this study. C_3 = C_3 photosynthesis; C_3-C_4 = C_3-C_4 intermediate; C_4 = C_4 photosynthesis. If C_4, either NAD-malic enzyme (NAD-ME) or NADP-malic enzyme (NADP-ME) type. C_4 anatomy either fimbristyloid (F), chlorocyperoid (C), rhynchosporoid (R), or eleocharoid (E). Inclusion of data for Eleocharis vivipara under the C_3 and the C_4 NAD-ME columns accounts for the mismatch of the totals and grand total. The classification follows Chapter 9.

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Figure 6.1

Figures 6.1A-F: Transverse sections of LR White embedded culms (A, D-F) and leaves (B and C) of Cyperaceae showing primary vascular bundles. PBS, parenchymatous bundle sheath; MS, mestome sheath; PCR, photosynthetic carbon reduction (or Kranz) tissue. Scales = 20 µm.

Figure 6.1A: *Fimbristylis polytrichoides* with fimbristyloid anatomy. Note three sheath layers: viz., PCR tissue in the boundary layer position, thickened mestome sheath and well developed outer parenchymatous bundle sheath.

Figure 6.1B: *Pycreus polystachyos* with chlorocyperoid anatomy. Note PCR tissue in the boundary layer position surrounded by the mestome sheath. A partial PBS is also evident (unlabelled arrows) in this vein.

Figure 6.1C: *Rhynchospora subtenuifolia* with rhynchosporoid anatomy with only two sheath layers. PCR tissue occupies the mestome sheath position and is surrounded by an incomplete PBS. Note the centrifugal chloroplasts in the PCR tissue. Secretory cells (SC) are a common feature in Cyperaceae. Inset: part of the same section between crossed polarizers shows the thickened walls of the mestome sheath (arrows) and the metaxylem vessel elements (MX; cf. Ueno et al. 1986, who state that the mestome sheath is absent).

Figure 6.1D: *Eleocharis acuta* showing C₃ anatomy. Note the mestome sheath surrounded by a PBS, both containing very few organelles. The boundary layer cells are small and also contain few organelles.

Figure 6.1E: *E. caespitosissima* with C₄ anatomy. Note PCR tissue between the metaxylem vessel elements and the laterally adjacent mestome sheath, scattered chloroplast position within PCR cells and small fibre strands (FS).

Figure 6.1F: *E. pusilla*, a C₃-C₄ intermediate species. Note the enlarged boundary layer cells (unlabelled arrows) with many chloroplasts, and small fibre strands (FS).
Chapter 7

Photosynthetic pathway-related ultrastructure of C₃, C₄
and C₃-like C₃-C₄ intermediate sedges (Cyperaceae),
with special reference to Eleocharis

Abstract

The ultrastructure of photosynthetic organs (leaf blades and culms) was investigated in 8 species from 4 genera of sedges: viz., Fimbristylis (C₄ fimbristyloid anatomy), Pycreus (C₄ chlorocyperoid anatomy), Rhynchospora (C₄ rhynchosporoid anatomy) – all NADP-ME type, and hitherto uninvestigated C₃, C₄ (eleocharoid anatomy, NAD-ME type) and C₃-like C₃-C₄ intermediate species of Eleocharis. Ultrasructural characteristics previously reported for the former anatomical types are largely confirmed, though some evidence of poorly developed peripheral reticulum in C₄ rhynchosporoid sedges is presented. Sedges, regardless of anatomical and biochemical type, possess a suberized lamella in photosynthetic organs which is invariably present in and confined to the mestome sheath cell walls, though it is often incomplete in the radial walls. By contrast with other C₄ sedges, NAD-ME Eleocharis species and the C₃-like C₃-C₄ intermediate E. pusilla possess abundant mitochondria and chloroplasts with well stacked grana in the PCR (Kranz)/bundle sheath cells. Peripheral reticulum is well developed in NAD-ME species in both PCR and PCA (C₄ mesophyll) chloroplasts, but differs from that seen in chlorocyperoid and fimbristyloid type sedges. Suberized lamella and starch grains (well preserved), and granal stacks (poorly preserved) are identifiable in dried herbarium material (Eleocharis). The significance of the ultrastructural similarities between the C₄ NAD-ME and C₃-C₄ intermediate Eleocharis species is discussed.

Introduction

Ultrastructural differences in the chloroplasts (presence or absence of peripheral reticulum and convolute or parallel arrangement of the thylakoid systems) of some C₄ sedges possessing chlorocyperoid, fimbristyloid and rhynchosporoid anatomy (Chapter 6), have been related to differences in the proximity of the photosynthetic carbon reduction (PCR or ‘Kranz’) and primary carbon assimilation (PCA or C₄ mesophyll) tissues in relation to metabolite transport (Ueno et al. 1988). Apart from this, and by
contrast with the existence of a substantial body of information on C₄ anatomical variation in the Cyperaceae (e.g., see Sharma and Mehra 1972; Lerman and Raynal 1972; Raynal 1973; Takeda 1972), ultrastructure of the family has received relatively little attention (see also Black and Mollenhauer 1971; Laetsch 1971; Carolin et al. 1977; Gilliland and Gordon-Gray 1978; Jones et al. 1981). The assumption that all C₄ sedges were NADP-ME has probably been a disincentive, but the desirability of extended comparative ultrastructure work has become apparent with the discovery of the ‘eleocharoid’ anatomical-type and its association with NAD-ME type photosynthesis (Bruhl et al. 1987; Chapters 5-6). For example, if the ultrastructural/biochemical correlations obtained in grasses apply to sedges (see e.g., Laetsch 1974; Hattersley 1987 and references therein), the NAD-ME species would be expected to have PCR cell chloroplasts with abundant grana and mitochondria, by contrast with the NADP-ME species which have agranal PCR cell chloroplasts and about a one-to-one ratio of mitochondria in the PCR and PCA cells. Before the discovery of NAD-ME Eleocharis species with the PCR in the border parenchyma position (Bruhl et al. 1987; Chapters 5-6), it had seemed that biochemical type could be predicted from anatomy alone (Ueno et al. 1986). Indeed, it seems that further C₄ Eleocharis species with eleocharoid anatomy (i.e. with the PCR intervening between the metaxylem vessel elements and the mestome sheath, and without an obvious parenchymatous bundle sheath) will prove to be NAD-ME. However, the NAD-ME Eleocharis retroflexa ssp. retroflexa now seems to be variable for the anatomical trait (i.e. the metaxylem vessel elements often interrupt the border parenchyma cells), as is the recently discovered C₄ E. retroflexa ssp. subtilissima (Chapter 5), which casts some doubt on the prediction of their biochemical type from anatomy. Further, Ascolepis capensis (related to species with chlorocyperoid anatomy), and Bulbostylis paradoxa and Nemum equitans (related to species with fimbristyloid anatomy, and possessing a well defined parenchymatous bundle sheath) also have PCR tissue in the border parenchyma which intervenes between the metaxylem vessel elements and the mestome sheath (Appendix 1; see also Chapter 6). Therefore, these species cannot be confidently typed on the basis of anatomy alone. Ultrastructural/biochemical correlates may allow more reliable biochemical typing of sedges on the basis of anatomical/ultrastructural criteria, possibly even from herbarium material (cf. Hattersley and Perry 1984).

This study compares the ultrastructure of recently described variants in Eleocharis with that of the other known C₄ and C₃ anatomical types. Dried material of Eleocharis retroflexa and E. subcancellata has been examined, to assess the possibility of using
ultrastructure to type C₄ sedges from herbarium material, and to extend the comparison of the suberized lamella between fresh and dried material (Hattersley and Perry 1984).

Methods and Materials

Plants were grown from field collected material or seed, under half shade in glasshouses maintained between 35°C (day maximum) and 15°C (night minimum), and regularly fertilized with Ruakura nutrient solution (Smith et al. 1983). All identities were checked using appropriate literature. Vouchers will be lodged at CANB: Eleocharis acuta, JJB125; E. geniculata, JJB231; E. pusilla, JJB682; E. caespitosissima, JJB399; E. retroflexa subspecies retroflexa, C2967; Fimbristylis tetragona, JJB546; Pycreus polysystachyos, JJB309; Rhynchospora rubra, JJB573.

The mid-third of youngest, fully expanded leaves or culms were sliced into small segments under fixative. Culms of conventionally dried specimens of Eleocharis retroflexa and E. subcancellata were also prepared according to schedule 1 below. In order to improve the quality of fixation and infiltration, and to permit close comparison with the results of Ueno et al. 1988, three schedules were applied to the fresh material:

1) 2.5% glutaraldehyde in 50 mM cacodylate buffer, pH 7, for 2 h, washed twice in buffer, over 1 h, post-fixed in 1% OsO₄ for 2 h at room temperature, washed in water, dehydrated in a graded ethanol series (15%, 30%, 50%, 70%, 90%, 95% twice, 100% twice, for 15 mins each), infiltrated for 24 h in LR White at room temperature, and embedded in fresh LR White for 12 h at 60°C under vacuum;

2) 2.5% glutaraldehyde and 2% formaldehyde in 30 mM Pipes buffer, 16 h at 4°C, washed three times in buffer over 30 mins, left in buffer for 12 h at 4°C, post-fixed in 1% OsO₄ for 16 h at 4°C, washed in buffer three times over 1 h, dehydrated in an ethanol series, as above but 30 mins per step, infiltrated in LR White with four changes over one week, and embedded in fresh LR White as above; and

3) Method similar to that of Ueno et al. (1988): 5% glutaraldehyde in 50 mM sodium phosphate buffer at 4°C, washed briefly in buffer three times, and overnight at 4°C, post-fixed in 2% OsO₄ for 6 h at 4°C, rinsed in buffer and left overnight in buffer at 4°C, washed in distilled H₂O, dehydrated and embedded as for (2).

Transverse sections were cut with a LKB 2128 ultramicrotome, double-stained with uranyl acetate and lead citrate, and examined in a Hitachi 600 electron microscope.
The ultrastructural features of interest here were constant regardless of the fixation schedule employed, though longer infiltration times resulted in fewer artifacts of sectioning.

**Results and Discussion**

Table 7.1 summarizes the ultrastructural features observed in a sample chosen to represent all the known biochemical and anatomical types in the Cyperaceae, paying particular attention to the variation in *Eleocharis*. The observations on C₃ (Fig. 7.1A) and C₄ chlorocyperoid, fimbristyloid (Fig. 7.1B) and rhynchosporoid (Fig. 7.1C and E) species largely confirm earlier observations on C₃ and NADP-ME species by Laetsch (1971), Carolin *et al.* (1977), Gilliland and Gordon-Gray (1978), Jones *et al.* 1981 and Ueno *et al.* (1988). Nevertheless, confidence in generalizations drawn from the available ultrastructural observations on Cyperaceae must be tempered with caution, given the small size of the sample. For rhynchosporoid anatomy this comprises only *Rhynchospora rubra*, which has been examined in three studies with more or less consistent results. The fimbristyloid and chlorocyperoid types have been better surveyed: 3 genera/11 species and 5 genera/27 species respectively, although no *Rhynchospora* species with chlorocyperoid anatomy has been investigated.

The following ultrastructural characteristics of NADP-ME sedges with chlorocyperoid, fimbristyloid or rhynchosporoid anatomy are confirmed here: 1) the convoluted thylakoid membrane pattern (Fig. 7.1B) in PCR chloroplasts of fimbristyloid and chlorocyperoid sedges⁴; 2) the more usual parallel arrangement of the thylakoid system in the rhynchosporoid species (Fig. 7.1C); 3) the agranal or at best poorly stacked thylakoid membranes; and 4) the more or less 1:1 ratio of mitochondria in the photosynthetic carbon reduction (PCR or ‘Kranz’) cells to those in the primary carbon assimilation (PCA or C₄ mesophyll) cells. NAD-ME species with eleocharoid anatomy (Figs 2A-C) and the intermediate *Eleocharis pusilla* (Fig. 7.2D and F) exhibit a distinct suite of ultrastructural features (Table 7.1); i.e., well stacked grana in the PCR/bundle sheath chloroplasts and abundant mitochondria in the PCR/bundle sheath cells.

---

1. Not all thylakoids are convoluted and this has led Gilliland and Gordon-Gray (1978) to describe the thylakoid system in *Kyllinga* (chlorocyperoid anatomy) and *Fimbristylis dichotoma* (fimbristyloid anatomy) as parallel, while Carolin *et al.* (1977) described the thylakoid system in PCR chloroplasts of *K. brevifolia* as contorted, but still with large areas of parallel flattened lamellae.
Fewer sections were examined of either of the C₃ species than the other species sampled, but they also exhibit a few granal chloroplasts in the border parenchyma position, while numbers of mitochondrial profiles for these cells (Fig. 7.1A) varies from equalling to slightly exceeding numbers for mesophyll cells. The stroma of the bundle sheath chloroplasts appears to be more electron dense than that of the mesophyll cells in all the C₄ species examined (e.g. Fig. 7.2C). Starch grains are larger and generally more abundant in the PCR chloroplasts of *Rhynchospora rubra* (Fig. 7.1C) and in the PCR (Figs 2A, C and E) and PCA (Fig. 7.2D) chloroplasts of the C₄ *Eleocharis* species than in any of the other species examined.

A suberized lamella has been found in walls of cells in the mestome sheath position in all sedges examined, regardless of anatomical or biochemical type (Figs 1A-E and 2A and C-F); Carolin *et al.* 1977; Ueno *et al.* 1988). Ultrastructurally the suberized lamella seen in these sedges resembles that found in the Poaceae (cf. O’Brien and Carr 1970; Laetsch 1974; Hattersley and Browning 1981; cf. Ueno *et al.* 1988; Gunning and Steer 1975). It consists in trans-section of two parallel osmiophilic bands separated by a lighter zone (Figs 1D-E). Where the suberized lamella traverses plasmodesmata, it widens (Figs 1E, 2A and D) and consists of several alternating osmiophilic and light bands. In leaves of C₄ Poaceae, suberized lamellae vary in occurrence and position. For example, most NADP-ME grasses possess a complete suberized lamella in the outer tangential wall of the PCR tissue (which constitutes the mestome sheath) and only a patchy one aligning the inner tangential and radial walls; most NAD-ME grasses possess a complete suberized lamella in the walls of the mestome sheath, but the PCR/parenchymatous bundle sheath cell walls lack a suberized lamella; and most PCK species have a complete suberized lamella in the walls of the mestome sheath and the suberized lamella of the PCR/parenchymatous bundles sheath cell complete in the outer tangential walls but patchy along the radial walls (Prendergast *et al.* 1987; Hattersley 1987). In the Cyperaceae, by contrast, the suberized lamella always occupies the inner and the outer tangential walls of the mestome sheath (cf. Carolin *et al.* 1977; Ueno *et al.* 1988: though the latter observed the suberized lamella in the mestome sheath in *R. rubra*, they avoided naming these cells ‘mestome sheath’ – but see Gilliland and Gordon-Gray 1978). The distribution of suberized lamella in the radial walls of the mestome sheath of sedges, however, is somewhat variable. A continuous suberized lamella in radial walls, beautifully illustrated by Ueno *et al.* (1988 pp.147-148), appears to be the exception rather than the rule. More often the suberized lamella is discontinuous in at least one of the radial walls of adjacent cells (Figs 1A-E, 2D). The adjacent segments of the discontinuous lamellae sometimes end at the same distance.
from the opposite tangential walls (Fig. 7.1D). In any case, the zone near the ends of
the suberized lamella or between them is somewhat more electron dense than much of
the remainder of the secondary wall (Fig. 7.1D-E), consistent with the presence of a
casparian strip or of a similarly water impermeable material (cf. Böcher and Oleson
1978; Hattersley 1987). Considering putative apoplastic transport between PCA and
PCR tissue, the PCR cell chloroplasts are separated from PCA cells by a suberized
lamella in both outer and inner tangential walls of the mestome sheath in species where
the PCR tissue is in the border parenchyma position. By contrast, where the PCR tissue
occupies the mestome sheath, the PCR cell chloroplasts are only separated by a
suberized lamella in the outer tangential walls of the mestome sheath.

Chloroplast position in C₄ grasses may represent different compromises between
the demands of maximizing rates of PCR-PCA metabolic transport on the one hand, and
of reducing rates of CO₂ leakage on the other (Hattersley and Browning 1981). The
correlation between biochemical type and chloroplast position in the sedges does not
always correspond to the situation seen in grasses (e.g., NAD-ME grasses with
centripetal chloroplasts and NAD-ME sedges with scattered chloroplasts; see Hattersley
1987). In C₄ sedges the presence of a suberized lamella irrespective of biochemical type
could be seen as removing one of the constraints, as it relates to CO₂ leakage, on
chloroplast position within the PCR cells.

Prominent peripheral reticulum, representing invagination of the inner of the two
chloroplast envelope membranes (cf. Laetsch 1974; Gunning and Steer 1975), was
identified by Carolin et al. (1977) in chloroplasts of chlorocyperoid and fimbristyloid-
type species. Ueno et al. (1988) also generally found peripheral reticulum in these types,
though they indicated that it was more abundant in PCR than PCA chloroplasts, and
even tabulated its absence from the PCA chloroplasts of some species. In Rhynchospora
rubra they noted it only in PCA chloroplasts. In the present study, prominent peripheral
reticulum was confirmed not only in species with chlorocyperoid and fimbristyloid
anatomy, but also in association with eleocharoid anatomy (Figs 2A-C). In the former
types the electron transparent areas are often dumb-bell shaped (cf. Carolin et al. 1977;
Jones et al. 1981) while in the C₄ Eleocharis species they are more or less circular in
profile (Fig. 7.2A-B). My observations suggest that there is a poorly developed
peripheral reticulum, or at least a peripheral reticulum-like zone in the PCR chloroplasts
of R. rubra (Fig. 7.1C). The peripheral reticulum bounds or defines electron transparent
regions of the chloroplasts referred to by Carolin et al. (1977) and Ueno et al. (1988)
as vesicles. However, their status as ‘vesicles’ (rather than being some form of reticulate
inter-membrane region) needs confirming, e.g. via serial sections, to demonstrate that each transparent region is indeed a separate entity.

The phenomenon of a peripheral reticulum and associated light regions may be an artifact of fixation (see Laetsch 1971, 1974): artifactual vesiculation has been described by Mersey and McCully (1978). Even so, it is a constant feature, notwithstanding different fixation schedules and preparation in different laboratories. Where well developed, it occurs in relatively closely related groups of species (Chapter 9), and evidently has some taxonomic value. Ueno et al. (1988) proposed that the development of the peripheral reticulum in species with chlorocyperoid and fimbristyloid anatomy is related to rapid metabolite transport, compensating for the higher resistance proposed for C₄ sedges where the PCR is separated from the PCA by the mestome sheath, as compared with species possessing rhynchosporoid anatomy where PCR and PCA tissues are adjacent. Peripheral reticulum in grasses seems never to have been critically examined in this context with respect to the C₄ subtypes. The presence of well developed peripheral reticulum in the sedges with eleocharoid anatomy, where the border parenchyma cells constitute the PCR tissue, is consistent with the notion of its involvement in metabolite transport (Ueno et al. 1988). However, the different appearance of the peripheral reticulum in the eleocharoid species, together with their being biochemically distinct, suggests that it may have evolved independently here in connection with some as yet unknown function or a related but not identical one.

The suberized lamella in *Eleocharis retroflexa* and *E. subcancellata* remains intact after drying (Fig. 7.2D), as in grasses (Hattersley and Perry 1984). Not surprisingly, the chloroplasts are poorly preserved in such material: the peripheral reticulum and mitochondria are mostly not recognizable or are obviously altered, and the electron transparent regions (or ‘vesicles’) are greatly enlarged; the stroma and the thylakoid systems are disrupted, though grana are apparent; and starch grains are well preserved (Fig. 7.2D). The consistency of the ultrastructural features that were observed in both fresh and herbarium material of *Eleocharis retroflexa* (which has also been biochemically typed) allows for some confidence in the typing of material from herbarium material. Thus, on the basis of abundant PCR chloroplasts with grana and many starch grains, and a C₄ d13C value and eleocharoid anatomy (see Chapters 5-6), *E. subcancellata*, is predicted to be C₄ and NAD-ME. Prediction of C₃-like C₅-C₄ intermediates in *Eleocharis* could be based on C₃-like d13C values combined with C₄-like leaf anatomy, poorly developed starch grains and less abundant bundle sheath chloroplasts.
A striking feature of NAD-ME sedges and of the apparently C₃-C₄ intermediate, *E. pusilla*, is the abundance of mitochondria in the border parenchyma cells (Figs 7.2A, C, D and F). These chlorenchymatous cells typically contain more than six mitochondria per profile and often many more (with some counts of 30 per profile). By contrast, the number of mitochondria per PCR cell profile in chlorocyperoid, fimbristyloid, and rhynchosporoid species is usually less than six. Both chloroplasts and mitochondria are less abundant in the border parenchyma cells of C₃ sedges, but there is sufficient variability within and between the C₃ species to suggest a need for more detailed examination, which might usefully start with C₃ *Eleocharis* species. Size profiles of the border parenchyma mitochondria were not calculated, but in the NAD-ME and intermediate species they appear to be at least as large as those of the mesophyll.

The elevated number of mitochondria in the PCR cells of the NAD-ME species is not surprising, given that mitochondria are the site of decarboxylation in NAD-ME species (Hatch and Mau 1973; Hatch and Kagawa 1974a-b; Kagawa and Hatch 1975). Abundant bundle sheath mitochondria are also a feature of C₃-like C₃-C₄ intermediates (see e.g. Holaday et al. 1984; Hylton et al. 1988; Rawsthorne et al. 1988). These mitochondria are involved in a ‘glycine shuttle’, where glycine from the mesophyll is transported to the bundle sheath cells for decarboxylation in the mitochondria (Monson et al. 1984; see also Edwards and Ku 1987). Hylton et al. (1988) demonstrated, via in situ immunogold labeling of leaves, that glycine decarboxylase is present only in bundle sheath mitochondria in C₃-C₄ intermediates of *Flaveria* and *Moricandia*. More detailed studies of *Eleocharis pusilla* are needed to establish whether glycine decarboxylase is restricted to its bundle sheath mitochondria (cf. Hylton et al. 1988; Rawsthorne et al. 1988) together with more elaborate gas exchange experiments, designed to test whether the response of CO₂ compensation point to changing O₂ pressures fits the predictions of the model for C₃-like C₃-C₄ intermediates (see von Cammerer 1989).

The functional and evolutionary significance of the similarities between the NAD-ME and C₃-like C₃-C₄ intermediate sedges are not known. Both have abundant mitochondria associated with scattered, granal chloroplasts located in the border parenchyma position. In both, the mitochondria probably serve as the site for decarboxylation (albeit perhaps for different metabolites). The sedges concerned are relatively closely related, all being members of *Eleocharis*, a helophytic to hydrophytic genus. The recent discovery of intraspecific variation of photosynthetic pathway in *Eleocharis vivipara* (Ueno et al., 1988; with C₃ submerged forms and C₄ NAD-ME terrestrial forms) , which may even be reversible, invites speculation as to the origin and stability of the C₄-like features in *E. pusilla*, and should encourage investigation
of the genetic and molecular basis of $C_4$ expression in this genus. Ecological considerations suggest that the extreme and changeable micro-environments inhabited by its species may have been decisive in the appearance of these photosynthetic pathway variations (see also Chapter 5).
Table 7.1. Ultrastructural characteristics of leaves and culms in the Cyperaceae sampled

C₃-C₄ = C₃-C₄ intermediate, C = chlorocyperoid C₄ anatomy, E = eleocharoid C₄ anatomy, F = fimbrylstyloid C₄ anatomy, R = rhynchosporoid C₄ anatomy, NADP-ME, NADP-malic enzyme, NAD-ME, NAD-malic enzyme, MS = mestome sheath, PCR = primary carbon reduction ('Kranz'), Grana: + = well developed, – = absent or at most stacks of three or fewer appressed thylakoids, Mitochondrial profiles are expressed on a per cell basis, BP = border parenchyma, Peripheral reticulum: + = poorly developed, ++ = well developed, n.a. = not applicable, 'blanks' = not scored.

<table>
<thead>
<tr>
<th>Photosynthetic pathway/ species</th>
<th>Photosynthetic organ</th>
<th>C₄ anatomical type</th>
<th>C₄ biochemical type</th>
<th>Location of suberized lamella</th>
<th>Border parenchyma and/or PCR cells chloroplasts</th>
<th>Mitochondrial profiles: Peripheral reticulum</th>
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<td></td>
<td></td>
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<td></td>
<td>Position</td>
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<td>n.a.</td>
<td>MS</td>
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<td>border parenchyma</td>
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<td>n.a.</td>
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</tr>
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<td>n.a.</td>
<td>MS</td>
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<td>MS</td>
<td>scattered</td>
<td>border parenchyma</td>
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<td>MS</td>
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<td>F</td>
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<td>MS</td>
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<tr>
<td>Pycreus polystachyos</td>
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<td>C</td>
<td>NADP-ME</td>
<td>MS</td>
<td>centrifugal</td>
<td>border parenchyma</td>
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<td></td>
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<tr>
<td>Rhynchospora rubra</td>
<td>leaf</td>
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<td>NADP-ME</td>
<td>MS</td>
<td>centrifugal</td>
<td>mestome sheath</td>
</tr>
</tbody>
</table>
Figures 7.1A-E: Transmission electron micrographs of fresh leaf blades and photosynthetic culms of sedges (cut transversely).

Figure 7.1A: *Eleocharis acuta* (C₃): only mestome sheath (MS) cell walls have a suberized lamella (SL and arrow heads). The suberized lamella (arrow heads) is discontinuous in the radial walls (RW). Inner tangential wall (ITW). The border parenchyma (BP) cells contain mitochondria (M) and one to few chloroplasts with grana (G), none are apparent in mestome sheath or parenchymatous bundle sheath (PBS) cells. Scale = 5 µm.

Figure 7.1B: *Pycreus polystachyos* (C₄): the ‘photosynthetic carbon reduction’ (PCR) cell in the border parenchyma position, internal to the mestome sheath (MS, without chloroplasts), has three centrifugal chloroplasts. Note the electron dense stroma (ST), convoluted thylakoid system, and peripheral reticulum (PR). Mitochondrion (M). The suberized lamella (arrow heads) occupies the mestome sheath and is discontinuous in the radial walls (RW). Scale = 2 µm.

Figure 7.1C: *Rhynchospora rubra* (C₄): mestome sheath cell (PCR site of this species) with chloroplasts showing electron dense stroma (ST), parallel agranal thylakoid system, and abundant starch grains (SG). The arrows indicate the position of the peripheral reticulum, appearing as a less electron dense zone. Mestome sheath (arrow heads). Radial wall (RW, cf. Fig. 7.1E). Scale = 1 µm.

Figure 7.1D: *Eleocharis retroflexa* ssp. *retroflexa* (C₄): showing the junction of two mestome sheath (MS) cells. The suberized lamella in places (SL) has a ‘tramline’ appearance, and is discontinuous in the radial wall (RW). The arrow heads indicate the extent of the suberized lamella, but note that the ‘gap’ is relatively electron dense. Primary carbon reduction cell (PCR). Scale = 1 µm.

Figure 7.1E: *Rhynchospora rubra* (C₄): the radial wall with pit field and suberized lamellae (arrow heads; Fig. 7.1C) at a higher magnification. The upper left suberized lamella (arrow) has a ‘tramline’ appearance. The upper suberized lamella is discontinuous, while the lower one is continuous and widened where it is traversed by plasmodesmata (PD, sectioned obliquely) in the pit field. Scale = 0.5 µm.
Figures 7.2A-F: Transmission electron micrographs of fresh (A-D and F) and dried (E) photosynthetic culms of *Eleocharis* (cut transversely).

Figure 7.2A: *E. caespitosissima* (C₄): part of a border parenchyma cell (the PCR site), internal to the mestome sheath (top left), with chloroplasts and mitochondria (M). Note the well stacked grana, starch grains (SG), and well developed peripheral reticulum (PR) with abundant electron transparent regions. Suberized lamella (arrow heads) in the mestome sheath wall is traversed by plasmodesmata (PD). Scale = 1 µm.

Figure 7.2B: *E. caespitosissima* (C₄): part of chloroplast of PCR cell showing well stacked grana (G), peripheral reticulum (PR) and associated electron transparent areas (asterisk). Scale= 0.2 µm.

Figure 7.2C: *E. caespitosissima* (C₄): photosynthetic carbon reduction cell (PCR) in the border parenchyma position with abundant chloroplasts (some with prominent starch grains) and mitochondria (M). A suberized lamella (arrow heads) occupies the walls of the mestome sheath (MS). Note the peripheral reticulum (PR) of chloroplasts in both the C₄ mesophyll or ‘primary carbon assimilation’ (PCA) and PCR cells. Scale = 4 µm.

Figure 7.2D: *E. pusilla* (C₃-C₄): border parenchyma cell (BP) showing mitochondria (M), and three scattered chloroplasts with well stacked grana (G). Suberized lamella (arrow heads) in the mestome sheath (MS) walls is traversed by plasmodesmata (PD) and is discontinuous in the radial walls (RW). Inner tangential wall (ITW). Scale = 2 µm.

Figure 7.2E: *E. retroflexa* ssp. *retroflexa* (C₄): ‘photosynthetic carbon reduction’ (PCR) cell in the border parenchyma position with disrupted chloroplasts. Note grana (arrows) and starch grains (unlabelled). The suberized lamella (SL) in the mestome sheath (MS) cell walls is intact. ‘Primary carbon assimilation’ (PCA) cell contents poorly preserved except for the starch grains (SG). Scale = 2 µm.

Figure 7.2F: *E. pusilla* (C₃-C₄): border parenchyma (BP) cells, with chloroplasts and abundant mitochondria (M), adjacent to the mestome sheath cell walls (top) with suberized lamella (arrow heads). Scale = 2 µm.
Automated identification and data retrieval

Introduction

Automation, in this case using the DELTA system (Dallwitz 1980; Dallwitz and Paine 1986), provides significant advantages over manual accumulation and maintenance of taxonomic descriptive data. For example, DELTA data can be translated into various formats for classificatory analyses (cf. Chapter 9), interactive identification, information retrieval and key-making (Watson 1987; Watson et al. 1988, 1989). The use of this methodology encourages the collection of comparative data against a character list incorporating mutually exclusive states, resulting in properly contrasting alternatives for identification. Other advantages of automation include the convenience of making corrections and additions, and the relative ease with which operationally efficient printed sequential keys can be produced for particular subsets of taxa and/or characters. By contrast, manually produced keys are often structurally inefficient, commonly fail to provide real contrasts and are difficult or impossible to revise in the light of new information.

All printed sequential keys, however, compare poorly with interactive systems such as ONLINE (Pankhurst and Aitchison 1975) or INTKEY (Dallwitz and Paine unpublished, but see Watson and Dallwitz 1988, Watson et al. 1989). The latter allow relatively easy, rapid and flexible identification, even of fragmentary material, and INTKEY in particular provides a wide array of ways of retrieving information for various purposes (see Watson et al. 1988, 1989 and examples therein). Watson’s data bank for world grass genera has served as a testing ground for the development of new technologies for identification and information retrieval, which are helping generate testable hypotheses in other disciplines (e.g. Amarasinghe and Watson 1989) and starting to greatly extend the range of taxonomic services for other disciplines (see Thomasson 1987; Thomasson et al. 1986). Thomasson called for the development of similar “computer banks of macromorphological and micromorphological” data of the Cyperaceae; and I hope that the data gathered in the course of my Ph.D. work, and organized via CONFOR and INTKEY, will go some way to satisfying his expressed requirement.
Interactive identification and data retrieval

Appendix 3 of this thesis is a floppy disk, carrying a complete INTKEY version of my data bank (see Appendix 1) for the sedge genera of the world, for use on MS-DOS microcomputers. Instructions for installing the data and the program are given in the file ‘README.1ST’. INTKEY is supplied with built-in prompts, and detailed operating instructions are accessible via HELP commands while the user is operating the program. Table 8.1 provides a summary of the facilities offered, and Watson et al. (1989) amply demonstrate both its flexibility in application and its capacity to cope with a very large data bank. It is necessary here only to exemplify the possibilities now open in relation to Cyperaceae, and to indicate how INTKEY has been used during the present study.

Examples 8.1-2 and Table 8.1 were produced directly from INTKEY output, with minimal editing. Comments (in italics) were added subsequently, though these too could have been inserted in the original LOG file using the COMMENT command. To save space some characters were replaced with dots in Example 8.1, the HELP facilities were listed together in Table 8.1, and the descriptions in Example 8.2 were edited into two columns. Concise examples are illustrated here, but in both cases the sessions could easily be extended; e.g. in Example 8.1 to provide a complete or partial description of the monotypic Lepironia, and in Example 8.2 to investigate further character state correlations pertinent to structural/functional relationships. The Plates (1-33) referred to in the INTKEY displays correspond with those presented in Chapter 3. The facility to display such illustrations directly within INTKEY is currently being developed (Dallwitz, work in progress; cf. Watson et al. 1989).

Example 8.1 illustrates the use of the commands BEST and DIFFERENCES which greatly assist in pursuing identifications, and also of TOLERANCE. The latter can be implemented to allow for possible errors either from the user or in the data, and is particularly useful when dealing with fragmentary material or where character interpretations are uncertain. This example represents a situation for which a printed key would usually offer no solution, and as such is a good illustration of both the scope of my data, and the versatility of INTKEY in dealing with a subset of characters relevant to the identification. It also highlights the ability of INTKEY and the data to provide taxonomic services to other disciplines, in this case for a museum conservator. Example 8.2 demonstrates use of the program and the data for information retrieval. It exemplifies searching for characters by name, use of the keyword REMAINING to specify taxa, use of the DESCRIBE command, and the ease with which lists of names and descriptions of taxa can be obtained for particular purposes. Taken together, these examples
demonstrate the flexibility of INTKEY, the ability of the sedge data bank to address practical problems, and the desirability of including in taxonomic descriptions a wide variety of features including anatomy, physiology, and ecology, to maximize the possibilities for applications over a wide range of research projects. In the present study to date INTKEY has been used to check the data, provide lists of taxa and summaries of character state distributions (Chapter 9), prepare diagnostic descriptions of groups (cf. Appendix 1), and cross-reference with classification (e.g. Table 9.5) and other correlates (e.g. photosynthetic pathways, see Table 5.4).

**Printed Keys**

The program KEY (Dallwitz 1974; Dallwitz and Paine 1986) for constructing identification keys provides for the specification of relative reliabilities of the characters and flexible treatment of intra-taxon variability. Subsets of taxa (e.g. for the production of regional keys) and/or characters (e.g. for keys based on vegetative anatomy) can be used to construct special-purpose keys, and can readily be extracted automatically from the main data set using INTKEY. Characters can be designated for use at particular positions in the key should this be thought desirable, and confirmatory characters can be presented where available.

Example 8.3 represents a general purpose key. The character reliability settings (see below) were chosen to facilitate ease of use, although some microscopic characters were necessary to achieve the fully resolved key. The latter has not been extensively tested in practice, though it appears to be quite practicable. It was produced as presented fully automatically, by directly linking the KEY output with the program TYPSET (Dallwitz and Zurcher 1988). Obviously inappropriate ‘characters’ in the main character list (Chapter 3; number of species, taxonomic groups, etc.) have been excluded. To cope with poorly scored descriptions, missing values have been treated as variable (see below). It will be observed that all the taxa are resolved, notwithstanding the inclusion of poorly scored genera, subgenera and variants provided with separate descriptions (cf. Chapter 2). While it would have been possible to obtain a tidier result by omitting the worst trouble-makers (e.g. *Rhynchocladium*) from the key, the present example effectively demonstrates the capacity of KEY and of the data to generate complete keys, according to user preferences and requirements. A significant factor leading to the repetitious appearance in the key of certain taxa and the need to resort occasionally to anatomy is the difficulty of dealing with variable taxa and character dependency patterns in the context of any large sequential key. For example, variability of inflorescence morphology in *Fimbristylis* accounts for its appearance four times. Some features
familiar to botanists are absent from the key. For example, a feature characteristic of many Northern Hemisphere species, viz. the perigynium (a tubular, flask-shaped spikelet phylly), is dependent upon spikelet phyllys being present and tubular (Chapter 3). ‘Perigynium’ is applicable to only 24 of the descriptions, and many of the taxa are variable for it. ‘Spikelet phyllys constituting perigynia’ is therefore not a very effective separator when considering the family as a whole, consequently it does not appear in this key.

Little effort has been expended on this example, it being felt that availability of the INTKEY version renders printed keys more or less obsolete. It has seemed sufficient for the present purpose, a) to demonstrate that a combination of data, CONFOR and KEY permits the flexible generation of printed keys to the genera of Cyperaceae; and b) to point out that both the data and the requisite programs are freely available on request for persons wishing to generate printed keys for their own use and to their own specifications.
Example 8.1. Identify fragmentary sterile culm material, suspected as being Cyperaceae, from a Papua New Guinean basket. A log file is opened to record the session for future reference.

INTKEY version: 19-JUL-89.
M.J. Dallwitz and T.A. Paine, CSIRO Division of Entomology, Australia.

World Sedge Genera 20:12:15 18-OCT-89
J.J. Bruhl, Research School of Biological Sciences, ANU, Canberra

Log opened.

Enter command: MATCH I O U
MATCH set to Inapplicables, Unknowns, Overlap.

Enter command: SET TOLERANCE 0
TOLERANCE set to 0.
132 taxa remain

Enter command: KEYWORDS CHARACTERS

CHARACTER KEYWORDS
Used
AVailable
ALL
SYnonyms
MOrphology
SHeaths
LiGules
CULM Epidermis
CULM Anatomy
CULM Characters
LEAF Epidermis
LEAF Anatomy
PHotosynthesis
FLoral
FEmale-fertile spikelets
MAle-fertile spikelets
PErianth
ANdroecium
POllen
Hypogynium
GYnoecium
EMbryo
CYtology
SPecies numbers
Distribution
GOetghebeur’s classification
NEarest neighbours
Bruhl’s classification
ECology
COmments
LIterature
SAmple
Use keywords for culm characters and distribution to explore the culm and distributional characters.

Enter command: INCLUDE CHAR CULMC DIST
83 characters included.

Enter command: CHARACTERS AVAILABLE
11: <plant> indumentum <culms, leaves, and or sheaths: colour>
13: lateral shoots <whether originating at the base of the uppermost culm internodes>
17: culms <whether possessing complete septa>

69: culms <mid-third of uppermost internode, whether possessing stomata>
70: <culm> stomata <position relative to the epidermals - best seen in transverse section>
71: <culm> stomata <whether obscured by projections from the adjacent epidermal cells, not to be confused with erect papillae>

77: culms <mid-third of uppermost internode, whether from their inception hollow or solid>

107: culm 'maximum cells-distant count' <after Hattersley and Watson 1975: excluding the parenchymatous bundle sheath>

338: <world distribution: this 'character' intended primarily for convenience in key-making>
340: Australasian distribution:
341: floristic kingdoms: <after Takhtajan 1969. Data for Takhtajan's floristic regions (see below)>

Use four of the available culm characters

Enter command: 17
17: culms <whether possessing complete septa>
   1. with complete septa <includes septate-nodulose> <Plates 3.5-6>
   2. without complete septa <implicit>

Enter value: 1
10 taxa remain
13. Baumea
21. Capitu.larina
29. Chorizandra
30. Chrysitrix
41. Cyperus subgen. Cyperus
48. Eleocharis (C3)
74. Lepidosperma
75. Lepironia
87. Neesenbeckia
108. Schoenoplectus

Enter command: 77
77: culms <mid-third of uppermost internode, whether from their inception hollow or solid>
   1. initially hollow <Plates 3.5-6>
   2. initially 'solid' <includes 'reticulate' and 'spongy'> <Plates 9.6, 11.1>

Enter value: 1
7 taxa remain
21. Capitularina
29. Chorizandra
30. Chrysitrix
41. Cyperus subgen. Cyperus
48. Eleocharis (C3)
75. Lepironia
87. Neesenbeckia

Enter command: 70
70: <culm> stomata <position relative to the epidermals - best seen in transverse section>
   1. sunken <Plate 8.6>
   2. flush <Plates 10.7, 11.7, 12.2>
   3. raised <Plates 7.4, 8.7, 9.7>
Enter value: 1
Also setting -
69: culms
   1. with stomata
5 taxa remain
29. Chorizandra
30. Chrysitrix
41. Cyperus subgen. Cyperus
75. Lepironia
87. Neesenbeckia

Enter command: 71
71: <culm> stomata <whether obscured by projections from the adjacent epidermal cells, not to be confused with erect papillae>
   1. obscured by projections from the adjacent epidermal cells <Plates 5.5-6, 7.6, 8.6>
   2. not obscured by projections from the adjacent epidermal cells <Plates 5.8, 8.2>
Enter value: 1
4 taxa remain
29. Chorizandra
30. Chrysitrix
75. Lepironia
87. Neesenbeckia

Request the program to suggest suitable characters from those available.

Enter command: BEST

SEPN. BEST CHARACTERS
0.81 66: <culm> silica bodies <whether present>
0.42 338: <world distribution: this 'character' intended primarily for convenience in key-making>
0.33 76: culm trans-section <mid-third of the uppermost internode, terms after Metcalfe 1971>
0.21 67: <culm> silica bodies <location, with respect to the epidermis>
0.25 16: culms <whether fibrous or herbaceous>
0.25 72: <culm> subsidiaries in surface view <shape>
0.25 74: <culm> subsidiaries in transverse section <shape>
0.16 62: <culm> epidermal cells in transverse section <whether radially elongated>
0.16 101: <culm> sclerenchyma <i.e. caps and girders: whether in direct contact with all of the vascular bundles>
0.10 100: <culm> sclerenchyma <distribution>
End of available BEST characters.
Enter command, or <CR> to get the next set of BEST characters: 66
66: <culm> silica bodies <whether present>
   1. present <Plate 6.4>
   2. absent
Enter value: 2
3 taxa remain
29. Chorizandra
30. Chrysitrix
75. Lepironia
Enter command: 80
80: <culm> pith <whether with translucent tissue>
   1. with translucent tissue <Plates 8.5, 10.1, 11.2, 12.8>
   2. without translucent tissue <Plate 9.3>
Enter value: 2
Also setting -
79: culms
   1. medullated
   2 taxa remain
30. Chrysitrix
75. Lepironia

To find suitable characters to complete the identification, list the differences between Chrysitrix and Lepironia for culm epidermal and anatomical characters

Enter command: DIFFERENCES REMAINING CULMEPIDERMS CULMANATOMY
89: <culm> vascular 'rings' completely embedded in chlorenchyma <number>
30. Chrysitrix
   0
75. Lepironia
   1
102: <culm> sclerenchyma <i.e. the caps and/or girders: whether coalescing to form a 'ring'>
30. Chrysitrix
   2. not coalescing to form a 'ring' (when applicable)
75. Lepironia
   1. coalescing to form a 'ring' (when applicable)
103: <culm> strands <whether all aligned with the vascular bundles>
30. Chrysitrix
   1. all aligned with the vascular bundles (when applicable)
75. Lepironia
   2. not all aligned with the vascular bundles (when applicable)
105: <culm> spongy mesophyll <whether present>
30. Chrysitrix
   2. absent
75. Lepironia
   1. present

4 differences between taxa.

Enter command: 102
102: <culm> sclerenchyma <i.e. the caps and/or girders: whether coalescing to form a 'ring'>
   1. coalescing to form a 'ring' <Plates 8.4, 9.7, 11.6>
   2. not coalescing to form a 'ring' <Plate 9.5>
Enter value: 1
Also setting -
100: sclerenchyma
   2. comprising girders
   3. forming caps on the vascular bundles
1 taxon remains
75. Lepironia

To allow for the possibility of an interpretative or data error, retrieve all genera differing from Lepironia in terms of only 1 of the characters used, and check that Lepironia actually occurs in New Guinea.

Enter command: SET TOL 1
TOLERANCE set to 1.
14 taxa remain
( 1) 14. Becquerelia
(1) 29. Chorizandra
(1) 30. Chrysitrix
(1) 34. Costularia brevicaulis
(0) 75. Lepironia
(1) 80. Mapaniopsis
(1) 87. Neesenbeckia
(1) 94. Phylloscirpus
(1) 95. Pleurostachys
(1) 103. Rhynchocladium
(1) 106. Rhynchospora (C4 chlorocyperoid)
(1) 117. Sumatroscirpus
(1) 125. Trichoschoenus
(1) 131. Volkiella

Enter command: **340**

340: Australasia distribution:
1. Tasmania
2. New South Wales
3. Australian Capital Territory
4. Victoria
5. Western Australia
6. Queensland
7. Northern Territory
8. South Australia
9. New Guinea
10. New Zealand
11. not known in Australasia <implicit>

Enter value: 9
1 taxon remains
75. Lepironia

Conclude the session. The output file becomes available. Ethnographic notes by Kern (1974 p.462) include that statement that Lepironia “in New Guinea ... is used ... for basket-making”.

Enter command: **FINISH**
Output files-
sample.egs
Example 8.2. Describe the C₄ genera from Malesia in terms of C₄ anatomical and biochemical type and ecology.

Enter command: MATCH 0
MATCH set to Overlap.

Enter command: SET TOL 0
TOLERANCE set to 0.
132 taxa remain

List the available photosynthetic pathway characters.

Enter command: CHAR PHOTO
163: <photosynthetic pathway: of the culms, leaves or inflorescence bracts, predicted anatomically or via δ¹³C or Γ values, or established biochemically>
164: <C₄> anatomical type <of the culms and/or leaves, determined from the primary vascular bundles>
165: <C₄> biochemical type <as determined by enzyme assay: data from Ueno et al. 1986, and Bruhl et al. 1987, Species samples in parentheses>
166: δ¹³C value range <literature sources in parentheses>
167: Γ value range <literature sources in parentheses>

Enter command: 163
163: <photosynthetic pathway: of the culms, leaves or inflorescence bracts, predicted anatomically or via δ¹³C or Γ values, or established biochemically>
  1. C₃
  2. C₃-C₄ intermediate
  3. C₄

Enter value: 3
27 taxa remain

Search for geographic characters which include Malesia.

Enter command: CHAR "MALESIA"
343: Paleotropical subkingdoms: <after Takhtajan 1969>
347: Indomalesian subkingdom regions: <after Takhtajan 1969>

Enter command: 347
347: Indomalesian subkingdom regions: <after Takhtajan 1969>
  1. Indian
  2. Indo-Chinese
  3. Malesian <Malayan>
  4. Papuan

Enter value: 3
Also setting -
343: Paleotropical subkingdoms:
  3. Indomalesian
  4. Polynesian
  5. Neocaledonian
Also setting -
341: floristic kingdoms:
  2. Paleotropical
13 taxa remain
1. Abildgaardia (C₄)
19. Bulbostylis
41. Cyperus subgen. Cyperus
61. Fimbristylis
71. Kyllinga
76. Lipocarpha
81. Mariscus
85. Monandrus
99. Pycreus
100. Queenslandiella
102. Remirea
105. Rhynchospora (C4 rhynchosporoid)
122. Torulinium

Describe the remaining taxa in terms of selected characters.

Enter command: DESC 164-165 ECOL
1. Abildgaardia <Vahl> (C4)
   164: anatomical type
   1. fimbristyloid
165: biochemical type
   2. NADP-ME
360:
   2. open habitats
361:
   2. helophytic
   3. mesophytic
362:
   2. glycophytic
363:
   2. calcifuge
364:
   1. weedy
   2. not weedy

85. Monandrus <Vorster>
   164: anatomical type
   2. chlorocyperoid
360:
   2. open habitats
361:
   2. helophytic
   3. mesophytic
362:
   2. glycophytic
363:
   2. calcifuge
364:
   1. weedy
   2. not weedy

99. Pycreus <P. Beauvois>
   164: anatomical type
   2. chlorocyperoid
165: biochemical type
   2. NADP-ME
360:
   2. open habitats
361:
   1. hydrophytic
   2. helophytic
   3. mesophytic
362:
   1. halophytic
   2. glycophytic
364:
   1. weedy
   2. not weedy

100. Queenslandiella <Domin>
   164: anatomical type
2. glycophytic
364:
  1. weedy
  2. not weedy

61. Fimbristylis <Vahl>
164: anatomical type
  1. fimbristyloid
165: biochemical type
  2. NADP-ME
360:
  2. open habitats
361:
  2. helophytic
362:
    1. halophytic
    2. glycophytic
363:
    1. calcicole
    2. calcifuge
364:
    1. weedy
    2. not weedy

71. Kyllinga <Rottboell>
164: anatomical type
  2. chlorocyperoid
165: biochemical type
  2. NADP-ME
360:
  2. open habitats
361:
  2. helophytic
362:
    1. halophytic
    2. glycophytic
363:
    1. calcicole
    2. calcifuge
364:
    1. weedy
    2. not weedy

76. Lipocarpha <R. Brown>
164: anatomical type
  2. chlorocyperoid
165: biochemical type
  2. NADP-ME
360:
  2. open habitats
361:
  2. helophytic
362:
  2. glycophytic
363:
  2. calcifuge
364:
  1. weedy
  2. not weedy

81. Mariscus <Vahl>
165: biochemical type
  2. NADP-ME

2. chlorocyperoid
360:
  2. open habitats
361:
  3. mesophytic
362:
    2. glycophytic
364:
    1. weedy

102. Remirea <Aublet>
164: anatomical type
  2. chlorocyperoid
360:
  2. open habitats
361:
  3. mesophytic
362:
    1. halophytic
363:
    1. calcicole
364:
    2. not weedy

105. Rhynchospora <Vahl corr. Wild.> (C4 rhynchosporoid)
164: anatomical type
  4. rhynchosporoid
165: biochemical type
  2. NADP-ME
360:
  2. open habitats
361:
  3. mesophytic
362:
    1. halophytic
    2. glycophytic
363:
    2. calcifuge
364:
    2. not weedy

122. Torulinium <Desvaux ex Hamilton>
164: anatomical type
  2. chlorocyperoid
165: biochemical type
  2. NADP-ME
360:
  2. open habitats
361:
  2. helophytic
362:
    1. halophytic
    2. glycophytic
363:
    2. calcifuge
364:
    1. weedy
    2. not weedy
Example 8.3. General Key to Sedge Genera of the World

Characters – 374 in data, 326 included, 175 in key.
Items – 154 in data, 132 included, 220 in key.

RBASE = 1.40 ABASE = 2.00 REUSE = 1.00 VARYWT = 0.70

Characters included 3–164 168–178 180–320 322–332 338


Items included 1–132

1(0). Plants monoecious, with all spikelets unisexual. .............................. 2
Plants bisexual, with bisexual spikelets. ........................................... 26
Plants dioecious. ............................................................................. 190

2(1). Floral bracts present. ............................................................... 3
Floral bracts absent. ...................................................................... 15

3(2). Lateral branch inflorescences ‘conipaniculate’ ......................... 4
Lateral branch inflorescences ‘planipaniculate’. .............................. Becquerellia
Lateral branch inflorescences anthelate. ........................................ 8
Lateral branch inflorescences capitate. .......................................... 9

4(3). Culms ‘central’; culm intercostal cell anticlinal walls sinuate; leaf blade vascular bundles in one row. ........................................ 5
Culms ‘axillary’; culm intercostal cell anticlinal walls straight; leaf blade vascular bundles ‘zig-zagged’. ................................. Everardia

5(4). Spikelet prophylls bract-like; rachillae persistent; leaf blade palisade mesophyll present; cotyledon ‘markedly widened’. .......... 6
Spikelet prophylls tubular; rachillae deciduous; leaf blade palisade mesophyll absent; cotyledon not markedly widened. ............ Schoenoxiphium

6(5). Female-fertile spikelets laterally compressed; floral bracts distichous; each flower enclosed directly by a distal floral bract; floral bracts of male spikelets distichous; style divided for about half its length. .................. 7
Female-fertile spikelets terete; floral bracts tristichous; each flower enclosed directly
by its subtending floral bract; floral bracts of male spikelets tristichous; style divided nearly to base. ................................. \textit{Lagenocarpus}

7(6). Style longer than the fruit; culm subsidiaries in transverse section smaller than the adjacent epidermal cells; culm parenchymatous bundle sheaths with extensions; leaf blade subsidiaries in transverse section smaller than the adjacent epidermal cells; leaf blade midrib anatomically asymmetrical. ................................. \textit{Acritulus}

Style about as long as the fruit; culm subsidiaries in transverse section similar in size to the adjacent epidermal cells; culm parenchymatous bundle sheaths without extensions; leaf blade subsidiaries in transverse section similar in size to the adjacent epidermal cells; leaf blade midrib anatomically symmetrical. ................................. \textit{Scleria}

8(3). Plant indumentum purple; culms armed with prick-le-hairs; anther apiculus obtuse; culms 'not photosynthetic'; style about as long as the fruit. ................................. \textit{Bisboecklera}

Plant indumentum not purple; culms without prick-le-hairs; anther apiculus acute; culms photosynthetic; style shorter than the fruit. ................................. \textit{Calyptracarya}

9(3). Culms 'central'. ................................................. 10

Culms 'axillary'. .................................................. 14

10(9). Female-fertile spikelets laterally compressed. ................................................. 11

Female-fertile spikelets terete. ................................................. 12

11(10). Rachillae vestigial; terminal flower present; style-base continuous with the fruit apex; culms with a hypodermis; abaxial leaf blade epidermal cells regular and rectangular. ................................. \textit{Diplacrum}

Rachillae contracted; terminal flower absent; style-base sharply differentiated from the fruit apex; culms without a hypodermis; abaxial leaf blade epidermal cells irregular. ................................. \textit{Scleria}

12(10). Sheath apices indumented; lateral inflorescence branches elongated; stigmata 3; floral bracts 'aristate'. ................................................. 13

Sheath apices glabrous; lateral inflorescence branches contracted; stigmata 1 to 2; floral bracts acute. ................................................. \textit{Exochogyne}

13(12). Sheath apices n-shaped; inflorescence gynandrous; rachillae contracted; culms without prick-le-hairs; inflorescence prophylls epulvinate. ................................. \textit{Lagenocarpus}

Sheath apices 'truncate'; inflorescence with the sexes mixed; rachillae vestigial; culms armed with prick-le-hairs; inflorescence prophylls adaxially pulvinate. ................................. \textit{Becquererelia}

14(9). Sheath apices n-shaped; sheath apices glabrous; ligules present; inflorescence gynandrous; inflorescence 'conipaniculate'. ................................................. \textit{Trilepis}

Sheath apices 'truncate'; sheath apices indumented; ligules absent; inflorescence with the sexes mixed; inflorescence capitulate. ................................................. \textit{Cephalocarpus}

15(2). Leaves spirally disposed. ................................................. \textit{Cymophyllus}

Leaves distichous. ................................................. \textit{Carex subgen. Carex}

Leaves tristichous. ................................................. 16

16(15). Rachillae distally hooked; androecial meristems present in the female-only flowers. ................................................. \textit{Uncinia}

Rachillae distally straight; androecial meristems absent. ................................................. 17
17(16). Lateral inflorescence branch bases enclosed. ........................................ 18
Lateral inflorescence branch bases exposed. ..................................................... 24

18(17). Inflorescence elongated. ................................................................. 19
Inflorescence contracted. .............................................................................. 23

19(18). Culm silica bodies present. ................................................................. 20
Culm silica bodies absent. .......................................................... Vesticarex

20(19). Lateral branch inflorescences 'conipaniculate' ..................................... 21
Lateral branch inflorescences 'planipaniculate'. .............................................. Carex subgen. Indocarex
Lateral branch inflorescences capitate. .......................................................... 22

21(20). Adaxial sides of the leaf sheaths similar in texture to the abaxial sides; leaf blade palisade mesophyll present. ....................................................... Carex subgen. Indocarex
Adaxial sides of the leaf sheaths differing in texture from the abaxial sides; leaf blade palisade mesophyll absent. ...................................................... Schoenoxiphium

22(20). Culm parenchymatous bundle sheaths with extensions ....................... Carex subgen. Carex
Culm parenchymatous bundle sheaths without extensions. ........................... Carex subgen. Indocarex

23(18). Subtending bracts non-overlapping; anther apiculus 5 to 10 percent of anther length; culm intercostal cells irregular; culm parenchymatous bundle sheaths with extensions. ............................................................... Carex subgen. Carex
Subtending bracts imbricate; anther apiculus 10 percent of anther length or more; culm intercostal cells regular and rectangular; culm parenchymatous bundle sheaths without extensions. ............................................................... Carex subgen. Primocarex

24(17). Anther apiculus 5 to 10 percent of anther length. ............................... 25
Anther apiculus 10 percent of anther length or more. ................................. Carex subgen. Primocarex

25(24). Inflorescence prophylls present. ......................................................... Schoenoxiphium
Inflorescence prophylls absent. ................................................................. Carex subgen. Vignea

26(1). Plants with hermaphrodite flowers. ....................................................... 27
Plants without hermaphrodite flowers. .......................................................... 168

27(26). Plants with a fenugreek odour. ............................................................ 28
Plants without a fenugreek odour. ................................................................. 30

28(27). Lateral inflorescence branch bases enclosed; floral bracts deciduous; primary inflorescence bracts without prickle-hairs; inflorescence prophylls epulvinate; leaf blade midrib with a secondary bundle abaxial to the primary bundle. ............................................................... Monandrus
Lateral inflorescence branch bases exposed; floral bracts persistent; primary inflorescence bracts armed with prickle-hairs; inflorescence prophylls adaxially pulvinate; leaf blade midrib without a secondary bundle abaxial to the primary bundle. ............................................................... 29

29(28). Stamens 2; inflorescence elongated; leaf blade trans-section 'flanged V-shaped'; leaf blade 'maximum cells-distant count' one; spikelet prophylls adaxially pulvinate. ............................................................... Queenslandiella
Stamens 3; inflorescence contracted; leaf blade trans-section 'V-shaped'; leaf blade 'maximum cells-distant count' more than one; spikelet prophylls epulvinate. ............................................................... Courtoisina
30(27). Floral bracts present. .................................................. 31
Floral bracts absent. ......................................................... 163

31(30). Each flower enclosed directly by its subtending floral bract. ........................................ 32
Each flower enclosed directly by a distal floral bract. ....................................................... 115

32(31). Female-fertile spikelets laterally compressed. ........................................................... 33
Female-fertile spikelets dorsiventrally compressed. ........................................................... 56
Female-fertile spikelets terete. ................................................................. 61

33(32). Style-base enlarged-bulbous, or enlarged-pyramidal. ............................................... 34
Style-base not enlarged. ................................................................. 45

34(33). Floral bracts increasing in length acropetally. ............................................................. 35
Floral bracts similar in length along the spikelet. ............................................................... 36
Floral bracts decreasing in length acropetally. ................................................................. 42

35(34). Culms armed with prickle-hairs; proximal sterile bracts 3 or more; style indumented;
style-base deciduous; culm ‘maximum cells-distant count’ one. ........................................... Abildgaardia (C₄)
Culms without prickle-hairs; proximal sterile bracts 0 to 2; style glabrous; style-base persistent; culm ‘maximum cells-distant count’ more than one. Eleocharis (C₃)

36(34). Sheath apices ‘truncate’; culm stomata flush to raised; filaments desiccating. ............ 37
Sheath apices V-shaped; culm stomata sunken; filaments markedly elongating. .................. Androtrichum

37(36). Rachillae contracted; style-base sharply differentiated from the fruit apex; mesocarp fibrous. ................................................................. 38
Rachillae elongated; style-base continuous with the fruit apex; mesocarp spongy. .......... Anosporum

38(37). Inflorescence always restricted to a solitary spikelet. ............................................... 39
Inflorescence at least sometimes comprising more than a solitary spikelet. ................... 41

39(38). Culm parenchymatous bundle sheaths present; embryo ‘constriction’ absent. ........ 40
Culm parenchymatous bundle sheaths absent; embryo ‘constriction’ present, above the coleorhiza. ............................................................... Eleocharis (C₃)

40(39). Style-base persistent; culm ‘maximum cells-distant count’ more than one; adaxial sides of the leaf sheaths similar in texture to the abaxial sides; culm spongy mesophyll absent; culm palisade mesophyll present.  Eleocharis (C₃)
Style-base deciduous; culm ‘maximum cells-distant count’ one; adaxial sides of the leaf sheaths differing in texture from the abaxial sides; culm spongy mesophyll present; culm palisade mesophyll absent. ........ Fimbristylis

41(38). ‘Basal spikelets’ present; anther basal appendages forming prominent spongy lobes.  Crosslandia
‘Basal spikelets’ absent; anther basal appendages not comprising spongy lobes. ............... Fimbristylis

42(34). Sheath apices indumented; long-rhizomatous; rachillae deciduous; anthers not apiculate; culms 100 cm high or more. Sphaerocyperus
Sheath apices glabrous; caespitose; rachillae persistent; anthers ‘apiculate’; culms 11 to 100 cm high. 43
43(42). Ligules present; rachilla internodes equal in length whether fertile or sterile; anther apiculus indumented; style about as long as the fruit; culm subsidiaries in transverse section smaller than the adjacent epidermal cells. *Abildgaardia* (C₃) Ligules absent; rachilla internodes of different lengths, the fertile ones elongated; anther apiculus glabrous; style longer than the fruit; culm subsidiaries in transverse section similar in size to the adjacent epidermal cells. .......... 44

44(43). Rachillae of indefinite growth; perianth absent; 'basal spikelets' absent; perennial; proximal sterile bracts 3 or more. .......... 44

45(33). Floral bracts persistent. .......... 46
Floral bracts deciduous. .......... 49

46(45). Ligules present; floral bracts spirally disposed; inflorescence elongated; stigmatic surface papillose; fruit epidermal cells longitudinally elongated. .......... 46

47(46). Leaves distichous; terminal spikelets present; hypogynium present; primary inflorescence bracts distichous; style-base sharply differentiated from the fruit apex. .......... 47

48(47). Plants lemon-scented; spikelet prophylls tubular; inflorescence prophylls epulvinate; inflorescence prophylls bract-like; spikelet prophylls epulvinate. .......... 48

49(45). Perianth present. .......... 50
Perianth absent. .......... 51

50(49). Rachillae deciduous; style indumented; style-base sharply differentiated from the fruit apex; culms 100 cm high or more. .......... 50

51(49). Floral bracts increasing in length acropetally; coleorhiza basal; germination pore perpendicular to the first first embryonic leaf primordium. .......... 51

52(51). Hypogynium present. .......... 52
Hypogynium absent. .......... 53

53(52). Terminal spikelets present. .......... 54
Terminal spikelets absent. .......... 54
54(53). Culm boundary layer cells `large`; culm boundary layer cells chlorenchymatous; culm `maximum cells-distant count` one; C4; culm parenchymatous bundle sheaths only adjacent metaxylem vessels. ........................................ 55
Culm boundary layer cells `small`; culm boundary layer cells non-chlorenchymatous; culm `maximum cells-distant count` more than one; C3; culm parenchymatous bundle sheaths interrupted by fibres. ................................. Cyperus subgen. Pycnostachys

55(54). Fruit laterally compressed. ........................................... Pycreus
Fruit dorsiventrally compressed. ........................................... Cyperus subgen. Cyperus
Fruit not compressed. ....................................................... Cyperus subgen. Cyperus

56(32). Ligules present; terminal spikelets present. ....................... 57
Ligules absent; terminal spikelets absent. ................................ 58

57(56). Rachillae deciduous; style indumented; style-base sharply differentiated from the fruit apex; culms 100 cm high or more. ........................................... Sumatrosceirpus
Rachillae persistent; style glabrous; style-base continuous with the fruit apex; culms 11 to 100 cm high. ................................................ Baeothryon

58(56). Spikelet prophylls present; inflorescence prophylls present. .... 59
Spikelet prophylls absent; inflorescence prophylls absent. ............... Ascolepis

59(58). Lateral inflorescence branch bases enclosed; primary inflorescence bracts distichous; style-base sharply differentiated from the fruit apex. ....... Volkiella
Lateral inflorescence branch bases exposed; primary inflorescence bracts tristichous; style-base continuous with the fruit apex. ......................... 60

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65(64). Leaves cauline; inflorescence terminal; fruit epidermal cells isodiametric; fruit not compressed; culm parenchymatous bundle sheaths interrupted by fibres. ......................................... Fuirena
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68(66). Inflorescence always restricted to a solitary spikelet. 69
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69(68). Style-base enlarged-bulbous, or enlarged-pyramidal; stigmatic papillae 'zoned'. ..
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78(63). Leaves cauline; inflorescence at least sometimes comprising more than a solitary spikelet; rachillae elongated; style-base not enlarged; style-base continuous with the fruit apex. ................. *Dulichium*

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79(63). Vernation conduplicate; leaf blades with a keeled midrib; leaf blade trans-section ‘V-shaped’; anther apiculus acuminate; anther apiculus indumented. ................. *Blysmus*

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differentiated from the fruit apex; second embryonic leaf primordium well
developed.  

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       leaf primordium rudimentary.  

       *Eleocharis* (C₃)  

88(87). Inflorescence terminal; stigmatic surface glabrous; fruit epidermal cells
isodiametric; mesocarp spongy; culms with a hypodermis.  

       Inflorescence pseudoaxillary; stigmatic surface papillose; fruit epidermal cells
       longitudinally elongated; mesocarp fibrous; culms without a hypodermis.  

       *Schoenoplectus*  

89(61). Leaf sheaths open to the base; leaf sheaths with margins overlapping distally; plants
'spiny'; culm substomatal chambers lined with sclereids; coleoptile sublateral.  

       Leaf sheaths tubular; leaf sheaths with entire margins; plants without spines; culm
       substomatal chambers without sclereids; coleoptile basal.  

       *Reedia*  

90(89). Leaves cauline.  

       Leaves radical.  

       *Fuirena*  

91(90). Sheath apices indumented.  

       Sheath apices glabrous.  

       *Bulbostylis*  

92(91). 'Basal spikelets' present; coleorhiza basal.  

       'Basal spikelets' absent; coleorhiza lateral.  

       *Fimbristylis*  

93(92). Rachillae becoming enlarged and woody with age; rachillae deeply pitted; anther
basal appendages forming prominent spongy lobes; culm epidermal cells in
transverse section 'radially elongated'; culm silica bodies absent.  

       Rachillae not becoming enlarged and woody with age; rachillae not deepy pitted;
anther basal appendages not comprising spongy lobes; culm epidermal cells in
transverse section isodiametric; culm silica bodies present.  

       *Tylocarya*  

94(93). Style-base continuous with the fruit apex; stigmatic papillae 'foot-like'; stigmatic
papillae not zoned; embryo 'constriction' present, above the coleorhiza.  

       Style-base sharply differentiated from the fruit apex; stigmatic papillae 'long';
stigmatic papillae 'zoned'; embryo 'constriction' absent.  

       *Eleogiton*  

95(92). The fertile rachilla internodes thick and corky at maturity.  

       The fertile rachilla internodes neither thick nor corky at maturity.  

       *Eleocharis* (C₃)  

96(95). Style-base persistent; culm 'maximum cells-distant count' more than one; adaxial
sides of the leaf sheaths similar in texture to the abaxial sides; culm spongy
mesophyll absent; culm palisade mesophyll present.  

       Style-base deciduous; culm 'maximum cells-distant count' one; adaxial sides of the
leaf sheaths differing in texture from the abaxial sides; culm spongy mesophyll
present; culm palisade mesophyll absent.  

       *Fimbristylis*  

97(90).
<table>
<thead>
<tr>
<th>Number</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>98(97).</td>
<td>Rachillae of indefinite growth; inflorescence anthelate; lateral inflorescence branches elongated; caespitose; inflorescence prophylls adaxially pulvinate. Torulinium Rachillae of definite growth; inflorescence capitulate; lateral inflorescence branches contracted; long-rhizomatous; inflorescence prophylls epulvinate. Remirea</td>
</tr>
<tr>
<td>101(100).</td>
<td>Floral bracts persistent.                                                                                           Floral bracts deciduous.</td>
</tr>
<tr>
<td>102(101).</td>
<td>Sheath apices indumented; fruit epidermal cells isodiametric; culm parenchymatous bundle sheaths interrupted by fibres. Sheath apices glabrous; fruit epidermal cells longitudinally elongated; culm parenchymatous bundle sheaths complete. Schoenoplectus</td>
</tr>
<tr>
<td>103(102).</td>
<td>Lateral branch inflorescences anthelate; spikelet prophylls present; culm trans-section circular; primary inflorescence bracts without prickle-hairs; inflorescence prophylls epulvinate. Nemum Lateral branch inflorescences capitulate; spikelet prophylls absent; culm trans-section triangular; primary inflorescence bracts armed with prickle-hairs; inflorescence prophylls adaxially pulvinate. Oxyccaryum</td>
</tr>
<tr>
<td>104(101).</td>
<td>Leaves cauline.                                                                                                  Leaves radical.</td>
</tr>
<tr>
<td>105(104).</td>
<td>Culms fibrous; style longer than the fruit; fruit dorsiventrally compressed; adaxial sides of the leaf sheaths differing in texture from the abaxial sides; culm epidermal zones wider costally than intercostally. Scirpus Culms herbaceous; style about as long as the fruit; fruit not compressed; adaxial sides of the leaf sheaths similar in texture to the abaxial sides; culm epidermal zones wider intercostally than costally. Fuirena</td>
</tr>
<tr>
<td>106(104).</td>
<td>Ligules present.                                                                                                  Ligules absent.</td>
</tr>
<tr>
<td>107(106).</td>
<td>Inflorescence terminal; fruit epidermal cells isodiametric; culm epidermal cell outer walls thick; culm parenchymatous bundle sheaths interrupted by fibres; culm palisade mesophyll absent. Scirpus Inflorescence pseudoaxillary; fruit epidermal cells longitudinally elongated; culm epidermal cell outer walls moderately thickened; culm parenchymatous bundle sheaths complete; culm palisade mesophyll present. Schoenoplectus</td>
</tr>
<tr>
<td>108(106).</td>
<td>Embryo ellipsoid; cotyledon not markedly widened. Isolepis Embryo mushroom-shaped; cotyledon 'markedly widened'. Schoenoplectus</td>
</tr>
<tr>
<td>109(100).</td>
<td>Hypogynium present; culms fibrous; style-base sharply differentiated from the fruit apex; anther apiculus 5 to 10 percent of anther length; culm subsidiaries in transverse section similar in size to the adjacent epidermal cells. Ficinia Hypogynium absent; culms herbaceous; style-base continuous with the fruit apex;</td>
</tr>
</tbody>
</table>
anther apiculus 10 percent of anther length or more; culm subsidiaries in transverse section larger than the adjacent epidermal cells.  10.  

| 110(100). Hypogynium present; style-base sharply differentiated from the fruit apex. | 11 |  
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| 116(115). Female-fertile spikelets gynandrous. | 117 |
| 116(115). Female-fertile spikelets androgynous. | 125 |
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| 117(116). Stamens 3. | 118 |
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| 118(117). Rachilla internodes equal in length whether fertile or sterile; the fertile rachilla internodes 'straight'; style-base enlarged-bulbous, or enlarged-pyramidal; floral bracts indumented; culm parenchymatous bundle sheaths interrupted by fibres. | 119 |
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\[ \text{Gymnoschoenus} \]

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120(119). Floral bracts persistent. 121

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121(120). Perianth present; culm palisade mesophyll present; endocarp light; mesocarp not oily. 122

Perianth absent; culm palisade mesophyll absent; endocarp dark; mesocarp oily. 124

122(121). Inflorescence 'conipaniculate'; style-base persistent. 123

Inflorescence capitate; style-base deciduous. 123

123(122). Stigmata 3; culm silica bodies luminal; culm stomata flush to raised; culms initially 'solid'; perianth of 'scales'. 124

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124(120). Sheath apices indumented; ligules obtuse; ligules glabrous; culms without complete septa; primary inflorescence bracts armed with prickle-hairs. 126

Sheath apices glabrous; ligules acute; ligules indumented; culms with complete septa; primary inflorescence bracts without prickle-hairs. 127

125(116). Leaves distichous. 128

Leaves tristichous. 129

126(125). Sheath apices 'truncate'; lateral branch inflorescences 'conipaniculate'; rachillae persistent; style-base sharply differentiated from the fruit apex; fruit trans-section elliptical. 130

Pleurostachys

Sheath apices V-shaped; lateral branch inflorescences 'planipaniculate'; rachillae deciduous; style-base continuous with the fruit apex; fruit trans-section triangular. 131

Rhynchochladium

127(116). Floral bracts spirally disposed. 132

Floral bracts distichous. 133

Floral bracts tristichous. 134

128(127). Rachilla internodes equal in length whether fertile or sterile; the fertile rachilla internodes 'straight'. 135

Rachilla internodes of different lengths, the fertile ones elongated; the fertile rachilla internodes flexuose. 136

129(128). Inflorescence 'conipaniculate'; coleoptile sublateral; coleorhiza subbasal. 137

\[ \text{Lepidosperma} \]

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Inflorescence capitate; coleoptile lateral; coleorhiza basal. \[ \text{Actinoschoenus} \]

130(128). Sheath apices indumented; ligules indumented; anther apiculus acute; stigmatic surface papillose; rachillae winged adjacent to the flowers. 131

Schoenus

Sheath apices glabrous; ligules glabrous; anther apiculus acuminate; stigmatic surface glabrous; rachillae wingless. 132

Ptilanthelium
131(115). Stamens 1. ............................................. *Hypolytrum*  
Stamens 2. ............................................. 132  
Stamens 3. ............................................. 135  
Stamens 4 or more. ..................................... 159

132(131). Sheath apices ‘truncate’; inflorescence proliferous; stigmatic surface glabrous.  
Sheath apices V-shaped; inflorescence not proliferous; stigmatic surface papillose.  

133(132). Perianth present; endocarp membranous; adaxial sides of the leaf sheaths differing  
in texture from the abaxial sides; endocarp light.  
Perianth absent; endocarp sclerenchymatous; adaxial sides of the leaf sheaths similar  
in texture to the abaxial sides; endocarp dark.  

134(133). Leaf sheaths with margins overlapping distally; sheath apices indumented; lateral  
inflorescence branch bases enclosed; subtending bracts non-overlapping; terminal  
spikelets present.  
Leaf sheaths with entire margins; sheath apices glabrous; lateral inflorescence  
branch bases exposed; subtending bracts imbricate; terminal spikelets absent.  

135(131). Sheath apices indumented.  
Sheath apices glabrous.  

136(135). Lateral shoots originating only at the base of the uppermost culm internode.  
Lateral shoots originating below the base of the uppermost culm internode.  

137(136). Perianth members persistent on the rachilla; culms herbaceous.  
Perianth members deciduous with the fruit; culms fibrous.  

138(137). Style divided for about half its length; culm intercostal cells irregular; culm  
epidermal cell outer walls thick; culm mesophyll translucent tissue absent.  
Style divided for much less than half its length; culm intercostal cells regular and  
rectangular; culm epidermal cell outer walls moderately thickened; culm  
mesophyll translucent tissue present.  

139(137). Plants ‘spiny’.  
Plants without spines.  

140(139). Leaf blade silica bodies luminal; leaf blade trans-section ‘thickly crescentiform’;  
fruit not rugose; leaf blades glabrous; leaf blade subsidiaries in transverse section  
larger than the adjacent epidermal cells.  
Leaf blade silica bodies ‘external’; leaf blade trans-section ‘thinly crescentiform’;  
fruit ‘rugose’; leaf blades indumented; leaf blade subsidiaries in transverse section  
similar in size to the adjacent epidermal cells.  

141(136). Plants with a ‘trunk’.  
Plants without a ‘trunk’.  

142(141). Leaf sheaths with margins overlapping distally; female-fertile spikelets  
androgynous; rachilla internodes of different lengths, the fertile ones elongated;  
perianth absent; the fertile rachilla internodes flexuose.  
Leaf sheaths with entire margins; female-fertile spikelets gynandrous; rachilla
internodes equal in length whether fertile or sterile; perianth present; the fertile rachilla internodes ‘straight’ .......................................................... Lophoschoenus

143(141). Lateral inflorescence branch bases enclosed. .............................................. 144
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Anthers not yellow-green. ................................................................. 145

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146(145). Leaves distichous; lateral branch inflorescences ‘conipaniculate’; leaf blades unifacial; inflorescence ‘conipaniculate’; primary inflorescence bracts scale-like. .......................................................... Machaerina
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147(145). Rachillae deciduous; style-base continuous with the fruit apex. ........ Rhynchocladium
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152(151). Female-fertile spikelets laterally compressed. .............................................. 153
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153(152). Leaves distichous; lateral branch inflorescences ‘conipaniculate’; female-fertile spikelets gynandrous; caespitose; rachillae persistent. ........... Epischoenus
Leaves tristichous; lateral branch inflorescences ‘planipaniculate’; female-fertile spikelets androgynous; long-rhizomatous; rachillae deciduous. ........ Rhynchocladium

154(151). Leaf sheaths with margins overlapping distally; spikelet prophylls absent; style indumented; fruit apex beakless. ........... Epischoenus
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155(154). Sheath apices ‘truncate’; subtending bracts non-overlapping; terminal spikelets present; rachillae contracted; culm trans-section circular. ........ Trichoschoenus
Sheath apices V-shaped; subtending bracts imbricate; terminal spikelets absent; rachillae vestigial; culm trans-section triangular. ........ Hypolytrum

156(150). Vernation conduplicate; ‘basal spikelets’ absent; culms fibrous; leaf blade trans-section ‘V-shaped’; anthers not yellow-green. .............. 157
Vernation ‘curved’; ‘basal spikelets’ present; culms herbaceous; leaf blade trans-section ‘thickly crescentiform’; anthers yellow-green. ........ Trianoptiles
157(156). Leaf blade parenchymatous bundle sheaths interrupted by fibres. .......................... Rhynchospora (C₃)

Leaf blade parenchymatous bundle sheaths only adjacent metaxylem vessels. .......................... Rhynchospora (C₄ chlorocyperoid)

Leaf blade parenchymatous bundle sheaths ‘irregular’. .................................................... Rhynchospora (C₄ rhynchosporoid)

158(149). Lateral inflorescence branch bases enclosed; female-fertile spikelets with only hermaphrodite flowers; spikelet prophylls absent; ‘basal spikelets’ present; inflorescence elongated. .......................... Trianoptiles

Lateral inflorescence branch bases exposed; female-fertile spikelets androgynous; spikelet prophylls present; ‘basal spikelets’ absent; inflorescence contracted. .......................... Syntrinema

159(131). Female-fertile spikelets laterally compressed. .......................... 160
Female-fertile spikelets dorsiventrally compressed. .......................... Hypolytrum
Female-fertile spikelets terete. .......................... 161

160(159). Lateral shoots originating only at the base of the uppermost culm internode; culms ‘central’; vernation conduplicate; leaves tristichous; spikelet prophylls present. .......................... Tetrariopsis

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161(159). Leaves cauline; floral bracts spirally disposed; primary inflorescence bracts spirally disposed; culms bulbous; culms glabrous. .......................... Causits
Leaves radical; floral bracts tristichous; primary inflorescence bracts tristichous; culms not bulbous; culms indumented. .......................... 162

162(161). Leaves ‘elaminate’; leaf sheaths with entire margins; lateral inflorescence branch bases exposed; female-fertile spikelets with only hermaphrodite flowers; floral bracts deciduous. .......................... Arthrostylis
Leaves laminate; leaf sheaths with margins overlapping distally; lateral inflorescence branch bases enclosed; female-fertile spikelets gynandrous; floral bracts persistent. .......................... Evandra

163(30). Spikelet prophylls present. .......................... 164
Spikelet prophylls absent. .......................... Rikilella

164(163). Leaf sheaths open to the base; sheath apices indumented; fruit apex beakless; margins of the spikelet prophylls indumented; culms without a hypodermis. .......................... Hellmuthia
Leaf sheaths tubular; sheath apices glabrous; fruit apex beaked; margins of the spikelet prophylls glabrous; culms with a hypodermis. .......................... 165

165(164). Rachis ‘widened’; inflorescence pseudoaxillary; fruit epidermal cells constituting hairs. .......................... Hemicarpha
Rachis not widened; inflorescence terminal; fruit epidermal cells smooth. .......................... 166

166(165). Female-fertile spikelets dorsiventrally compressed; perennial; culms fibrous; terminal flower present; adaxial side of the leaf sheaths cartilaginous. .......................... Nelmesia
Female-fertile spikelets terete; annual; culms herbaceous; terminal flower absent; adaxial side of the leaf sheaths membranous.
167(166). Spikelet prophylls bract-like; style-base continuous with the fruit apex; stigmata 1 to 2; fruit trans-section elliptical; the spikelet prophyll keels indumented.

\[Hypolytrum\]

Spikelet prophylls tubular; style-base sharply differentiated from the fruit apex; stigmata 3; fruit trans-section circular; the spikelet prophyll keels glabrous.

\[Principina\]

168(26). Leaf sheaths open to the base.

Leaf sheaths tubular. 169

169(168). Female-fertile spikelets laterally compressed.

\[Coleochloa\]

Female-fertile spikelets dorsiventrally compressed. 170

Female-fertile spikelets terete. \[Chrysitrix\]

170(169). Floral bracts present; fruit epidermal cells smooth; fruit winged.

Floral bracts absent; fruit epidermal cells constituting hairs; fruit wingless.

\[Hellmuthia\]

171(170). Spikelet prophylls subtending male flowers.

Spikelet prophylls sterile. 172

\[Capitularina\]

172(171). Inflorescence ‘conipaniculate’; terminal spikelets present; plants with a ‘trunk’; plants ‘spiny’; culm stomata not obscured by projections from the adjacent epidermal cells.

\[Scirpodendron\]

Inflorescence capitate; terminal spikelets absent; plants without a ‘trunk’; plants without spines; culm stomata obscured by projections from the adjacent epidermal cells. 173

173(172). Style-base enlarged-bulbous, or enlarged-pyramidal; floral bracts glabrous; anther apiculus acuminate; style indumented; style-base persistent.

\[Lepironia\]

Style-base not enlarged; floral bracts indumented; anther apiculus obtuse; style glabrous; style-base deciduous. \[Chorizandra\]

174(168). Inflorescence ‘conipaniculate’.

Inflorescence ‘planipaniculate’ 181

Inflorescence anhelate. 183

Inflorescence capitate. 186

175(174). Perianth present.

Perianth absent. 176

176(175). Leaves distichous; leaf sheaths with margins overlapping distally; floral bracts deciduous; leaf blades deciduous; culm stomata sunken. \[Coleochloa\]

Leaves tristichous; leaf sheaths with entire margins; floral bracts persistent; leaf blades persistent; culm stomata flush to raised. 177

177(176). Subtending bracts non-overlapping; rachillae contracted; stigmatic surface papillose; fruit beak apiculate; perianth ‘cupular’.

\[Scleria\]

Subtending bracts imbricate; rachillae vestigial; stigmatic surface glabrous; fruit beak subulate; perianth of ‘scales’. \[Afrotrilepis\]

178(175). Lateral branch inflorescences ‘conipaniculate’.

Lateral branch inflorescences ‘planipaniculate’. \[Principina\]

Lateral branch inflorescences capitate. 180
179(178). Spikelet prophylls bract-like; rachillae persistent; fruit beak apiculate; anther apiculus 10 percent of anther length or more; leaf blade palisade mesophyll present. .......................... 
Scleria
Spikelet prophylls tubular; rachillae deciduous; fruit beak acuminate; anther apiculus 5 to 10 percent of anther length; leaf blade palisade mesophyll absent. .......................... 
Schoenoxiphium

180(178). Subtending bracts non-overlapping; primary inflorescence bracts persistent; rachillae persistent; anther apiculus 10 percent of anther length or more; leaf blade bulliform cells present. .......................... 
Scleria
Subtending bracts imbricate; primary inflorescence bracts deciduous; rachillae deciduous; anther apiculus 5 to 10 percent of anther length; leaf blade bulliform cells absent. .......................... 
Kobresia

181(174). Plants ‘spiny’; culm silica bodies present; margins of the spikelet prophylls indumented; culm intercostal cells regular and rectangular; anthers with basally appended. .......................... 
Thoracostachyum
Plants without spines; culm silica bodies absent; margins of the spikelet prophylls glabrous; culm intercostal cells irregular; anthers basally unappendaged. .......................... 182

182(181). Style-base continuous with the fruit apex; stigmata 1 to 2; fruit trans-section elliptical; leaf bases not breaking down into fibres; adaxial side of the leaf sheaths cartilaginous. .......................... 
Hypolytrum
Style-base sharply differentiated from the fruit apex; stigmata 3; fruit trans-section circular; leaf bases breaking down into fibres; adaxial side of the leaf sheaths membranous. .......................... 
Paramapania

183(174). Spikelet prophylls subtending male flowers; endocarp light. .......................... 184
Spikelet prophylls sterile; endocarp dark. .......................... 
Diplasia

184(183). Plants differentiated into separate sterile laminate and fertile elaminate shoots; primary inflorescence bracts scale-like; stigmata 3; adaxial side of the leaf sheaths membranous; culms indumented. .......................... 
Paramapania
Plants not differentiated into sterile and fertile shoots; primary inflorescence bracts foliose; stigmata 1 to 2; adaxial side of the leaf sheaths cartilaginous; culms glabrous. .......................... 185

185(184). Sheath apices indumented; floral bracts indumented; style-base sharply differentiated from the fruit apex; fruit beak acuminate; fruit epidermal cells smooth. .......................... 
Exocarya
Sheath apices glabrous; floral bracts glabrous; style-base continuous with the fruit apex; fruit beak apiculate; fruit epidermal cells constituting hairs. 
Mapanipopsis

186(174). Ligules present; primary inflorescence bracts deciduous; culm tannin idioblasts absent; style terete. .......................... 
Kobresia
Ligules absent; primary inflorescence bracts persistent; culm tannin idioblasts present; style ‘flattened’. .......................... 187

187(186). Subtending bracts non-overlapping; rachillae contracted; terminal flower absent; anthers sterile proximally; stigmatic surface glabrous. .......................... 
Rhynchospora (C, rhynchosporoid)
Subtending bracts imbricate; rachillae vestigial; terminal flower present; anthers fully fertile; stigmatic surface papillose. .......................... 188
188(187). Inflorescence prophylls adaxially pulvinate; culm silica bodies absent. .... 189
Inflorescence prophylls epulvinate; culm silica bodies present. ........ Mapania

189(188). Style-base continuous with the fruit apex; stigmata 1 to 2; fruit trans-section
elliptical; leaf bases not breaking down into fibres; adaxial side of the leaf sheaths
cartilaginous. .......................................................... Hypolytrum
Style-base sharply differentiated from the fruit apex; stigmata 3; fruit trans-section
circular; leaf bases breaking down into fibres; adaxial side of the leaf sheaths
membranous. .......................................................... Paramapania

190(1). Culms 'central' .................................................. 191
Culms 'axillary' .......................................................... 194

191(190). Floral bracts present; spikelet prophylls bract-like. ................. 192
Floral bracts absent; spikelet prophylls tubular. .......................... 193

192(191). Female-fertile spikelets laterally compressed; floral bracts distichous; each flower
enclosed directly by a distal floral bract; floral bracts of male spikelets distichous;
style about as long as the fruit. ........................................... Scleria
Female-fertile spikelets terete; floral bracts tristichous; each flower enclosed directly
by its subtending floral bract; floral bracts of male spikelets tristichous; style
shorter than the fruit. .................................................... Didymiandrum

193(191). Anther apiculus 5 to 10 percent of anther length; culm intercostal cells irregular.  .
.......................................................... Carex subgen. Vignea
Anther apiculus 10 percent of anther length or more; culm intercostal cells regular
and rectangular. .......................................................... Carex subgen. Primocarex

194(190). Verration conduplicate; female-fertile spikelets terete; floral bracts tristichous; each
flower enclosed directly by its subtending floral bract; leaf blades persistent.  .
.......................................................... Everardia
Verration 'curved'; female-fertile spikelets laterally compressed; floral bracts
distichous; each flower enclosed directly by a distal floral bract; leaf blades
deciduous. .......................................................... Microdracoides
Chapter 9

Classification of the genera of Cyperaceae

Abstract

Descriptions of the 122 genera of Cyperaceae were automatically converted from a DELTA database to PAUP format and into distance matrices, for cladistic and phenetic analyses. Various subsets of characters and taxa were analyzed and the results scrutinized and compared with previous classifications of the family, including one recently derived from manual cladistic analyses. In dealing with these large data sets the cladistic analyses were more successful in providing reasonable hypothetical phylogenies than in providing classifications permitting useful generalization. The phenetically derived trees are in general similar to the cladograms, but they are more highly structured and correspond more closely with previously published manually derived cladograms. A suprageneric classification of the Cyperaceae is proposed, in which the genera are explicitly assigned to twelve tribes and two subfamilies. The interactive program INTKEY was used for preparing group descriptions and diagnoses, thus greatly facilitating comparisons among alternative classificatory solutions. Weaknesses of literature generalizations, particularly at higher taxonomic levels, highlight the need for more comparative data.

Introduction

The Cyperaceae have been the subject of suprageneric classification for 200 years, starting with de Jussieu’s (1789) division of the family into unisexual- and hermaphrodite-flowered groups. Interestingly, the latter have persisted to the present as subfamilies in most subsequent treatments, though further groupings (recognized today as tribes) were soon superimposed (e.g. Kunth 1815; Nees 1834, 1842). Many regional treatments have appeared, which sometimes involve suprageneric classificatory novelties but which provide incomplete coverage of the family (e.g. Chermezon 1937; Kern 1974; Tucker 1987 and references therein).

Table 9.1 summarizes the more recent, more or less comprehensive classifications of the Cyperaceae, set alongside the one proposed in the present study. Tribes and subfamilies are recognized in all these schemes, except that of Hooper (1973) who
adopted only tribes. The original division of the family using unisexual versus bisexual flowers is reflected in most of the classifications at subfamilial rank: the Diclines/Caricoideae comprise the unisexual flowered tribes and the Monoclines/Cyperoideae/Scirpoideae the bisexual flowered tribes. This distinction is not absolute, particularly in the proposed classification. The definition of flowers and spikelets has remained a matter of controversy, so the mapanioid genera (the Hypolytreae/Mapanieae/Mapanioideae) have been differently assigned depending upon whether their floral structures were interpreted as bisexual flowers with a ‘perianth’ or as spikelets of unisexual flowers (see also Chapter 4). The classifications of Bentham (1883) and Schultze-Motel (1964: nearly identical to Bentham’s, in terms of the groups recognized) at the subfamilial and tribal level were ostensibly based on flower and spikelet characters. Clarke’s (1908) classification was published posthumously without further explanation, but judging from his (1901) regional treatment of tropical Africa and (1909) illustrations, it at least took account of a broad range of inflorescence and floral characters. The classifications of Koyama have broadened, from being largely limited to consideration of floral, spikelet and inflorescence morphology (1961) to later inclusion of substantial evidence from fruit anatomy and vegetative anatomy (1969 and 1971). Seeming inconsistencies in his spikelet-structure evidence and the contentious nature of his interpretation of fruit anatomy have been pointed out by Eiten (1976a-b) and Goetghebeur (1985, 1986; see also Chapter 3). Hooper (1973) presents her classification, without subfamilies, in the form of a key to the tribes largely based on floral and spikelet characters.

More recent treatments of the Cyperaceae have been influenced by the accumulation of data on additional features: notably vegetative morphology and anatomy, with major contributions from Pfeiffer (1927) and Metcalfe (1971, and see references therein); variation in photosynthetic pathways (Lerman and Raynal 1972; Raynal 1973); and embryo morphology (van der Veken 1965; Verbelen 1970; van Linden 1971; Juget 1972; Vanhecke 1974). Goetghebeur’s (1986) thesis represents the most recent comprehensive account of the family. He recognizes seventeen tribes, a considerable increase in number over any earlier classification. However, Nees (1834, 1842) had already recognized the Chrysitricheae, Cladieae (Schoeneae pro parte), Ficinieae, and Fuireneae; Reichenbach (1828) and Raynal (1978) the Fimbristylideae (Abildgaardieae Lye 1973); and Pax (1897) and Eiten (1976a) the Bisboeckelereae. Various other tribes have been recognized (e.g. by Chermezon 1937; Eiten 1976a), and a detailed listing is given by Goetghebeur (1986). His interpretation of floral features is bound in the theories of Meeuse (1975, and references therein), but he utilizes a broad
spectrum of taxonomic characters, emphasizing features of floral and inflorescence morphology and embryo morphology. Goetghebeur's (1986) treatment represents the first attempt at application of cladistic method to the family as a whole. He seems not to have used a computer, but to have established transformation series of the morphological types a priori, rather than treating the features in terms of their unitary characters polarized by the outgroup (see Stevens 1980) and allowing "the characters to speak for themselves" (Meacham 1984 p.35).

Assumed familial relationships take on practical significance in choosing appropriate outgroups for cladistic analyses. Choice of outgroup to polarize the character state changes (i.e. to root the network) in cladistic analyses is of particular relevance to identifying basal ingroup members. Hutchinson (1973) considered Oreobolus to be the most primitive group of the Cyperaceae but did not argue the case, and Seberg (1988a) disputes it. Holttum (1948), Kern (1962), Kukkonen (1967), Kern (1974) and Goetghebeur (1986) took Scirpodendron as the putative ancestral sedge. Goetghebeur (the only one to employ cladistic method) used the Juncaceae as an outgroup, but makes no explicit statement regarding the limits of the outgroup employed or the characters used to polarize the ingroup characters. The Pandanales and the Poales/Poaceae have also been proposed as sister groups of the Cyperaceae. The former notion was based on overall similarity between the tropical genera Scirpodendron and Pandanus in habit and vegetative anatomy (Holttum 1948; Kern 1974; Meeuse 1975). However, Metcalfe (1971) found no evidence of such a relationship from vegetative anatomy. The supposition of a Poaceae–Cyperaceae relationship was based partly on overall similarity (Bentham 1883; Cronquist 1981), but mainly on chemical data (Clifford and Harborne 1969; Harborne 1982), with supporting evidence including ovule number, endosperm formation and seedling type (Dahlgren and Clifford 1982). More recently Clifford (1987) has argued that the flowers of grasses and sedges are synanthia in which trimery is a shared derived feature, but, the Juncaceae and five other families (not including the Cyperaceae) appear on the same clade in his study. By contrast, Campbell and Kellogg (1987) dismissed the Poaceae as a sister group of the Cyperaceae, arguing that the shared chemical characters are also found in relatively unrelated families and therefore probably represent convergence, and that other features important in this context (e.g. ligules) are probably not homologous between the Cyperaceae and Poaceae.

Shah (1967) tabulated ten similarities between the embryology of the Cyperaceae and Juncaceae, but only two rather generalized gynoecial features of ovule number and placentation linking the Cyperaceae and Poaceae. Juget (1972) also found congruence between the embryo formation in the Cyperaceae and Juncaceae, while Dahlgren and
Clifford (1982) listed basifixed anthers and polycentric centromeres as significant common features of these two families. Metcalfe (1971) concluded that the vegetative anatomy of the Juncaceae and Cyperaceae indicates close relationship, and there are also host-parasite data supporting this view (Savile 1979). The Juncaceae (ignoring the Thurniaceae, for practical reasons) seemed the most appropriate outgroup in relation to the present study, but the question has probably not yet been decided once and for all, and further analyses might reasonably include additional outgroups such as the Restionaceae.

In taking full advantage of comparative descriptions and the flexibility of the automated database taxonomic system DELTA (Dallwitz and Paine, 1986), I have investigated the relationships of the sedge genera of the world employing both phenetic and cladistic analyses; compared the results with previous classifications, especially with that of Goetghebeur (1986, which is particularly relevant in the present connection, given the overlaps in our data and methods: see Chapter 3); tested previous notions about which groups constitute the basal members of the family; and tested the robustness of emergent groups by analyzing different combinations of taxa and characters, and different character state interpretations. Finally I have proposed a suprageneric classification of the Cyperaceae, in which all the genera are explicitly assigned to tribes and subfamilies in association with detailed, comparative group descriptions (Appendix 1). Goetghebeur (1985 p.617) considered that high level groups are "not that important for information retrieval". I have a higher opinion of their potential worth, and have tried to arrive at a system of practical use for general purposes (e.g. in relation to experimental sampling, cf. Chapters 4-8) and which should serve as a guide for future taxonomic work within the family.

Phylogenetic approaches to classification (including cladistics) aim to unravel present-day relationships as part of a continuum of evolutionary change, in the belief that relationships which reflect historical reality will provide the best taxonomic model for prediction and generalization, as well as providing insights into evolutionary processes. There is infinite scope for varying the ways in which the organisms are described for taxonomic purposes, and of interpreting their diversity in terms of characters and character states. Phenetic analyses provide models of overall similarity of the organisms under study without (necessarily) imposing constraints due to evolutionary philosophy. Methods exist which cope (more or less) rationally with the ever-present problems of missing data, character dependencies and variable data. By contrast, cladistic analyses place a number of constraints (e.g. variable data cannot be analyzed, evolution is presumed to be dichotomous, not reticulate), but are supposed
to result in more powerful phylogenetic hypotheses. The effects of these constraints on the results of the cladistic analyses is considered below, in part by comparison with alternative classifications, with the phenetic results, and against the actual descriptions of the genera (Appendix 1). In the present context there are special (but not unusual or contrived) problems in obtaining comparative data. Contemplate, for example, the description of *Eleocharis* with elaminate leaves and an inflorescence reduced to a solitary spikelet. There is the concern regarding anatomical features which may be redundant through logical dependency, e.g. the link between various anatomical features and photosynthetic pathways. Of particular importance and controversy in the Cyperaceae is the uncertainty over the correct interpretations of inflorescences and flowers (Chapter 4). With these difficulties in mind, inclusion of a wide range of characters in the analyses seemed appropriate. Indeed, in the absence of detailed analyses it is generally impossible to determine *a priori* which characters are "taxonomically unimportant". This is particularly the case in supra-generic studies, where one commonly finds that characters which exhibit taxonomically useful discontinuities for some of the genera are otherwise largely uninformative or 'noisy'. There are additional reasons for inclusion of a wide range of characters in the present study. There was a desire to set photosynthetic pathways against taxonomy (see Chapters 5-7), and to balance the use of traditional floral and morphological suites of features with data from physiology and anatomy (see also Chapters 4 and 5). I have also aimed to incorporate enough data to provide flexibility in identification (see Chapter 8, Example 8.1) as well as a body of material offering scope for direct retrieval of information on a useful scale (see Chapter 8, Example 8.2). The latter aspect is increasingly becoming a worthwhile consideration, given the possibilities for delivering extensive new services to users of taxonomic systems and of taxonomically organized information (cf. INTKEY, Chapter 8 and Appendix 3).

Although most of the characters seem to show taxonomic patterns (see Appendix 1: Subfamilial and Tribal Descriptions), different analyses based on different suites of characters or computer strategies (Table 9.2), all of which seemed more or less valid on *a priori* grounds, have given somewhat different results (Appendix 4). This is in itself justification for having performed comparative analyses, since it clearly demonstrates the futility of establishing classifications upon small data sets and single analyses. In the context of the present study of the Cyperaceae one possibility for reducing the 'noise' and overcoming some of the technical problems of the cladistic programs might have been to analyze the family in terms of the groups (tribes) apparent from the initial
analyses or accepted in the literature. However, given the lack of consensus regarding tribal circumscriptions, that approach seemed hardly justifiable.

Analyzing the more than 100 generic descriptions has thus involved the use of numerous characters, and required the use of non-exhaustive cladistic algorithms. The phenetic and especially the cladistic programs employed allow for a number of parameters to be varied. The limits of the descriptions are also open to interpretation and alteration (e.g. via amalgamation of the subgeneric descriptions). Conducting comparative analyses under these circumstances is crucial. Simply running the data through a program and presenting the first result would clearly be unacceptable. To address this need analyses were undertaken which compared within and between phenetic and cladistic analyses (see below). Investigating the contributions of suites of features seemed appropriate given the variation in emphasis which has been given to them. Embryo morphology, questions relating to "what is a flower", culm anatomy, photosynthetic pathways and elaminate versus laminate taxa seemed particularly pertinent.

One of the difficulties in classifying plants is to choose between competing hypotheses. I have contemplated the results in terms of the apparent groupings (Appendix 4), the "apologists" and "change lists" (cladistic analyses) and the actual descriptions in the database (Appendices 1 and 3). A major concern has been the changes in the data between the version acceptable to the cladistic programs and the original descriptions. This misrepresentation of data in the translation from the ITEMS files (i.e. genuine taxonomic descriptions) to PAUPDATA (i.e. data acceptable for "phylogenetic analyses") is an unfortunate but unavoidable constraint of the cladistic analyses reflecting the inadequacy of the methods in the face of properly descriptive data. The two examples presented below from analysis #24 are typical of the mistranslation.

Example 9.1. Clade supported at node 204–219 by character 209: postulated change from "Spikelet prophylls not constituting perigynia" to "Spikelet prophylls constituting perigynia" (i.e. state 2 to state 1); see Fig. 9.7. + = exact match of encoded description with PAUPDATA description; * = encoded description variable for character; no marks indicate that the character is inapplicable for the generic description.

Trilepideae: *Afrotilepis*, *Coleochloa*, *Microdracoides*, *Trilepis*
Sclerieae: *Acriulus*, *Scleria*
Cariceae: *Carex +, Cymophyllus +, Kobresia *, *Schoenoxiphium*, *Uncinia +, Vesicarex +
Example 9.2. Clade supported at node 218-227 by character 165 changing from state 2 "C₄ Biochemical type NADP-ME" to state 1 "C₄ Biochemical type NAD-ME". * = the amalgamated encoded description is variable for the character; no marks indicate that the character is inapplicable for the generic description.

Scirpeae pro parte: Androtrichum, Anosporum, Blysmus, Bolboschoenus, Desmoschoenus, Egleria, Eleocharis * (i.e. the C₄ species), Eleogiton, Ficinia, Isolepis, Kyllingiella, Oxy Caryum, Phylloscirpus, Schoenoplectus, Scirpoides, Websteria

It will be observed that in both examples, missing values and inapplicables have become bogus data supporting the trees. These examples represent a widespread phenomenon, demanding very cautious interpretation of results.

With such considerations in mind, the results were carefully compared with those of Goetghebeur (1986), and where a number of options were apparent from the current analyses but no convincing argument to the contrary was present, the conservative line which agreed with his classification was accepted. Differences between the results of different analyses ranged from minor branch swapping to fundamental changes in group alliances. In the absence of one analysis which I was prepared to accept in full, I have looked for robust groups at different levels, and compared these with their constituent descriptions (Appendices 1 and 4). I have tried to identify aberrant results in terms of discrepancies between the "apolists" and the descriptions, and also anomalies most likely resulting from missing data or methodological constraints. In some cases the final decision has been rather arbitrary in the absence of a seemingly satisfactory solution, or in the presence of several more or less equally unsatisfactory results. These cases have been noted and usually point to the need for more or finer-scale data or better material for examination.

Methods and Materials

Data matrices for phenetic and cladistic analyses were generated automatically from the ITEMS file (cf. Chapter 2) using the CONFOR programs TODIS and TOPAU respectively (Dallwitz and Paine 1986).

The taxa

The taxa studied are those covered in the set of automated descriptions: i.e. 122 genera of Cyperaceae plus a number of subgenera, informal species groups and species which were described separately to permit exploration of their affinities (Chapter 2: i.e.,
in order to explore competing generic limits, to minimize variation in seemingly heterogeneous genera and to contemplate evolution of photosynthetic pathways). For some analyses, the segregates and some genera were coalesced automatically using INTKEY (see Chapters 3 and 5), and the resulting broader descriptions were substituted for them. In both the phenetic and the cladistic analyses, genera not sampled directly by me (‘poorly scored’ genera, cf. Chapter 2 and Appendix 1) were omitted from some of the analyses. In my preliminary cladistic analyses *Prionium* failed to unite with the remainder of the outgroup, and it was omitted from some of the subsequent analyses. *Hellmuthia* and *Phylloscirpus* were omitted in some cases because their unstable placement appeared to lead to the formation of spurious groups. I am aware that such operations can be construed as subjective massaging of the data. They are, however, inescapable in the face of missing data and the limitations of the available classificatory methods.

The Characters

The annotated character list is presented in Chapter 3. Characters inappropriate for classification were omitted from all classificatory analyses: viz. #1-2, 4, 9, 11, 12, 29-30, 46, 48, 58, 78, 84, 89-90, 92, 104, 128, 131, 145, 153, 158, 162-165, 188, 192, 210, 220-225, 227, 240, 251, 258, 263-264, 272, 277, 286, 301, 320, 321, 337-364. These include text ‘characters’; pseudocharacters such as ‘number of species’ and ‘taxonomy’; distributional and ecological ‘characters’, whose inclusion would preclude testing of biogeographical hypotheses (contrast Goetghebeur 1986, and see below); some very poorly scored characters (e.g. #285-286); ratios (e.g. #104); autapomorphs, which are uninformative at the level in question: e.g. characters #29-30); and characters included for their usefulness in other contexts (e.g. identification) where the states obviously involve homoplasy (e.g. #46 and 48). Additionally, 22 quantitative or ordered multistate characters (#17, 45, 47, 54, 56, 61, 64, 70, 72-74, 111, 113, 121, 123-125, 130, 134, 137, 140, 213, 233, 242, 244, 247, 256-257, 261, 266, 278-279, 281, 284, 288-289, 293, 302, 303, 310) were often omitted because the necessity for arbitrary ranging may be deleterious (cf. Archie 1985; Pimentel and Riggins 1987; but see Thiele and Ladiges 1988) while others, where appropriate, were converted into binary or more discrete multistate characters (e.g. #57 and 232: characters converted to presence/absence statements). Various subsets of the characters were also omitted from particular analyses (Table 9.2). To increase comparability between laminate and elaminate ‘genera’, and between those taxa with well developed or poorly developed culms, characters #92-98, 107, 145-150, 158 were substituted in the later analyses by #163-165, which summarize
photosynthetic pathway characteristics (see Chapter 3; Appendix 1). With these character deletions the comparative trees (Appendix 4: cf. #16 with 17) were much more highly chained, though the sequence of apparent groups was mostly the same. Replacement of anatomical characters with the corresponding photosynthetic pathway type characters did not greatly alter the pattern, though the more or less duplicate scoring of anatomical characters increased the apparent support (branch lengths) of the major clades in that version. Characters #369-372 represent differences between the Cyperaceae and the outgroup.

**Phenetic Analyses**

The DELTA format data were translated into a distance matrix using the program DIST (Dallwitz, unpublished, see "Changes" file), which utilizes the Gower metric. Overlapping character values between pairs of taxa were treated as matches (MATCH OVERLAP), thus contributing zero to distances. A flexible combinatorial clustering strategy (where the intensity parameter $\sigma=0$ gives UPGMA and $\sigma=1$ gives ISS) was employed, of which intensities of 0.2, 0.5 and 0.90 were used. This kind of clustering strategy is preferred by Abel and Williams (1985), and proved superior to conventional WUPGMA and various other phenetic algorithms in classificatory experiments with a large data set on the grass genera (Watson *et al.* 1985; Dallwitz, in press).

**Cladistic Analyses**

Character-state analyses were performed using PAUP (Swofford 1985). In translating the DELTA format data to PAUPDATA, any characters scored as variable within an item were treated as unknown for that item. The parameters used were ADDSEQ=CLOSEST, SWAP=GLOBAL, MULPARS, ROOT=OUTGROUP, MAXTREE=5 or 50, with or without WEIGHTS SCALE.

The only difference in parameters between analyses #1 and 2 was the weighting of the character states as equal in the former, and the characters as equal in the latter (i.e. without and with WEIGHTS SCALE respectively). The second strategy seems to be generally preferred because it avoids giving 'excessive' weight to a character simply because it has many states. Generally, the differences between the results were insignificant, with only some minor branch swapping evident. The significantly reduced tree length and the increase in the consistency index are necessary corollaries of the "scaling", as in analysis #2, and they do not necessarily indicate improved results.

The taxa were entered in the (mostly alphabetical) order of the ITEMS file, except for analyses #16 and 17 where the input order was rearranged to generally conform with the pattern of a phenogram (not presented) of the same data (Table 9.2). The eight genera
of Juncaceae were used as the outgroup, in line with the widespread supposition that the Cyperaceae and Juncaceae are sister taxa (see above and cf. Juget 1972; Goetghebeur 1986; Seberg 1988a). Material of Juncus, Luzula and Marsippospermum was examined directly for this purpose, the remaining genera being scored from the literature. The Juncaceae descriptions follow those of the sedge genera in Appendix 1.

Consensus trees for any particular analysis were highly resolved even when as many as 50 trees resulted. Polychotomies were restricted to a few genera of the outgroup and/or involved limited terminal branch swapping within the Cyperaceae. The resulting trees do not convey branch length information and direct application of "apolists" and "change lists" is not possible. Consensus trees could not be produced automatically for between-analysis comparisons. Given the constancy within analyses, it has been convenient, and has seemed sufficient, to scrutinize only the first tree of each analysis in detail. The attributes cited below are numbered according the main character list, while the states are those of the character list after conversion to PAUP format, resulting in some modified state boundaries.

The Descriptions

Appendix 1 contains a full set of the comparative descriptions included in the ITEMS file together with descriptions of the proposed subfamilies and tribes. The latter were produced via INTKEY and within-group variability is summarized numerically in terms of character state distributions. INTKEY was also used to obtain subfamilial and tribal diagnoses, the diagnostic character states being italicized in the full descriptions generated by CONFOR.

Results and Discussion

The thirty analyses are listed in Table 9.2, and presented in full in Appendix 4. The gross differences between the phenetic and cladistic analyses as a whole lie in the more highly structured nature of the phenogram set against the relatively extensively chained cladograms. The tribal groupings are almost exactly the same throughout. Their arrangement and order, however, is variable. In cladogram #24 the Hypolytreae are basal and the Cypereae apical, whereas the order in the phenogram and analysis #17 is more or less reversed (see also Table 9.2). Division of the cladograms into subfamilies was often less clear-cut than in the case of the phenograms.

Regarding cladistic analyses, the outgroup controls the polarization of the character states in converting the unrooted tree or network into a directed or rooted tree (Swofford
1985; see also Stevens 1980), and yet, as in the present case, preparation of appropriate outgroup descriptions is invariably outside the scope of, and ancillary to the work in hand. There are serious difficulties in applying a character list designed for one group (here the Cyperaceae) to another (the Juncaceae). Difficulties over the determination of homologies within the family are inevitably amplified with extension to the outgroup. For example, the interpretation of floral features within the Cyperaceae is controversial (Chapter 4), and judging from the variety of terms used to describe the floral bracts/glumes/prophylls/bracteoles/scales in the Juncaceae, similar problems of interpretation also exist there. In the context of the present study the only practicable option (fortunately a reasonable one, on the basis of the purported sister group relationship, see above), has been to assume that the basic structural patterns are consistent across the families.

The results of heuristic algorithms used in these cladistic analyses (unlike the comprehensive options, which are unavailable to data sets with more than about 19 taxa), are affected by input order (Swofford 1985). To investigate the influence of input order on the result, it was changed in two cases, from the normal order (e.g. #15: i.e. from that of the ITEMS file (see Appendix 4) which is essentially alphabetical within the ingroup and outgroup respectively), to an order derived from a phenetic analysis (Appendix 4: #16 and 17). In these cases the input order was as follows: the genera of the Juncaceae first, followed by Scirpodendron (the putative ancestral sedge according to some e.g. Kern 1962 and Goetghebeur 1986) and the rest of the Hypolytreae and so on according the order generated in a current phenogram. The length of altered input order tree decreased by 2 steps over 1447.6, or a trivial 0.15% difference, by comparison with the original input order tree. The consistency index remained the same. In the analyses with altered input order, the most basal genus was Dulichium and the Hypolytreae clade was positioned at the apex of the tree, by contrast with the original input order which resulted in the Hypolytreae being basal, next to the outgroup in the comparative analysis. Overall the major clades appeared constant for both analyses, with the exception of Cladium which shifted from between the Hypolytreae clade and Bisboeckelereae in a chained sequence in #16 to the base of the Schoeneae near the Rhynchosporeae in #15 (Fig. 9.6). These results also suggest (see above), that the major groupings are reasonably robust but that the rooting of the networks is rather labile, again emphasizing the need to study the outgroup more thoroughly, and even to try alternative or multiple outgroups.

The overall result of the omission of the embryo characters (Analysis #8: characters #321-332) was a tree similar to that of most of the other analyses, and in particular #5
and 12, in that all three were rooted near a clade including the Hypolytreae as a clade nested above the Bisboeckelereae, Sclerieae, Cariceae, Trilepideae, and Cryptangieae, and *Evandra*. Generally the major groups (e.g. Schoeneae and Hypolytreae) were recognizable as usual, with a few genera seemingly misplaced. For example *Nelmesia* (one of the ‘poorly scored’ genera) shifted from the Abildgaardieae to the Cypereae, basal to *Volkieila* and *Ascolepis*. The high degree of congruence between trees including and excluding embryo characters may reflect congruence of these characters with the data as a whole, or it may mean that they are more or less superfluous (i.e. involve a high degree of homoplasy). In fact, both of these notions are probably correct. For example, in analysis #24, contrast the high level of uniformity in embryo type within the Cypereae and the Trilepideae, with the reversion four-times to the *Juncus*-type embryo and the six-times parallel development the *Carex*-type embryo across the Cyperaceae (cf. Figs 9.1 and 9.7-8; Appendix 4).

Contemplating character dependencies, the eleven descriptions comprising solely elaminate species were omitted from analysis #12, in order to increase the applicability of the characters to the remaining taxa and identify conflicts in previous analyses that could hereby be resolved. All elaminate genera will essentially be relatively poorly scored given the large number of characters dependent on the possession of leaf blades. The taxa omitted were *Abildgaardia* (the C3 species), *Actinoschoenus, Androtrichum, Arthrostylis, Egerlia, Eleocharis* (the C3 species and the C4 species), *Lepironia, Pseudoschoenus, Trichoschoenus*, and *Websteria*. Analysis #1 shares the same parameters, but included all the descriptions. The major difference between these analyses is that the removal of the elaminate was sufficient to allow the tree to root at the outgroup. Some minor branch swapping was also evident. This result provides some confidence that the inclusion of the elaminate, as such, has not skewed the results unduly.

The culm anatomical characters (#57-107) were omitted from analyses #10 and 11 to investigate their influence, and in particular whether they represented double-weighting of the vegetative anatomical (i.e. culm and leaf blade) characters. Regardless of whether the ‘poorly scored’ genera were included (#10) or excluded (#11), the same three main groups were evident as in other analyses (Appendix 4; see below). In the former case the "Eleocharideae" (see below) was placed near the Arthrostylideae and the Abildgaardieae, and in the latter within the Cypereae together with *Androtrichum*; removal of culm characters renders the descriptions for the elaminate genera largely ‘unknown’. These results, compared with cases where no taxa and only ‘general’ (Table 9.2: "G"; Analyses #3, 14, 18) characters were omitted, indicate no substantial
interaction with the culm anatomical characters on the groups formed. The results suggest that the value of culm characters in assigning leafless forms outweighs possible deleterious effects arising out of their redundancy elsewhere.

The characters obviously and directly relating to photosynthetic pathways (#92-98 105-107 140 142 146-151 159-162) were omitted in analysis #13. Two major groups were apparent. The first included the Scirpeae, Cypereae, Abildgaardieae, Arthrostylideae, and the Rhynchosporeae, containing C_3 and C_4 genera; the second, exclusively C_3, included the Schoeneae and the Sclerieae, Cryptangieae, Trilepideae, Bisboeckelereae, Cariceae, and Hypolytreae (except for *Hellmuthia*). The Rhynchosporeae was rendered polyphyletic with *Syntrinema* pairing with *Nelmesia* within a group comprising the "Eleocharideae", Arthrostylideae, Abildgaardieae and *Hellmuthia*. The C_3 and C_4 species of *Abildgaardia* constituted a sister group. The C_3 genera *Androtrichum*, *Anosporum*, *Oxycaryum*, and *Kyllingiella* were included in the predominantly C_4 Cypereae, but *Scirpoides* remained outside it. *Androtrichum* linked with *Sphaerocyperus*, and *Kyllingiella* with *Monandrus*. The pattern indicates that the features related to photosynthetic pathway omitted here influence the results seen in the other analyses, but they do not dominate them (e.g. the grouping of the Cypereae mostly remains the same). This suggests that there are other features less obviously or not directly associated with photosynthetic pathways which support similar patterns of relationships. If nothing else, the removal the photosynthetic pathway characters increases the weighting of those remaining. The association of *Nelmesia* and *Syntrinema* may reflect poorly scored descriptions rather than close taxonomic relationship, though the clustering of the remainder of the Rhynchosporeae within the Cyperoideae cannot be explained in like fashion. This analysis highlights the link between the sclerioids *sensu traditus* (see below) and the Schoeneae (Appendix 4).

The most apparent result of the omission of the floral characters (Appendix 4: Analysis #9) was the failure of the tree to root at the outgroup. *Prionium* linked with the Hypolytreae clade (minus *Chorizandra*, *Chrysitrix* and *Lepironia*) and the Sclerieae, while the remainder of the Juncaceae joined the Cariceae–Trilepideae clade. Judging generally from the analyses the monophyly of the outgroup as presented is relatively weakly supported. By contrast, the general pattern of relationships is robust and does not rely on controversial floral features.

The trees obtained from the classificatory analyses (Appendix 4) will now be discussed, with particular reference to the two subfamilies and twelve tribes recognized in Table 9.1 and 9.5. The earlier analyses (especially #1-13, Table 9.2) were useful in making gross comparisons involving various matrix modifications, but given some
changes in the encoded descriptions (see also #14-17, Table 9.2) and some obviously unsatisfactory results (e.g. analyses #1-2 and 9 where the cladograms rooted at the midpoint with the Cyperaceae represented as polyphyletic), their importance will be down-weighted in what follows. More reliance will be placed on the later analyses, and especially #17, 24 (cladistic) and 30 (phenetic) which emerge as the most satisfactory in terms of the considerations set out above. Indications of the extent of support for the proposed classification across the analyses and within some of the analyses are provided. Comparisons with other systems are made, primarily with that of Goetghebeur (1986). The conclusions set out the strengths and weaknesses of the proposed classification as perceived by me. Comparative group descriptions are provided in Appendix 4.

The Tribes

The Cypereae (Appendix 1, pp 419-424)

This group, as recognized here, includes seventeen genera, viz. Alinula, Ascolepis, Ascopholis, Courtoisina, Cyperus (subgenera Pycnostachys and Cyperus), Hemicarpha, Kyllinga, Lipocarpha, Mariscus, Monandrus, Pycreus, Queenslandiella, Remirea, Rikiella, Sphaerocyperus, Torulinium and Volkiella (Table 9.5).

In analysis #24 (Fig. 9.1) this clade is supported by ten features: annual (5,1), leaf blade septa visible adaxially (34,1), leaf blade palisade mesophyll adaxial (161,2), photosynthetic pathway $C_4$ (163,3), $C_4$ anatomical type chlorocyperoid (164,2), inflorescence ‘planipaniculate’ or anthelate (177,2), female-fertile spikelets laterally compressed (202,1), rachillae elongated (216,3), floral bracts distichous (239,2), and fruit laterally compressed (304,1), None of these characters are constant across the genera and most of them are extensively variable. Nevertheless, this clade appears in two cladistic analyses (#23-24) and two phenograms (#26-27). In analyses #1, 3-6, 9, 12, 17, the clade lacks Courtoisina and Cyperus subgenus Pycnostachys. In #8 the clade also lacks Courtoisina and Cyperus subgenus Pycnostachys while Nelmesia is included, in #19 and 20 the clade lacks Sphaerocyperus, and Kyllingiella is basal to the clade. In #10, 16, 25, and 28-30 the latter is clearly included in the clade/cluster. In #7 and 22 Anosporum and Oxycaryum are included, in #13 Anosporum, Oxycaryum and Androtrichum are included, and in #11, Anosporum, Oxycaryum, Kyllingiella and the ‘Eleocharideae’ are included in the clade.

Even when only the last series of analyses is contemplated (i.e. #18-30) for the reasons given above, Kyllingiella in particular, and to a lesser extent Anosporum and
Oxycaryum are candidates for inclusion in this clade. This close relationship is highlighted by the fact that the excluded genera are members of the Scirpeae group (see below), above which the clade comprising the Cypereae was nested in the cladistic analyses. In the phenetic analyses the group was also reasonably robust and constituted a clearly separate cluster from Scirpeae, even when Kyllingiella appeared in the Cypereae group (#25, 28-30).

Within the Cypereae two more or less distinct groups were often apparent. In analysis #24 (Fig. 9.1) Monandrus to Courtoisina constitute a paraphyletic group and Sphaerocyperus to Alinula a monophyletic clade; however, in most other cases the two groups were apparent and both constituted clades (Appendix 4).

The tribe Cypereae as defined here is not novel. It corresponds with Raynal’s (1973 Pl. 8) Cyperus lineage delimited at the base by the occurrence of distichous floral bracts, and to Goetghebeur’s (1986 p.172) Cypereae clade without the basal and unresolved branch including Scirpoides, Oxycaryum, Androtrichum, and Kyllingiella. Indeed, the Sphaerocyperus to Alinula clade described above coincides with Raynal’s group of genera which possess single flowered spikelets. This is despite the relevant character (i.e. #251 hermaphrodite flowers, number per spikelet) having been deleted from my analyses (i.e. while the attribute is indicated parsimoniously in the ‘apolist’ and ‘changelist’ it contributed zero to the branch lengths). Examination of the ‘apomorphy list’ for analysis #24 reveals that this character is also congruent here. Lipocarpha, Rikiella and Hemicarpha were lumped by Goetghebeur (1986; see also Tucker 1987), however in most analyses, including #24, the three genera appear to be resolved, though the sister pair of Hemicarpha and Rikiella could reasonably be amalgamated. A number of other members of the Cypereae are more contentious. For example, Cyperus subgenus Cyperus has a zero branch length and forms a trichotomy in this analysis (with Pycreus and the rest of the clade) and is separated from subgenus Pycnostachys. Species level studies would be appropriate to clarify the generic limits here.

The Scirpeae (Appendix 1, pp 424-429)

This group includes 27 genera, namely Androtrichum, Anosporum, Baeothryon, Blysmopsis, Blysmus, Bolboschoenus, Desmoschoenus, Dulichium, Egeria, Eleocharis (the C₃ species and C₄ species), Eleogiton, Eriophoropsis, Eriophorum, Erioscirpus, Ficinia (and Ficinia subgenus Sickmannia), Fuirena, Hymenochaeta, Isolepis, Kyllingiella, Oreobolopsis, Oxycaryum, Phylloscirpus, Pseudoschoenus, Schoenoplectus, Scirpoides, Scirpus and Websteria (Table 9.5). The group is the most
poorly supported of those recognized here (Table 9.3). It was recognizable as paraphyletic in six analyses (#12, 19-20 22-24), monophenetic in #25 and polyphyletic/polyphenetic in the remainder. The polyphyletic nature of the group resulted from the inclusion of a foreign element or the exclusion of one or a few of the ingroup taxa, and disregarding these taxa would lead at least to the Scirpeae emerging as paraphyletic (e.g. disregarding the exclusion of Oxycaryum and Anosporum from the Scirpeae in #17, or the inclusion of the Arthrostylideae in #9).

In #24 (Fig. 9.2), in which the descriptions were amalgamated for 1) Blysmopsis and Blysmus; 2) Eleocharis the C₃ species and C₄ species; 3) Eriophoropsis, Eriophorum and Eriscirpus; and 4) Ficinia and Ficinia subgenus Sickmannia, three clades emerged. The most basal clade included Baeothryon, Bolboschoenus, Dulichium, Fuirena, Hymenochaeta, Pseudoschoenus and Scirpus, and was supported by six attributes: viz., habit ‘long-rhizomatous’ (3,1), ligules present (49,1), culm mesophyll ‘translucent tissue’ present (83,1), abaxial leaf blade epidermal cells irregular (109,2), lateral inflorescence branch bases enclosed (185,1), and margins of the spikelet prophylls indumented (215,1), though none are constant across the genera. The association of Scirpus with Baeothryon was common, and when included, Oreobolopsis usually paired with the latter.

Dulichium, Blysmus and Blysmopsis emerged as a monophyletic/monophenetic clade in 15 analyses (Table 9.4). In a number of cases in which the ‘Dulichieae’ clade occurred it was nested above other genera of the Scirpeae, while when Blysmopsis and Blysmus were amalgamated (cf. Goetghebeur 1986) it failed to pair with Dulichium. In analysis #19 nine characters strongly unite the three genera, which were recognized by Goetghebeur (1986) as the "Dulichieae". Most of these attributes are either constant across the three taxa or congruent with them. Only #206 and 290 are variable between the genera without overlapping scores. The pattern of evidence for and against the recognition of the three genera as a tribe is similar to that in the case of "Chrysitricheae" (see below). In both cases a small number of seemingly closely related (well supported) genera is involved, their respective sister group relationships are variable though they are often nested above their respective relatives. Recognition of these groups, therefore leads to a trade off in that either many more smaller groups need to be recognized to achieve robust (and seemingly monophyletic groups) or the remaining groups are rendered less robust. Although the "Dulichieae" appears to be reasonably well supported, the constitution of the surrounding genera is not particularly stable, and I prefer for the present to regard them as members of the more inclusive Scirpeae pending resolution of the remainder of the tribe (see below).
Similarly *Bolboschoenus, Hymenochaeta, Pseudoschoenus* and *Fuirena* appeared together or as near neighbours of the same minor clade in many of the cladistic analyses, but as the other members of the clade to which they belonged varied and as the group usually nested above other Scirpeae genera, they are not given any status here. Goetghebeur (1986) recognized the "Fuireneae" as comprising *Schoenoplectus, Fuirena, Pseudoschoenus, Bolboschoenus*, and *Hymenochaeta*. By contrast with the four genera grouping above, his "Fuireneae" never emerged in my analyses (phenetic or cladistic) as a monophyletic/monophenetic group, and only three times as a paraphyletic assemblage (#2-3; 12). Inspection of his cladograms reveals that the possition of *Fuirena* is unsupported and that the tribe is based only on the occurrence of the *Schoenoplectus*-type embryo.

*Eriophorum* (based on the amalgamated descriptions of *Eriophoropsis, Eriophorum, Erioscirpus*) constituted the second clade of the Scirpeae in #24 (Fig. 9.2). It is only supported by one attribute here (perianth members elongating with maturing of the fruit: 262,1); a feature not unique to them. The three genera when included separately in the analyses always failed to form a monophyletic group. *Erioscirpus* almost always was a member of a separate clade, or at least, paired with other genera. The amalgamated description of *Eriophorum* (analysis #24) was neither homogeneous nor highly distinct. Rather, the disparate embryo morphology of *Erioscirpus*, and the otherwise heterogeneous description for this ‘genus’ seem to account its intermediate and isolated position in #24. Goetghebeur’s (1986) cladogram of his "Scirpeae" included all three genera united by the same perianth attribute as above. He also included in this tribe *Scirpus, Trichophorum, Sumatrosirpus, Phyllosirpus* and *Baeothryon*. The results obtained in the present study show that this grouping emerged in ten analyses, but only as paraphyletic/paraphenetic groups (Table 9.4), suggesting that further work is required to resolve their relationships.

The third clade of the Scirpeae evident in tree #24 (Fig. 9.2) includes fifteen genera (*Androtrichum, Anosporum, Blysmus* (including *Blymopsis*), *Desmoschoenus, Egleria, Eleocharis* (the C₃ species and the C₄ species), *Eleogiton, Ficinia* (including *Ficinia* subgenus *Sickmannia*), *Isolépis, Kyllingiella, Oxycaryum, Phylloscirpus, Schoenoplectus, Scirpoides, Websteria*) supported by three characters: viz., culm palisade mesophyll present (106,1), leaf blade strands not all aligned with the vascular bundles (157,2), and C₄ biochemical type NAD-ME (165,1). Paradoxically the C₄ species of *Eleocharis* are the only members of this clade that are known to be NAD-ME type but they do not posses culm palisade mesophyll or leaf blades (Appendix 1).
Nevertheless, the current analyses do not support taxonomic segregation of *Eleocharis* on the basis of photosynthetic pathway differences.

*Eleocharis* (the C₃ species, and the C₄ species), *Egleria* and *Websteria* constitute a robust group (i.e. Goetghebeur’s 1985, 1986 "Eleocharideae"); appearing monophyletic in 17 of the analyses, paraphyletic/paraphyletic in seven (Table 9.4), though in most cases these genera were nested amongst various other genera of the Scirpeae.

In #24 (Fig. 9.2), for example, the "Eleocharideae" are supported by seven characters: viz., ‘basal spikelets’ female (172,1), rachillae of definite growth (217,2), style-base sharply differentiated from the fruit apex (294,2), style-base ‘enlarged-pyramidal’ (295,2), stigmatic papillae ‘zoned’ (300,1), fruit laterally compressed (304,1), and second embryonic leaf primordium ‘well developed’ (329,1). Only #294 is constant across the four genera, though the score for *Websteria* is equivocal (Appendix 1), while #300, 304 and 329 are unknown for at least one of them, with #304 only recorded for *Websteria*, and character #217 exhibits intra- and intertaxon variation. Goetghebeur (1986) separates the "Eleocharideae" from the Abildgaardieae (see below) by three attributes; inflorescence reduced to solitary spikelets, leaves elaminate, and *Eleocharis*-type embryo. The first two occur in at least some species of both of his neighbouring tribes (the Abildgaardieae and the Fuireneae). The last character can be reduced to a matter of whether the first embryonic leaf primordium is exerted (*Eleocharis*-type) or not (*Schoenoplectus*-type), however, my observations and Goetghebeur’s (1986 p.382 Figs 8.4.5C, 8.5.1C-D and G-I) drawings show this character to be variable for both *Eleocharis* and *Schoenoplectus*. The "Eleocharideae" rarely grouped with the Abildgaardieae, but often with the Scirpeae. In the latter cases, the four genera generally linked with *Fuirena* in the phenetic analyses, and with *Schoenoplectus* in the recent cladistic analyses. These results are not surprising, though they are controversial. Raynal (1973) and Goetghebeur (1986) have argued for the "Eleocharideae"–Abildgaardieae relationship, while Haines and Lye (1971) derived *Eleocharis* from the ancestor of *Schoenoplectus*. The "Eleocharideae" and Abildgaardieae (see below) share zoned stigmatic papillae, enlargement of the style base, and in some cases share various morphological features including inflorescences which always comprise solitary spikelets, and elaminate leaves. The "Eleocharideae" and *Schoenoplectus* share similar embryo types, very similar vegetative anatomy and morphology (including in some cases the last two features listed for the other grouping). The discovery of C₄ *Eleocharis* species (Bruhl *et al.* 1987; Ueno *et al.* 1988) has not lead to a resolution of this ambiguity, as the C₄ *Eleocharis* species differ from the
Abildgaardieae C₄ species anatomically (Chapter 8), ultrastructurally (Chapter 9), and biochemically (Chapter 8). Therefore, the relationship between the 'Eleocharideae' and *Schoenoplectus* indicated by the analyses is not invalidated. Indeed, it suggests a testable hypothesis that the latter may include NAD-ME C₄ sedges other than *Eleocharis*, or that *Schoenoplectus* and the "Eleocharideae" should prove to be more closely related at the molecular level than "Eleocharideae" and Abildgaardieae. As the relationships of the four genera are uncertain and as the genera are often nested above other Scirpeae genera, I have refrained, by contrast with Goetghebeur (1985, 1986), from recognizing the "Eleocharideae" as a tribe. A more profitable approach may be to direct attention towards establishing the limits of an "Eleocharideae" plus *Schoenoplectus* group.

The relationships of many of the other genera of the *Kyllingiella-Androtrichum* group apparent in #24 (Fig. 9.2), were rather labile. For example those of *Ficinia* and *Ficinia* subgenus *Sickmannia*, and of *Isolepis* and *Eleogiton* both varied from disassociation to sister group relationships. The variability inherent in the morphologically highly heterogeneous *Ficinia* no doubt accounted for its appearance as a nearest (or once to three times removed) neighbour of many genera (Appendix 1), and would also affect its clustering in the phenetic analyses. Variability in *Ficinia*'s description led to many of its characters being considered as unknowns for purposes of the cladistic analyses, and this would have increased its chance of linking with various genera in those analyses. The evidence from the analyses for including *Eleogiton* within *Isolepis* is reasonable but equivocal, for their association was not constant nor did it always involve a sister group relationship. A species level investigation of the two genera is still in order. Similarly, a species treatment of *Eleogiton, Isolepis, Ficinia* and *Scirpoides* is needed to deal authoritatively with the placement of *Isolepis nodosa* and *I. prolifera*. However, based on the use of INTKEY (Appendix 3) the former seems to be most closely allied to *Ficinia*, and the latter to *Isolepis* (cf. Wilson 1981).

*Desmoschoenus* more often paired with *Androtrichum, Scirpoides* or *Ficinia*, while *Phylloscirpus* was particularly unstable. *Phylloscirpus* linked with the Abildgaardieae, the Scirpeae or with *Hellmuthia*. Its description was based primarily on one of the five species, and its culm anatomy was not assessed. In analysis #13, without culm anatomy *Phylloscirpus* was interpositioned between the Abildgaardieae and most of the Arthrostylideae. Goetghebeur (1986) includes *Phylloscirpus* in his narrowly defined Scirpeae as the sister taxon of *Baeothryon*, but there was no support for this placement in my analyses (cf. Table 9.4; Appendix 4).

Neither the recognition of Goetghebeur’s (1986) series of small tribes (several of which never appeared as monophyletic/monophenetic in my analyses; Table 9.4) nor
the proposed recognition of a large and at best grade tribe (the Scirpeae) appears to be satisfactory. The latter is preferred only as a conservative and convenient means of dealing with these genera. Meanwhile, this tribe seems to be the one in greatest need of taxonomic effort in the Cyperaceae.

The Abildgaardieae (Appendix 1, pp 429-434)

A group of seven genera including Abildgaardia (the C₄ species and the C₃ species), Bulbostylis, Crosslandia, Fimbristylis, Nemum, Nelmesia, Tylocarya (Table 9.5), appeared as a monophyletic group in five analyses (#11-12, 22-24) and monophenetic in one (#25; Table 9.3). Material of Nelmesia and Nemum was not available and most analyses in which they were included failed to produce the Abildgaardieae as a monophyletic group (#1-4, 6, 8, 10, 13-14, 18, 28-30). A more obvious cause of the group appearing as paraphyletic/paraphenetic or polyphyletic/polyphenetic was the inclusion of a separate description for the two C₃ species of Abildgaardia; the Abildgaardieae, exclusive of the C₃ species of Abildgaardia, emerged intact in twelve analyses (#9, 14-21, 26, 27, 29). The behaviour of both Abildgaardia (the C₃ species), and the Arthrostylideae which often linked with the Abildgaardieae, is discussed below.

To evaluate the support for the Abildgaardieae, the features of the group were examined in the cases where they formed 1) a monophyletic group including all seven genera, but where the description of the C₃ species of Abildgaardia was omitted (#12; Appendix 4); 2) a monophyletic group in an analysis from which Nelmesia and Nemum were omitted (#19; Appendix 4); and 3) one where the last two genera were omitted and C₃ and C₄ species of Abildgaardia were amalgamated (#24; Fig. 9.3A).

In analysis #12 ten features unite the group: viz., culm trans-section circular or truncate circular (76,5), leaf blades ‘pilose’ (113,3), leaf blade hypodermis present (129,1), ‘basal spikelets’ borne above ground (171,1), floral bracts incompletely deciduous (236,2), style-base sharply differentiated from the fruit apex (294,2), stigmatic papillae ‘long’ (299,1), stigmatic papillae ‘zoned’ (300,1), fruit epidermal cells relatively ‘smooth’ (314,3), embryo turbinate (322,1), and germination pore perpendicular to the first embryonic leaf primordium (327,1).

In analysis #19 nine attributes support the group: viz., vernation ‘curved’ (24,2), leaf blades without a keeled midrib (36,2), culm trans-section circular or truncate circular (76,5), leaf blade trans-section ‘thinly crescentiform’ or ‘thickly crescentiform’ (127,2), leaf blade ‘translucent tissue’ absent (135,2), photosynthetic pathway C₄ (163,3), C₄ anatomical type fimbristyloid (164,1), the spikelet prophyll keels
indumented (214,1), floral bracts incompletely deciduous (236,2), and stigmatic papillae ‘zoned’ (300,1).

Nine characters also support the group in #24 (Fig. 9.3A): viz., ligules indumented (55,1), culm sclerenchyma not in direct contact with all of the vascular bundles (101,1), photosynthetic pathway $C_4$ (163,3), $C_4$ anatomical type fimbristyloid (164,1), ‘basal spikelets’ borne above ground (171,1), floral bracts incompletely deciduous (236,2), perianth absent (255,2), stigmatic papillae ‘zoned’ (300,1), and cotyledon ‘markedly widened’ (323,1).

There is a higher level of coincidence of characters supporting the group between the analyses in which Nelmesia and Nemum were omitted (i.e. #19 and 24: 163-164, 236, 300), than for the other two combinations (#12 and 19: 76, 300; #12 and 24: 300). The comments that follow relate to the ITEMS data for the group in terms of the original separate descriptions. Characters #294, 299, 300 are constant for all the taxa. Each of these features is paralleled outside the group, though #300 otherwise only occurs in the "Eleocharideae" (see above). Ten of the features (#24, 36, 101, 113, 127, 129, 135, 164, 171, 236, 327) are congruent but unknown, inapplicable, or variable for one or most of the genera, while the remainder (#55, 76, 163, 214, 255, 314, 322, 323) exhibit intergeneric variability. The leaf blade and photosynthetic pathways characters (#113, 127, 129, 135, 163-164) are all at odds with the description of Abildgaardia (the $C_3$ species). The sister group relationships are not stable for the Abildgaardieae in these analyses, but usually included the Cypereae and/or Scirpeae.

The sister group relationship of the Abildgaardieae with the "Eleocharideae" postulated by Goetghebeur (1986) and implied by Raynal (1973) was not generally substantiated by these analyses (Appendix 4), though the four eleocharoid descriptions (Eleocharis the $C_3$ and the $C_4$ species, Egleria and Websteria) plus Androtrichum formed the sister group of the Abildgaardieae in #3 and 5, and the "Eleocharideae" constituted a clade within the Abildgaardieae in #6 and 13 (though the Arthrostylideae were also included in these cases).

The sister group relationships within Abildgaardieae were unresolved across the analyses. Goetghebeur's tree is only partially resolved, and involves the spurious use of an 'embryo-type' character; his Tylocarya-type is a unique (autapomorphic) condition of the Fimbristyli-type, and my observations on the embryo of the $C_3$ species of Abildgaardia reveal Fimbristyli—Schoenoplectus-like embryo morphology. A broader sample for embryo morphology of Abildgaardia and Fimbristyli is warranted to determine the significance of these observations. Regardless of the possibility of
transferring one or both of the C\textsubscript{3} species back to *Fimbristyris* (see Chapter 2) the relationships of the Abildgaardieae remain largely unaltered.

**The Arthrostylideae** (Appendix 1, pp 434-437)

This is a small tribe of three monotypic genera (*Arthrostylis, Trachystylis*, and *Trichoschoenus*) and one tritypic (*Actinoschoenus*; Table 9.5). There might, therefore, be an expectation that the tribe is relatively homogeneous and taxonomically stable. This seems to be the case to the extent that the *Actinoschoenus, Arthrostylis, and Trachystylis* constituted a robust clade in most of the analyses (Appendix 4: #1-2, 4-5, 8, 10-12, 14, 18, 20-27). In #3 and 6 *Trichoschoenus* also was a member of the clade, in nine cases (#7-10, 13, 15-17, 19) the four genera constituted a paraphyletic group, while in many of the analyses in which *Trichoschoenus* was included, it failed to join directly the with the other three genera rendering them paraphyletic or polyphyletic (cf. Table 9.3). This may have resulted from the poorly scored description for *Trichoschoenus*, for which no material was examined. In addition to the leaf anatomical characters being inapplicable for this elaminate genus, almost no culm anatomical characters were able to be scored. It differs from the other three genera in possessing characters, in particular of the style base and fruit, which are at variance with those of the other members of the group, but which are typical of some Schoeneae (e.g. *Costularia* and *Oreobolus*), a fact noted by Raynal (1968), when he described *Trichoschoenus*. The embryo of *Trichoschoenus* is also of a kind typical of the Schoeneae.

In #24 (Fig. 9.3A) the clade of the three genera, i.e. exclusive of *Trichoschoenus* is supported by fifteen attributes: viz., leaves ‘elaminate’ (25,1), culm palisade mesophyll present (106,1), leaf blade ‘translucent tissue’ absent (135,2), leaf blade spongy mesophyll absent (159,2), leaf blade palisade mesophyll present (160,1), primary inflorescence bracts tristichous (189,3), floral bracts of each female-fertile spikelet deciduous collectively (237,2), floral bracts tristichous (239,3), perianth absent (255,2), hypogynium present (287,1), style-base deciduous (296,2), fruit apex beakless (308,2), fruit epidermal cells ‘cancellate’ (314,1), cotyledon ‘markedly widened’ (323,1), and germination pore parallel with the first embryonic leaf primordium (327,2). The characters can be evaluated across the four genera from the ITEMS data. Characters #255 and 323 are constant across the four genera. *Trachystylis* is variable for #237, and differs for #25 and 314, though the latter is dependent on the degree of magnification and *Trachystylis* probably should also be scored as ‘cancellate’ for this trait. *Trichoschoenus* is the odd-genus-out for #296 and 314, and unknown for #106, while
leaf blade characters (#135, 159, 160) apply only to *Trachystylis*, the others being elaminate.

The sister group to the Arthrostylideae (i.e. usually excluding *Trichoschoenus*) in most of the cladistic analyses was *Abildgaardia* (the C₃ species: #1-4, 6, 10, 20, 21) or the Abildgaardieae as a whole (11, 14-16, 28). Other sister group relationships included *Phylloscirpus* in analyses #7, 12, and 19; the Schoeneae in #26-27, and 30; the Rhynchosporoae and the Cyperoideae generally, or the Rhynchosporoae and Abildgaardieae #23-25; *Hellmuthia* #18, 22; and *Ptilanthelium* #5. *Trichoschoenus* formed sister group relationships with a similarly diverse group of taxa. These results point to a close relationship with the Abildgaardieae, and some authors have included *Arthrostylis* and *Actinoschoenus* in *Fimbristylis* or *Abildgaardia* (e.g. Kern 1974; Koyama 1974). This result seems to have been biased by the inclusion of the C₃ species of *Abildgaardia* as a separate description, and the anomalous behaviour, in particular of *Hellmuthia*, and *Phylloscirpus* in frequently linking with the Abildgaardieae. The omission of *Hellmuthia* and *Phylloscirpus*, resulted in a shift of the tribe away from the Abildgaardieae nearer the Schoeneae and Rhynchosporoae. Historically, this is also an unsurprising result, in that some authors have included or allied the genera of the Arthrostylideae in or near these tribes (e.g. Kuekenthal 1944, 1952; Blake 1969; Raynal 1968; see also Table 9.1).

To examine the support for the relationship of the Arthrostylideae with the Abildgaardieae, the attributes supporting, in #19 (Fig. 9.3B), the group including *Abildgaardia* (the C₃ species), *Hellmuthia*, and the Arthrostylideae (except for *Trichoschoenus*) were investigated in terms of the character state distributions of the these taxa together with *Trichoschoenus* for the ITEMS data. This is a well-supported clade representing twelve attributes: viz., leaves ‘elaminate’ (25,1), leaf sheath apices V-shaped (43,3), leaf blade ‘translucent tissue’ absent (135,2), rachillae of definite growth (217,2), proximal sterile bracts 1 or more (232,2), floral bracts incompletely deciduous (236,2), floral bracts of each female-fertile spikelet deciduous collectively (237,2), floral bracts tristichous (239,3), floral bracts increasing in absolute length acropetally (241,3), each flower enclosed directly by a distal floral bract (249,2), style-base ‘enlarged-pyramidal’ or conical (295,2), and coleorhiza basal (331,3). Attribute #25 links most of the Arthrostylideae to the C₃ Abildgaardieae species, but this feature is variable across the Abildgaardieae (and the Schoeneae). Character #135 unites *Hellmuthia* with *Trachystylis* but the character is inapplicable for the other members of the clade. Features #232, 236, 239, 241, and 295 are typical of the Abildgaardieae, the Schoeneae and the Rhynchosporoae. Attribute #43 links the Arthrostylideae with the
Schoeneae, and #217 with the Schoeneae and the Rhynchosporae. The Arthrostylideae, Schoeneae, Rhynchosporae, and Sclerieae share attribute #249, while #237 is a feature unique to the Arthrostylideae. There is support both for a relationship between the Arthrostylideae and the Abildgaardieae on one hand, and the Arthrostylideae and the Schoeneae/Rhynchosporae on the other. This ambiguity has not been resolved.

Goetghebeur's (1986) cladogram of the Arthrostylideae is supported by two features (viz., floral bracts of each female-fertile spikelet deciduous collectively, and the absence of a perianth), congruent with the present study, basal to the unsupported clade of the Rhynchosporae and the Schoeneae. All three constitute the sister group of the Cypereae. His presentation clearly favours a relationship of the Arthrostylideae with the Schoeneae and Rhynchosporae; all three are included (together with the Abildgaardieae) in his Cyperoideae.

A thorough examination of *Trichoschoenus* and of the features uniting the four genera is necessary to resolve these conflicts, and may even lead to the formers' placement within the Schoeneae, and thence to a resolution of much of the conflicting evidence presented above. Meanwhile it is convenient to accept the four genera as constituting a tribe.

*The Rhynchosporae* (Appendix 1, pp 437-441)

The Rhynchosporae (Figs 9.4A-B), composed of *Micropapyrus*, *Pleurostachys*, *Rhynchospora*, and *Syntrinema* (Table 9.5), emerged as a robust group (Table 9.3). The C\textsubscript{3} species, the C\textsubscript{4} rhynchosporoid species, and the C\textsubscript{4} chlorocyperoid species of *Rhynchospora* were provided with separate descriptions for most of the analyses, but they were amalgamated for #22-24. Material of *Pleurostachys* was not examined, and it was omitted from most of the analyses. The genera appeared as a monophyletic/monophenetic clade in most of the analyses (#1-2, 5-7, 9-11, 15-21, 23-25) including five of the cladistic analyses with *Pleurostachys*. In six analyses (#3-4, 8, 12-14) the Rhynchosporae formed a paraphyletic group and in two paraphenetic (#26-27), including five with *Pleurostachys*. In the remaining four cases (#22, 28-30) the Rhynchosporae formed a polyphyletic/polyphenetic group (four analyses, mostly phenetic, with *Pleurostachys*).

Ten attributes support the clade comprising the Rhynchosporae in analysis #18 (Fig. 9.4A), which includes *Pleurostachys* and the separate descriptions for the photosynthetic pathway variants of *Rhynchospora*: i.e., culm intercostal cells regular and rectangular (59,1), culm strands all aligned with the vascular bundles (103,1), abaxial
leaf blade epidermal cells regular and rectangular (109,1), leaf blade hypodermis absent (129,2), inflorescence capitate (177,3), primary inflorescence bracts distichous (189,2), stigmata up to 2 (297,1), fruit dorsiventrally compressed (304,2), cotyledon ‘markedly widened’ (323,1), coleoptile lateral (324,1).

Nine features support the clade comprising the Rhynchosporeae in #19, but here Pleurostachys had been omitted and the photosynthetic pathway segregates of Rhynchospora described separately: viz., leaf sheath apices glabrous (44,2), abaxial leaf blade epidermal cells regular and rectangular (109,1), leaf blade hypodermis absent (129,2), primary inflorescence bracts distichous (189,2), margins of the spikelet prophylls glabrous (215,2), floral bracts glabrous (245,2), stigmata up to 2 (297,1), stigmatic surface glabrous (298,2), and coleoptile lateral (324,1). By contrast, only four characters support the equivalent clade in #24 (Fig. 9.4B): i.e. female-fertile spikelets androgynous (200,2), functionally male-only flowers 1 per spikelet or more (254,2), stigmata up to 2 (297,1), and stigmatic surface glabrous (298,2). In this case not only was Pleurostachys omitted but Rhynchospora was represented by only one amalgamated description.

There is a high level of similarity of attributes supporting the clade between these analyses, with five characters appearing in both #18 and 19 (i.e. characters #109, 129, 189, 297, 324), two in common between #19 and 24 (#297, 298), and one of these is common to all three analyses (#297). The last feature is constant for all the members of the clade. Six (#44, 109, 200, 254, 298) are variable within one or a few of the descriptions but are congruent for all in terms of the ITEMS data. Characters #59 and 103 are also congruent with the cladogram despite being unknown or inapplicable for some, whereas #129 exhibits intra- and inter-taxon variability. Characters #189, 323, and 324 are unknown for most of them, highlighting the need in particular for further sampling for embryo characters.

The sister group relationships of the Rhynchosporeae are broadly explicable but ambiguous. In six analyses (#1-3, 6, 10, 15) its sister group was the Schoeneae. In most of the other cases the sister group included a number of tribes, either of a) the Schoeneae together with other tribes of the Caricoideae including the Caricaceae and Hypolytreae (e.g. #17-18); or b) tribes of the Cyperoideae, including the Arthrostylideae (e.g. #13-14, 19). Other sister groups included the Caricaceae with Dulichium, and Eleocharis (the C₄ species). The phenetic analyses generally clustered the Rhynchosporeae with either the Abildgaardieae or within the Schoeneae.

The within tribe sister group relationships were generally as follows: Syntrinema and rhynchosporoid C₄ species of Rhynchospora constituted a terminal pair, with the
addition in turn of the chlorocyperoid C₄ species, the C₃ species and Micropapyrus while Pleurostachys was basal. By contrast, with the amalgamation of the three groups of Rhynchospora and the exclusion of Pleurostachys, Rhynchospora and Micropapyrus paired and the C₄ Syntrinema was basal (#23-24) or separated (#22), implying, less convincingly, that in these latter cases that C₄ photosynthesis is an ancestral trait in the Rhynchosporae. Goetghebeur (1986) recognized the Rhynchosporae, comprising Pleurostachys and Rhynchospora. The latter is not supported by any features in his cladogram. He includes both Micropapyrus and Syntrinema in Rhynchospora prior to his analysis. Whilst they are clearly related, with vegetative anatomy providing useful information (see Chapter 5), the material available for examination has been inadequate to score a number of key features such as embryo morphology and some style and fruit characters. Thus, reduction of these monotypic genera may reasonably await a more detailed examination of them.

The Schoeneae (Appendix 1, pp 441-447)

Twenty-seven genera are included in this tribe, namely Baumea, Carpha, Caustis, Cladium, Costularia, Cyathochaeta, Cyathocoma, Epischoenus, Evandra, Gahnia, Gymnoschoenus, Lepidosperma, Lophoschoenus, Machaerina, Mesomelaena, Morelotia, Neesenbeckia, Oreobolus, Ptlanthelium, Reedia, Rhynchocladium, Schoenoides, Schoenus, Tetraria, Tetrariopsis, Trianoptiles and Tricostularia (Table 9.5). Costularia brevicaulis was described separately (see Chapter 3) but amalgamated with Costularia in analyses #22-24 (cf. Seberg 1986, 1987a-b; e.g. Fig. 9.5). The group appeared as a monophyletic clade in only five cases (#6-7, 9, 15 and 25) and was presented as polyphyletic/polyphenetic in eleven (Table 9.3). For example in #18 Microdracoides was included within the Schoeneae and Evandra was excluded.

In the phenetic analyses the Schoeneae constituted a monophenetic cluster in only #25. Otherwise it mostly formed a highly distinctive cluster, but was paraphenetic (#26, 28-30) by virtue of inclusion of all or part of either or both the Arthrostylideae and Rhynchosporae (see above). In #27 it was polyphenetic by the exclusion of Carpha and Trianoptiles. In the rest of the cladistic analyses Schoeneae constituted a paraphyletic group, often only by virtue of the segregation of Cladium, or Cladium and Rhynchocladium. Thus, the Schoeneae, are generally more robust than Table 9.3 indicates.

Analyses #14 and 15 contrast the inclusion of all the taxa with the omission of the ‘poorly scored’ genera respectively. In the former case the Schoeneae grade into the
scleroids sensu traditus, with Tetrariopsis, Morelotia and Lophoschoenus, and Evandra basal to the genera of the Cryptangieae (here paraphyletic) and Trilepideae (nested above the Cryptangieae), while Cladium is positioned above them at the base of the Hypolytreae. Omitting the ‘poorly scored’ genera led to the Schoeneae constituting a closer knit but paraphyletic group higher up in the cladogram, while the basal genus in the analyses changed from Oreobolopsis to the Hypolytreae. Other rearrangements were mostly minor. Although the Schoeneae, in particular, are affected by the inclusion or omission of the ‘poorly scored’ genera generally the similarities between the outcome of the two analyses far outweigh their differences. Not surprisingly, this result points to the need to examine material of the ‘poorly scored’ genera.

As the Schoeneae appeared as a paraphyletic group in both analyses #19 and 24 (Fig. 9.5), a comparison of the features supporting the group in #24 is made with that of #15 (Fig. 9.6) where the group emerged as a clade. Ten attributes support the Schoeneae clade in #15: viz., leaf sheaths with overlapping margins distally (41,1), leaf sheath apices V-shaped (43,3), leaf sheath apices indumented (44,1), leaf blades indumented (112,1), leaf blade hypodermis present (129,1), leaf blade hypodermal cells distinctly larger than the adjacent epidermal cells (132,1), leaf blade sclerenchyma in direct contact with all of the vascular bundles (155,2), leaf blade strands not all aligned with the vascular bundles (157,2), female-fertile spikelets gynandrous (200,1), and second embryonic leaf primordium not detectable (328,2). Examination of the ITEMS data reveals that none of them are constant across all the genera of the Schoeneae, though characters #41 and 43 are the most consistent.

Five chained clades in analysis #24 include the taxa (with the exception of Evandra) which constitute the Schoeneae. The node at the base of the Schoeneae group in #24 (which also includes most of the Cyperaceae) is supported by eight features: viz., leaf sheaths with overlapping margins distally (41,1), culm trans-section circular (76,5), leaf blade hypodermal cells distinctly larger than the adjacent epidermal cells (132,1), leaf blade ‘bulliform cells’ absent (133,2), leaf blade strands not all aligned with the vascular bundles (157,2), female-only flowers 0 per spikelet (252,1), style ‘flattened’, or markedly angular (290,2), and style-base ‘enlarged-pyramidal’ or conical (295,2).

The next highest node supports the same genera, but it omits Cladium, and thirteen characters are involved, though none are in common with those supporting the Schoeneae clade in analysis #15. They include vernation ‘curved’ (24,2), leaves distichous (26,2), leaf blades without a keeled midrib (36,2), leaf blade trans-section ‘thinly crescentiform’, or ‘thickly crescentiform’ (127,2), mid-leaf blade palisade mesophyll abaxial (161,1), primary inflorescence bracts distichous (189,2),
inflorescence prophylls bract-like (196,2), margins of the spikelet prophylls indumented (215,1), floral bracts deciduous (235,2), perianth present (255,1), style indumented (292,1), first embryonic leaf primordium present (325,1), and coleorhiza subbasal (331,2).

The five clades comprising the Schoeneae are examined in turn. The genus *Cladium* (whose author predated cladistics) is strongly supported in #24 by fifteen attributes, all of which this small homogeneous genus actually possesses. They include leaf blades with readily visible transverse septa (33,1), leaf bases not breaking down into fibres (39,2), culm parenchymatous bundle sheaths with extensions (99,1), leaf blades amphistomitic (120,3), leaf blade vascular bundles 'inverted' (141,1), leaf blade parenchymatous bundle sheaths with extensions (152,1), lateral branch inflorescences 'planipanicle' (i.e. corymbose) or anthelate (184,2), rachillae deciduous (218,1), floral bracts glabrous (245,2), stamens 2 (268,2), hypogynium present (287,1), mesocarp spongy (316,1), endocarp sclerenchymatous (318,1), endocarp 'dark' (319,1), and cotyledon not markedly widened (323,2). There is some direct overlap with the remainder of the Schoeneae for all of these characters, except for culm vascular bundle extensions (#99) where a few of the genera concerned have not been scored but those that have are without them. Characters #184 and 218 link *Rhynchocladium* with *Cladium*, though the former genus is variable for the second feature. In fact, although there is some support for the two genera as sister taxa, *Rhynchocladium* has been insufficiently described in this study (see also Koyama 1969, 1972) to allow definitive comments regarding its relationships. The attributes supporting *Cladium* at the base of the Schoeneae clade in analysis #15 include eleven in common with those supporting *Cladium* in #24 (namely #33, 99, 120, 141, 152, 218, 268, 287, 316, 318, and 319). Six further attributes in #15 support the distinctiveness of the basal clade comprising *Cladium*; viz., leaf blade 'bulliform cells' absent (133,2), leaf blade palisade mesophyll present (160,1), the spikelet prophyll keels glabrous (214,2), rachillae (female-fertile spikelets) 2. disarticulating below prophyll (219,2), floral bracts persistent (235,1), and perianth absent (255,2). Of these additional attributes of *Cladium*, #219,2 is shared within the Schoeneae by *Rhynchocladium* (and in part by *Tettraria*), seemingly further corroborating the *Cladium-Rhynchocladium* relationship, though this character may be linked to the deciduous nature of the rachilla. Goetghebeur (1986 pp.178-179) links the two genera in his cladogram of the Schoeneae solely on the basis that they both have "corymbiform deelbloemgestellen". Strict comparisons reveal that the lateral inflorescence branches in *Cladium* are more anthelate than corymbose; however, as these states may intergrade (see also #177) they were treated collectively as one state.
of character #184. Clearly Cladium is a distinctive member of the Schoeneae. Whether Cladium itself merits tribal or subtribal status, is a matter that should await a more thorough study of Rhynchocladium (especially to include vegetative anatomy and embryo morphology) in order to confirm their relationships with each other and to clarify their status vis a vis the rest of the Schoeneae. 

Tricostularia constitutes the next clade of the Schoeneae group in analysis #24 (Fig. 9.5), supported by three attributes: leaf blade sclerenchyma not in direct contact with all of the vascular bundles (155,1), anther apiculus indumented (280,1), and germination pore parallel with the first embryonic leaf primordium (327,2). In the context of the Schoeneae, none are unique to Tricostularia, though #327 comes close, with Tetraria being variable. Tricostularia did form a distinct clade in a number of the other analyses, while in #1-4, 7-10, 17, 19-20 it appeared basally on a small clade with Gymnoschoenus and Reedia near or within a clade including Schoenus, and in #9-10, 15, 21 it paired with Cyathocoma. The instability or isolated position of Tricostularia from analysis to analysis may be a result of its relatively high heterogeneity (a number of its species have been variously placed in Schoenus, Tetraria and Costularia). The generic limits of Tricostularia warrant further attention.

The next clade appearing in analysis #24 (Fig. 9.5), includes Tetraria, Neesenbeckia, Reedia, Gymnoschoenus, Mesomelaena, Schoenus, Episcoenus, Caustis, Machaerina, Lepidosperma, and Baumea, supported by six attributes: culm sclerenchyma not coalescing to form a ‘ring’ (102,2), culm palisade mesophyll present (106,1), leaf blade trans-section circular, or ‘elliptical’ (127,5), leaf blade ‘translucent tissue’ more or less adaxial to vascular bundles (136,2), pollen grains many aperturate (285,2), and fruit ‘stalked’ (306,1). None of the attributes are constant across the clade, though the members are more or less united in most of the analyses.

Common variations on this clade involve the inclusion of Tricostularia (#14, 15 19; see above); the linking of Neesenbeckia and Cyathocheta (#2, 6, 7, 10); and the exclusion of Caustis and its pairing with Gahnia (#3-4, 7, 10, 20). The last outcome is unsurprising given that the former is an extremely weak member of the former clade in #24: at odds with attributes #102 and 127, not applicable for 136, unknown for 285 and variable for 306. By contrast, the minor groups apparent in this clade, e.g. a) Schoenus, Episcoenus and Mesomelaena, and especially b) Machaerina, Baumea, and Lepidosperma are robust across the analyses. Baumea and Machaerina have been lumped by some authors (e.g. Koyama 1956; Kern 1959). Blake (1969 p.23) stated that there were "big differences in the fruit" between Baumea and Machaerina (viz. fruit whether winged and stalked, whether the pericarp is very thin and brittle or possess a
spongy mesocarp and bony endocarp), but my observations seem to indicate that these are largely quantitative, rather than qualitative features, and a more thorough study of the characters is needed.

Another very robust, and a novel minor group comprises Gymnoschoenus and Reedia (see also above; Figs 9.5-6). It is supported by nine attributes in #24: leaf sheaths with overlapping margins distally (41,1), culm substomatal chambers lined with bridging sclereids (75,1), culm strands all aligned with the vascular bundles (103,1), leaf blades indumented (112,1), leaf blade substomatal chambers lined with bridging sclereids (126,1), leaf blade trans-section ‘thinly crescentiform’ or ‘thickly crescentiform’ (127,2), leaf blade hypodermis present (129,1), lateral inflorescence branches contracted, the secondary rachides not visible (182,2), and spikelet prophylls more or less equalling the subtending bracts in length (206,2). Attributes #75 and 127 seem to be unique to these two taxa, though Metcalfe (1971) described this feature in some other taxa, his observations were not corroborated in the present study (see also Chapter 3). The other anatomical features are not unique to the two genera either, but collectively strongly corroborate the relationship, while the first attribute (#41) is a more general feature of the Schoeneae, and #182 is unknown for Gymnoschoenus. The two genera were chained (rather than paired) in all but the two most weakly clustered phenograms (i.e. #25 and 28). Other authors usually consider Gymnoschoenus, Mesomelaena and Ptilanthelium to be closely related (e.g. Wilson 1981b; Goetghebeur 1986), indeed Bentham (1878) included all three genera in Mesomelaena. Interestingly, Goetghebeur’s (1986 p.178) cladogram provides no features supporting his clade of these three genera.

Seven genera of the Schoeneae (viz. Gahnia and Cyathochaeta, Tetrariopsis, Morelotia and Lophoschoenus, and Cyathocoma and Costularia including Costularia brevicaulis) appear as the next clade in analysis #24 (Fig. 9.5), supported by only three attributes: culms armed with prickle-hairs (18,1), leaf blades markedly infolded when dry (37,1), and ligules indumented (55,1). None of these attributes are particularly constant across the members of the clade. Inspection of the other analyses reveals several general patterns of relationships. Morelotia, Lophoschoenus, Tetrariopsis, and often Evandra constitute a robust group (e.g. in trees #3-4, 6-9, 11-12, 15-14, 17-19, 21). Four attributes support the four genera in the example from #15 (Fig. 9.6); i.e.; plants with a ‘trunk’ (6,1), leaf bases breaking down into fibres (39,1), culms indumented (63,1), leaf blade hypodermal cells not larger than the adjacent epidermal cells (132,2). Of these only character #132 is constant across the four genera. Despite the seemingly low level of support in this particular analysis, data retrieval via INTKEY indicates that the four
genera have a very large number of attributes in common. Nevertheless *Gahnia* and *Cyathochaeta* also have affinities with the *Schoenus*-group of genera (see above). *Cyathocoma* never paired with *Tetraria* despite being a segregate of that genus (see Levyns 1947c; Goetghebeur 1986). It linked with *Tricostularia* in analysis #21, while more often it paired with *Costularia* (e.g. #6-7, 15-16, 18). *Costularia* never form a sister relationship with *Lophoschoenus* (treated as subgenera by Raynal 1974, modified from Kuekenthal, 1939a) and often they were placed on different major clades within the Schoeneae. In the analyses where *Costularia brevicaulis* was analysed separately it always failed even to associate with *Tetraria* and it usually failed to pair with *Costularia*, however, it mostly appeared in the same clade or an adjacent paraphyletic one to the latter. While support for the relationship of *Costularia brevicaulis* with *Costularia* was found, its qualification may in part be due to the limited amount of material and time available to study this segregate; for culm anatomy was not investigated, and the presence or absence of pseudopetioles not adequately assessed. In a number of cases (e.g. #3, 8-9, 11-12, 15, 19, 21) *Costularia* appeared within a clade near *Oreobolus* (see below).

*Oreobolus* and *Schoenoides*, and *Ptilanthelium*, *Trianoptiles* and *Carpha*, constitute another robust group within the Schoeneae. In analysis #24 (Fig. 9.5) they are supported by three attributes: leaf blades amphistomic (120,3), lateral inflorescence branches contracted (182,2), and coleoptile basal (324,3). Despite the apparently limited support indicated by these characters in terms of their number and variability across the five genera in this analysis, the group also emerged as a clade in #7, 10, 14, 15 (Fig. 9.6), 17-18, 20, 23-24, and in #3, 8-9, 11-12 without *Ptilanthelium*. Support for Kuekenthal’s (1939c) recognition of a close relationship between *Carpha* and *Ptilanthelium* is apparent in most of the analyses, with *Carpha* joining at the base of the *Ptilanthelium* and *Trianoptiles* pair.

Even when the Schoeneae constituted the basal clade in the analysis, *Oreobolus* was highly nested in the group; i.e. the results provide no support for the notion that it is particularly ‘primitive’ within the family (cf. Seberg 1988a, but contrast Hutchinson 1973).

Seberg (1986, 1988a-b) in an investigation of the phylogenetic relationships of *Oreobolus* recognized *Oreobolus oligocephalus* as a monotypic genus *Schoenoides*. He employed a subset of *Costularia* as the outgroup. Evaluation of his cladogram of their relationships (e.g. 1988a p.129 Fig. 2) reveals a number of debatable morphological interpretations. *Bulbostylis*, *Microdracoides*, *Costularia pro parte*, *Oreobolus* and *Schoenoides* were cited as genera in which the lateral shoots only originate at the base
of the uppermost culm internodes. Within the Schoeneae this growth pattern also occurs in *Tetrariopsis*, and some *Lepidosperma* and *Tricostularia* species. Seberg (1988a p.127) stated that "Distichous leaves rarely occur in the Cyperaceae ... and are not found in any related genus except *Costularia*". In fact, 27 genera of the Cyperaceae have distichous or spirodistichous leaves, including most genera of the Schoeneae (Appendix 1: 17 out of 27). He stated that the pseudopetirole is found in the Cyperaceae only in *Oreobolus* and *Schoenoides*, however, they are present in at least some species of *Costularia, Eleogiton, Ficinia, Isolepis, Mesomelaena, Oreobolopsis* (see Koyama and Guaglianone, 1987 Fig. 1), *Schoenus*, and are also clearly present in at least *Oxychloe* of the Juncaceae (see Barros 1953). Culm and/or leaf blade silica bodies "external" (i.e. forming cones seated on the epidermis; characters #67 and 118) are more widespread than Seberg stated. They occur in *Actinoschoenus, Costularia* (including *Costularia brevicaulis*), *Cyathocoma, Episcoenus, Neesenbeckia, Oreobolus, and Schoenoides*. The external silica bodies in *Actinoschoenus* do seem to be homologous with those of e.g. *Oreobolus* (see Chapter 3) by contrast with Seberg (1986, 1988a-b). *Episcoenus* is variable for this trait, while the ‘external’ silica bodies on culms of *Costularia* were not readily detectable. A well-developed hypodermis is given as a synapomorphy for part of *Costularia* equivalent to subgenus *Chamaedendron* plus *Costularia brevicaulis*; however, *C. brevicaulis* does not possess a hypodermis, while an adaxially complete hypodermis is present in *Cyathocoma, Gymnoschoenus, Reedia, Tricostularia*, and at least some *Lophoschoenus, Mesomelaena*, and *Tetraria* species.

*Schoenoides* is supported in Seberg's cladogram by two features, one of which is "subcapitate inflorescences". Kern (1974 p.682) describes the inflorescences of *Oreobolus* as "...almost capitate...", indeed, Seberg's own description of *Oreobolus ambiguus* (1988a p.151) includes "Inflorescence subcapitate...". This leaves a solitary autapomorphy supporting *Schoenoides* in his treatment. In my analysis #24 (Fig. 9.5) two features support *Schoenoides*: viz., mid-culm mesophyll 'translucent tissue' present (83,1), and spikelet "prophylils" lateral (205,1). The latter is equivalent to Seberg's "prophyl of the coflorescences split to the base". The sample of *Oreobolus* for culm anatomy is as yet limited, and the feature (#83,1) may occur in *Oreobolus*. In the meantime, the justification for maintaining the monotypic *Schoenoides* appears weak. The synapomorphy for *Oreobolus* of one-flowered spikelets is also relatively weak. Thirteen genera of the Schoeneae, including *Schoenoides*, have spikelets which may bear solitary flowers, although *Oreobolus* is the only one for which this trait is constant.

Regarding the Schoeneae, there are several areas of broad agreement between the results of the present study and those of Goetghebeur (1986), in particular the isolated
sister-group relationship of *Cladium* and *Rhynchocladium*, and the close relationship between *Carpha*, *Trianoptiles*, *Oreobolus* and *Costularia*. Goetghebeur, however, includes *Lophoschoenus* in *Costularia*. They are widely separated from one another in my analyses. I discount analyses which do not recognize a clade comprising *Baumea*, *Machaerina* and *Lepidosperma*. His placement of *Morelotia* near *Gahnia* seems to reflect their nomenclatural history rather than similarity based on shared features (see above; cf. Appendices 1 and 4). The similarity between *Gahnia* and *Reedia* recognized by Goetghebeur (1986) probably owes much to superficial phenotypic similarity. Much of the disparity between the results of our analyses for the internal structure of the Schoeneae may be due to his inappropriate and sometimes erroneous use of a geographic ‘character’, i.e. "20. Areal: pantropisch ... Australië". For example, he included *Reedia* (a monotypic genus from temperate south-west Western Australia), *Lepidosperma* (which has centres of diversity in the Sydney region of temperate New South Wales and south-west Western Australia), and *Trianoptiles* (which is restricted to southern Africa) in the pantropical clade.

At least some of the constituent groups of the Schoeneae described above may well justify tribal status (e.g. the *Oreobolus* group); however a more detailed study of the Schoeneae to determine more precisely the limits of these additional groups should precede any formal recognition. Some of the genera are clearly in need of a species revision to determine generic limits, e.g. *Costularia*, *Tetraria* and *Tricostularia*.

The Cryptangieae (Appendix 1, pp 447-450)

The Cryptangieae, composed of *Cephalocarpus*, *Didymiandrum*, *Everardia*, *Exochogyne* and *Lagenocarpus* (Table 9.5), appear in seventeen of the cladistic trees as a monophyletic or paraphyletic clade, and as a mono- or paraphenetic group in all the phenetic analyses (Table 9.3). In a number of cases the four genera constituting the Trilepideae (see below) were nested above the Cryptangieae rendering the latter paraphyletic (Table 9.3). Two main alternatives suggest themselves, either to distinguish the four genera of the Cryptangieae as a group or to recognize both the Cryptangieae and Trilepideae genera in a single group. The correlation of the paraphyletic status of Cryptangieae with the Trilepideae as a nested group may be due to an undesirable interaction of the two groups, because by contrast, the Trilepideae also often linked with the Cariceae (#6-9, 16-18, 22-24) and in almost all of these cases members of both the Cryptangieae and Trilepideae constituted monophyletic groups, thus providing a more resolved hypothesis. More of the recent cladistic analyses provide support for the former
option of recognizing the Cryptangieae separate from the Trilepideae, and all of the phenetic analyses are congruent with this conclusion.

The tribe Cryptangieae is well supported in analysis #24 (Fig. 9.7) with eight synapomorphs, but, the situation here is confounded by the inclusion of *Evandra*, which is probably misplaced, since it appears elsewhere in other analyses (see above). The attributes supporting the clade in #24 are leaf sheath apices n-shaped (43,1), culm indumentum costal (65,2), leaf blade sclerenchyma not in direct contact with all of the vascular bundles (155,1), leaf blade sclerenchyma girders or caps of the main veins not encasing parenchyma (156,2), lateral inflorescence branching pattern ‘prophyllar’ (181,2), floral bracts, female-fertile spikelets tristichous (239,3), floral bracts of male spikelets tristichous (253,2), and anther apiculus indumented (280,1). The character state distributions on the cladogram indicate that #181 and 253 are constant and do not vary outside the clade, while only 43, 155, and 253 are subject to homoplasy within it. By contrast, examination of the real descriptions (cf. ITEMS, Appendices 1 and 4) reveals much more variability, mostly associated with the inclusion of *Evandra* in this clade. Of the attributes supporting the clade, *Evandra* is the only one with V-shaped leaf sheath apices, and it is inapplicable for #156. The high level of support for *Evandra* (branch length of 12.5) itself arouses suspicion that this genus may be misplaced here. In fact, almost all of the attributes are unique to *Evandra* in the context of this clade, though they include a number of features typical of the Schoeneae. Therefore, the tribe Cryptangieae is accepted here, exclusive of *Evandra*.

The purported intergeneric relationships of the four members are not at all constant across both the phenetic and cladistic analyses. Many highly different trees were obtained, including the one presented by Goetghebeur (1986). His tree, however intuitively appealing, is in fact highly unresolved, and he includes a number of superfluous features which are unique (autapomorphs) to individual genera. More detailed comparative studies of the species of these genera are needed. Meanwhile, for practical purposes the genera are better treated separately rather than reverting to the sensu lato circumscription of *Lagenocarpus* (i.e. including *Didymiandrum*, *Cephalocarpus* and *Everardia*: cf. Gilly 1941a-b, 1942 and Koyama and Maguire 1965).

*The Trilepideae* (Appendix 1, pp 450-453)

*Afrotrilepis*, *Coleochloa*, *Microdracoides*, and *Trilepis* (Table 9.5) constitute one of the most robust groups in my analyses, appearing as a monophyletic/monophenetic clade/group in all but two of the trees (Table 9.3: where *Microdracoides* joined the
Schoeneae, see above). Generally one of two patterns emerged. Either the Trilepideae were nested above a paraphyletic assemblage of the Cryptangieae (#1-2, 4-5, 10-15, 19-21; see above), or appeared as the sister group to the Cariceae (#6-8, 16-18, 22-24). In the phenetic analyses the Trilepideae clustered separately (not nested) as part of a larger group including the Bisboeckelereae, Sclerieae, and Cryptangieae.

Twelve attributes unite the four genera of the Trilepideae in analysis #24 (Fig. 9.7): viz., leaves distichous (26,2), leaf blades deciduous (38,1), ligules indumented (55,1), culm strands not all aligned with the vascular bundles (103,2), leaf blades indumented (112,1), leaf blades amphistomic (120,3), rachillae vestigial (216,1), perianth present (255,1), anthers basally unappendaged (274,2), fruit beak hollow (309,2), fruit epidermal cells ‘constituting hairs’ (314,2), and coleorhiza subbasal (331,2). As is common, when considering the whole tree, all these attributes involve homoplasy. Nevertheless, the ingroup is largely constant for them. According to the analysis only characters #26, 38, 55, and 314 are variable within the group. Two of these changes (leaves tristichous and leaves persistent) link *Afrotrilepis* and *Trilepis*. Examination of the ITEMS data reveals somewhat more variation, for example only *Coleochloa* is scored for #274. Further, *Microdracoides* is inapplicable for #55 and unknown for 331 and this contributes to the uncertainty of its position; the only genus with ‘smooth’ fruit.

Goetghebeur (1986) also recognizes the Trilepideae, based on inflorescence- and embryo-type characters and distichous floral bracts, with the tribe as the sister group to the Cryptangieae. He presents a fully resolved cladogram of the four genera (not withstanding that *Microdracoides* is indicated as having spiraled leaves; they are in fact spirodistichous). By contrast, my analyses indicate that the intergeneric relationships in the Trilepideae are unresolved (see Appendix 4).

The Cariceae (Appendix 1, pp 453-458)

*Carex* (composed of the subgenera *Primocarex*, *Vignea*, *Indocarex*, *Carex*), *Cymophyllus*, *Kobresia*, *Schoenoxiphium*, *Uncinia*, *Vesicarex* (Table 9.5) constitute a robust group which appeared as a monophyletic/monophenetic clade/group in all but two of the analyses (Table 9.3), providing strong support for its status as a monophyletic group. In analyses #22-24, where the subgenera of *Carex* were amalgamated, the genus was markedly more ‘variable’ and the PAUPDATA were correspondingly less resolved. The combination of a strong clustering intensity (0.90) and the inclusion of all taxa resulted in *Nelmesia* (one of the ‘poorly scored’ genera) linking with the Cariceae causing the latter to be paraphenetic (Appendix 4: Analysis #30).
Sixteen attributes support the Cariceae clade in #24 (Fig. 9.7): viz., leaf sheath apices ‘truncate’ (43,2), leaf sheath apices glabrous (44,2), culm sclerenchyma, not coalescing to form a ‘ring’ (102,2), the leaf blade indumentum intercostal (114,1), leaf blade palisade mesophyll absent (160,2), lateral inflorescence branch bases exposed (185,2), primary inflorescence bracts deciduous (190,1), female-fertile spikelets terete (202,3), spikelet prophylls longer than the subtending bracts (206,1), spikelet prophylls subtending female flowers (207,3), spikelet prophylls tubular (208,2), rachillae elongated (216,3), floral bracts absent (231,2), style-base ‘enlarged-pyramidal’ or conical (295,2), fruit indumentum ‘papillose’ (315,1), and cotyledon not markedly widened (323,2). Fourteen attributes support the Cariceae in #19: ligules present (49,1), culm tannin idioblasts absent (85,2), culm strands all aligned with the vascular bundles (103,1), leaf blade tannin idioblasts absent (138,2), terminal spikelets absent (199,2), spikelet prophylls longer than the subtending bracts (206,1), spikelet prophylls subtending female flowers (207,3), spikelet prophylls tubular (208,2), spikelet prophylls constituting perigynia (209,1), rachillae disarticulating below prophyll (219,2), floral bracts absent (231,2), stamens 3 (268,3), fruit indumentum ‘papillose’ (315,1), and coleoptile lateral (324,1).

The most surprising omission from the former group of attributes is that of #209,1 (spikelet prophylls constituting perigynia). Inspection of the "change lists" reveals that it appears but once on the cladogram in analysis #24 between the nodes 219 and 204, i.e. the feature appears as a synapomorphy linking the Sclerieae, Trilepideae, and Cariceae. No doubt the variability recorded for this trait in Kobresia and Schoenoxiphium (cf. Kern 1962), and the amalgamation of the Carex subgenera (invariant for this feature) contribute to this result.

Characters #207 and 231 appear from the "change lists" to be constant for the Cariceae, but the latter is in fact not scored for Kobresia and Schoenoxiphium. Several other characters are variable for a few of the taxa (e.g. #208, 323 and 43). The other characters are very variable across the clade, with only one or two members possessing the purported shared-derived condition (e.g. see #114, 160, 206, 216, 295 above).

The attributes supporting the Cariceae in analysis #19 are generally more constant across the clade (in terms of the ITEMS data). Characters #207 and 268 are constant, five others (#103, 199, 219, 231, 315) are constant as far as they have been scored. Another five (#85, 138, 208, 209, 324) are variable for some genera but are otherwise congruent, while only #206 is variable between the genera of the Cariceae.

The sister group relationships of the clade were of three general types. In earlier analyses the Cariceae generally paired with Dulichium or Cladium. By contrast, in the
more recent cladistic analyses the sister group comprised various combinations of the Trilepideae, Cryptangieae, Bisboeckelereae, and Sclerieae. The four tribes collectively constituted the ‘sister’ in the phenetic analyses, while the Trilepideae alone linked with the Cariceae in seven analyses (#6-8, 16-18, 24). The last two results were the most robust.

Within the Cariceae a number of robust groups were apparent, though these did not include the subgenera of Carex (which never formed a monophyletic group), nor the group composed of Kobresia and Schoenoxiphium (which were paired only in #1-2, 18, 20). Variability within the genera (e.g. in characters #208-210) could explain the failure of the latter two to form a sister group relationship. By comparison, Goetghebeur’s (1986 p.184) cladogram for the Cariceae shows no synapomorphs for these two genera, and only one distributional ‘autapomorphy’ defining Schoenoxiphium. The intrageneric relationships of Carex have received a great deal of attention, yet even questions regarding the monophyly of the genus and its subgenera remain subject to contention. (cf. Savile and Calder 1953; see also Tucker 1987 and references therein).

In the present study, the subgenera Vesicarex and Indocarex formed a sister group relationship in most analyses (#1-10, 12, 14-15, 20). This result contrasts with reduction to synonymy of the monotypic Vesicarex with Carex subgenus Carex by Mora-Osejo (1982; cf. Goetghebeur 1986). Carex subgenus Primocarex, Cymophyllus and Uncinia formed a robust clade in all the cladistic analyses (except for #22-24, e.g. Fig. 9.7, where the subgenera were amalgamated; Uncinia and Cymophyllus still united). In the phenetic analyses Carex subgenus Primocarex and Uncinia were paired, but Cymophyllus linked at the base of the Cariceae. The character concerned with occurrence of staminal meristems in the female-only flowers (#270) united the two or three taxa, regardless of the amalgamation of the subgenera. This feature is in fact scored present only for Cymophyllus and Uncinia, and its occurrence in a clade characterized by strictly unisexual flowers is of considerable relevance to questions regarding the evolution of unisexuality and bisexuality in the Cyperaceae (see also Chapter 4).

The Sclerieae (Appendix 1, pp 458-461)

Scleria and Acriulus linked with the Cariceae (#22), the Cryptangieae (#17), or more usually some combination of the Bisboeckelereae (see below), Cryptangieae, Cariceae, Trilepideae, and Hypolytreae. Given the lack of a clear consensus as to the sister group relationships of Scleria and Acriulus, combined with their emergence as a
monophyletic clade in most analyses, they are conveniently recognized as a tribe (Tables 9.3 and 9.5).

The tribe Sclerieae (represented by the amalgamation of descriptions of Scleria and Acriulus) is supported in #24 (Fig. 9.7) by four attributes: ligules acute (53,1), leaf blade sclerenchyma not in direct contact with all of the vascular bundles (155,1), coleoptile basal (324,3), and second embryonic leaf primordium ‘well developed’ (329,1). Acriulus is inapplicable for #53 but the remaining attributes are constant for the two genera. In analysis #19, where Scleria and Acriulus have been described separately, nine attributes support the Sclerieae clade: viz., culms bulbous (22,1), culm pith with air cavities (81,1), culm strands all aligned with the vascular bundles (103,1), leaf blades amphistomic (120,3), leaf blade ‘translucent tissue’ absent (135,2), leaf blade strands all aligned with the vascular bundles (157,1), style-base deciduous (296,2), coleoptile basal (324,3), second embryonic leaf primordium ‘well developed’ (329,1). Scleria is variable for five of these attributes (#33, 81, 120, 135, 296), and Acriulus is inapplicable for #103, but the three remaining characters are constant for both genera. Only the embryo characters, #324 and 329, support the Sclerieae in both of these trees, emphasizing the importance of these features. Similarly, this tribe is supported in Goetghebeur’s (1986) cladogram by embryo ‘characters’ (i.e. “Embryo ... Fimbristylis-type”, but see below).

In most of the analyses the cupular structure at the base of the fruit in Scleria, Acriulus, Diplacrum, and Becquerelia was treated as constituting a perianth (see Chapter 3 and 4). Other authors (e.g. Kern 1974; Franklin Hennessy 1985; Goetghebeur 1986) have interpreted it as a hypogynium, but the evidence either way is equivocal. Thus, the four taxa in contention (some other genera unambiguously possess a hypogynium) were rescored for analysis #20 in line with the alternative interpretation. The marginally shorter tree length in #20 for the comparable analysis #19 is readily accounted for by the increase in the number of unknown values in the former resulting from the changes in descriptions. The effects of the changes in the data on relationships apparent in tree #20 were not limited to those taxa whose descriptions were altered.

The local behaviour remained the same for the four taxa whose descriptions were modified, i.e. Acriulus and Scleria paired, and Diplacrum and Becquerelia chained respectively with the hypogynium character simply treated in Analysis #20 as highly homoplasious. Rather than strengthening the relation between the four genera in Analysis #20, in line with the pattern described by Goetghebeur (1986), the increase in the similarity between our data for this analysis (#20) resulted in an increase in the disparity between Scleria and Acriulus on one hand and Diplacrum and Becquerelia on the other. He linked Sclerieae (including Scleria and Acriulus) and Bisboeckelereae
(including \textit{Diplacrum} and \textit{Becquerelia}), with Trilepideae and Cryptangieae (all four constituting an unresolved subfamily, the Sclerioideae), the Cariceae was treated as a separate subfamily linked to the Sclerioideae. Only then, basal to and somewhat nested in the Cyperoideae do the Rhynchosporeae and Schoeneae appear. If the cupula in the four genera is in fact a perianth then the result from analysis #20 suggests that Goetghebeur is correct in his allocation of tribes to his Sclerioideae clade, but for the wrong reasons; he supports the grouping of the Sclerieae and Bisboeckelereae on the basis of 'two' possibly logically dependent attributes: "disc (or hypogynium) well developed" and "glumellae (or perianth) absent". The hypothesis presented in #20 of a close link between the \textit{Scleria} and Schoeneae is appealing as it broadly reflects the branching patterns of the inflorescence, floral bract morphology and habit, while the Cryptangieae may well be more homogeneous with the relocation of \textit{Exochogyne} to the Sclerieae. These relationships can to some extent be put to the test with the inclusion of \textit{Koyamaea} (Thomas and Davidse 1989) in the analyses. In any case the results obtained from #20 should stimulate further analysis of this controversy.

\textit{The Bisboeckelereae} (Appendix 1, pp 461-465)

This group, composed of \textit{Becquerelia}, \textit{Bisboeckelera}, \textit{Calyptrocarya}, \textit{Diplacrum} (Table 9.5), appeared as a monophyletic clade in two of the later analyses (#22 and 24). Elsewhere it formed a paraphyletic or paraphenetic group (#1-6, 8-9, 11-21, 23, and 26-27, 29-30 respectively), though \textit{Becquerelia} separated off in #15 and 17 and \textit{Diplacrum} was isolated in #7, 10, 18, 25 and 28. Often when the four genera formed a paraphyletic group, this appeared basal to the Hypolytreae clade (Table 9.3: e.g. #1-5, 8-9, 10-13, 19-20), with \textit{Scleria} and/or \textit{Acriulus} at the base of this combined clade.

In #24 (Fig. 9.7) nine attributes unite the Bisboeckelereae clade: leaf sheath apices 'truncate' (43,2), culm parenchymatous bundle sheaths with extensions (99,1), culm sclerenchyma not coalescing to form a 'ring' (102,2), leaf blade 'translucent tissue' absent (135,2), lateral inflorescence branches gynandrous (183,1), spikelet prophylls of the female-fertile spikelets absent (203,2), floral-bract indumentum on the keel (246,2), fruit indumentum 'hispid' (315,3), and first embryonic leaf primordium detectable (325,1). All these attributes are paralleled outside the clade, although #183 co-occurs only in \textit{Exochogyne}. Furthermore, only characters #183 and 325 are fully scored and constant, while #102 and 246 provide the most dubious support for the clade, being variable or unknown for all but \textit{Diplacrum}. Characters #43, 135 and 203, are each variable for some of the four genera, but they are nevertheless congruent with the clade.
An alternative to recognizing the Bisboeckelereae as a four-genus clade would be to include these genera together with the Hypolytreae (possibly also including Scleria and Acriulus) in a larger group as suggested by analyses (#1-5, 7-8, 10-13, 19-20). For example, in #19 the Bisboeckelereae (paraphyletic) and Hypolytreae (except for Hellmuthia) constitute a clade supported by eleven attributes: leaf blade septa visible adaxially (34,1), leaf bases not breaking down into fibres (39,2), culms with a hypodermis (87,1), culm sclerenchyma not coalescing to form a ‘ring’ (102,2), leaf blades ‘glabrous’ (112,2), the leaf blade indumentum abaxial (115,1), leaf blade ‘luminal’ silica bodies globular (119,2), female-fertile spikelets gynandrous (200,1), terminal flower present (250,1), stamens 1 (268,1), and anthers with ‘basal appendages’ (274,1). Inspection of the character state distributions reveals that characters #39, 87, 102, and 112 are subject to homoplasy both within and outside this clade. Only #119 appears to be constant and without homoplasy in this context. In fact, the data for each of the ‘Bisboeckelereae’ genera on this clade are variable for this character, i.e. the genera all have both conical and globular silica bodies in the leaf blades (cf. the descriptions, Appendix 1). Further, globular leaf blade silica bodies do occur elsewhere (e.g. Bolboschoenus). This example suggests that the silica body types should be treated independently.

Character #200 also appears constant within the clade, but is inapplicable for the ‘Bisboeckelereae’. By contrast #250 is well scored, and constant, for this clade. Eiten (1976a-b) has demonstrated that apparently terminal flowers in a number genera of Cyperaceae are in fact axillary, and suggested that the terminal flowers seen in the Bisboeckelereae may eventually be shown to be similarly axillary, though she found no evidence to support that contention.

In deciding between the above approaches, i.e. the recognition separately of the Bisboeckelereae or collectively of the Bisboeckelereae-Hypolytreae group, the following factors were considered. The different cladograms give roughly equal support for the both options; the limits of the former are, however, more certain than the latter. Thus, Scleria and/or Acriulus often join the group while the Cryptangieae rarely do. In all the phenetic analyses the mapanioids constitute a major and separate group. This pattern is also evident in some of the final series cladistic analyses. The recognition of the Bisboeckelereae tribe constituting four genera is advocated as a reasonable but tentative solution to the equivocal results.

The within-group relationships are also somewhat unresolved, though the terminal members are Bisboeckelera and Calyptrocarya in analyses #3-4,7, 13-20, and 25-30. Diplacrum segregated on a separate branch rendering the other three genera paraphyletic
or polyphyletic in a minority of the cladistic analyses (#10 as sister taxon to Scleria and Acriulus, and 18 as sister taxon to Cariceae and Trilepideae) and paraphenetic or polyphenetic in the phenetic analyses (#25-30, as sister taxon to Scleria and Acriulus).

*Diplacrum* often has been included in *Scleria* (e.g. Koyama 1961, 1967b; Kern 1974; Wilson 1983), and there is strong phenetic support for their decision (Appendix 4: Analyses 25-30). The placement of *Diplacrum* in a majority of cladistic analyses, however, affords only equivocal support for the phenetic result. The option of including *Scleria* and *Acriulus* together with the Bisboeckelereae has some appeal as a compromise solution, but is discounted based on the equivocal evidence summarized above. The proposed position (Table 9.5) is conservative in agreeing with Goetghebeur's (1986) circumscription of the Bisboeckelereae and the bitypic Sclerieae (comprising *Scleria* and *Acriulus*), which he considered as sister taxa. He listed one synapomorphy for the Sclerieae: occurrence of the *Fimbristylis*-type embryo, which is inappropriate given that *Diplacrum* also exhibits it. Of the three features by which he supported the Bisboeckelereae, "spikelets unisexual" is a feature for which the Sclerieae is variable. Thus, his cladogram for these two groups is virtually unresolved, emphasizing their contentious nature.

The *Hypolytreae* (Appendix 1, pp 465-469)

The tribe *Hypolytreae sensu lato* here include 14 genera, viz. *Capitularina, Chorizandra, Chrysitrix, Diplasia, Exocarya, Hellmuthia, Hypolytrum, Lepironia, Mapania, Mapaniopsis, Paramapania, Principina, Scirpodendron*, and *Thoracostachyum* (Table 9.5). This group appears in its entirety in four of the five phenetic analyses (Table 9.3: #25-29), but under higher clustering intensity (0.9) and the inclusion of the 'poorly scored' genera in analysis #30 *Hellmuthia* separated from it. *Hellmuthia*, formerly included in *Scirpus*, is the most recent addition to this long-standing tribe (Haines and Lye 1976). It also failed to associate with the Hypolytreae in all the cladistic analyses, suggesting that the group (including *Hellmuthia*) is polyphyletic. The remaining 13 genera were mostly depicted as a robust clade, but *Chorizandra, Chrysitrix* and *Lepironia* sometimes segregated together and apart from the majority of the group (though in these cases not with *Hellmuthia*), further engendering suspicion that the Hypolytreae may be polyphyletic (cf. Table 9.3).

The genera of the Hypolytreae (exclusive of *Hellmuthia*) usually nested directly above the Bisboeckelereae or some combination of the sclerioids *sensu traditus*
(sometimes closely associated with the Cariceae; #3, 7-8, 10, 12-14, 16-21). Otherwise the Hypolytreae formed a separate clade near the sclerioids (#6, 11, 22-24).

The Hypolytreae (exclusive of Hellmuthia) appeared as a polyphyletic assemblage in a number of cases with Chorizandra, Chrysitrix and Lepironia nested in the Schoeneae (either as the sister taxon to Neesenbeckia: #1-2, 4, 9; or Epischoenus: #5). Except for Chorizandra, Chrysitrix, Lepironia the remaining genera of the Hypolytreae did not constitute stable groups. Chorizandra, Chrysitrix, and Lepironia invariably formed a terminal clade; and in 13 of the cladistic analyses (#6-8, 10-11, 13, 16-18, 21-24) Capitularina was their sister group (i.e. the group comprising Chorizandra, Chrysitrix, and Lepironia and Capitularina was almost as robust as that restricted to the first three).

Hellmuthia linked with Chorizandra, Chrysitrix and Lepironia in phenograms #25 and 28, and with Capitularina (and thence with Chorizandra, Chrysitrix and Lepironia) in phenograms #26-27, 29-30. When Hellmuthia separated from the rest of the group it aligned in various ways: a) mostly with some or all of the Arthrostylidiaceae (see above), Phylloscirpus and Abildgaardia (the C₃ species: #1, 5, 7, 13-20, 22, 30); b) as the sister taxon or basal to Desmoschoenus (#2-4, 6, 8-9, 11); or c) with Pseudoschoenus and Erioscirpus (#10).

The Hypolytreae (without Hellmuthia) is supported in #24 (Fig. 9.8) by thirteen attributes: viz: leaf blades with readily visible transverse septa (33,1), plants with ligules obtuse (53,2), plants without hermaphrodite flowers (169,2), inflorescence prophylls adaxially pulvinate (195,1), subtending bracts imbricate (197,2), terminal spikelets absent (199,2), female-fertile spikelets dorsiventrally compressed (202,2), spikelet prophylls lateral (205,1), spikelet prophylls subtending male flowers (207,1), the spikelet prophyll keels indumented (214,1), fruit dorsiventrally compressed (304,2), mesocarp spongy (316,1), and endocarp sclerenchymatous (318,1). All of these characters are subject to reversals or parallelism across the whole analysis; within the clade only characters #169, 195, 197, and 205 appear to be constant; and of these Principina is not scored for #205 and Hypolytrum is variable for it.

In #19 fourteen synapomorphies support the clade: viz. leaf sheath apices V-shaped (43,3), leaf sheath apices glabrous (44,2), leaf blade silica bodies absent (117,2), mid-leaf blade strands not all aligned with the vascular bundles (157,2), plants bisexual, with at least some bisexual spikelets (168,2), lateral inflorescence branches with the sexes mixed (183,3), lateral inflorescence branch bases exposed (185,2), terminal spikelets absent (199,2), female-fertile spikelets dorsiventrally compressed (202,2), spikelet prophylls lateral (205,1), floral bracts glabrous (245,2), fruit 'winged' (305,1), fruit
‘stalked’ (306,1), and first embryonic leaf primordium absent (325,2). As in #24 homoplasy is a feature of all of these characters across the analysis, with only characters #168, 183, and 185 constant within the clade.

The case for including Chorizandra, Chrysitrix, and Lepironia in the Schoeneae group (see analyses #1-2, 4-5, and 9) can be assessed from the results of analysis #9. Here ten attributes appear to link them with Neesenbeckia: namely, leaf blade septa visible adaxially (34,1), culm silica bodies ‘external’ (67,3), culms initially hollow (77,1), culm sclerenchyma coalescing to form a ‘ring’ (102,1), culm spongy mesophyll absent (105,2), leaf blade silica bodies ‘external’ (118,3), leaf blade ‘translucent tissue’ absent (135,2), inflorescence pseudoaxillary (176,2), primary inflorescence bracts with one much longer (187,2), and anther apiculus indumented (280,1). Of these, #67 and 118 ascribe an attribute to the three genera where it is fact inapplicable (and therefore appears in the PAUP data matrix as an unknown) because culm silica bodies are absent from them. Similarly, #34 and 135 are inapplicable to Lepironia (and applicable only to some species of the other two genera). Character #77 is variable for Chorizandra and 280 is variable for Chorizandra and Chrysitrix, and thus they appear as unknown. The number and quality of characters uniting these four genera are thus less substantial than they appear at first sight, and the case for including Chorizandra, Chrysitrix, and Lepironia in the Schoeneae is poor. Most of the remaining characters occur sporadically in one or a few species of a number of genera (e.g. #77) or are widespread in the family (e.g. #176 and 187), suggesting a high level of homoplasy and, perhaps reflecting ecologically related convergence. Eleven attributes unite Chorizandra, Chrysitrix, and Lepironia in the same analysis: viz., leaf sheaths open to the base (40,1), culm silica bodies absent (66,2), leaf blades indumented (112,1), leaf blade silica bodies absent (117,2), leaf blade strands all aligned with the vascular bundles (157,1), inflorescence contracted (175,2), inflorescence capitate (177,4), floral bracts similar in absolute length along the spikelet (241,2), each flower enclosed directly by its subtending floral bract (249,1), stigmata up to 2 (297,1), and fruit ‘winged’ (305,1). All are congruent in whole or part with the Hypolytreae (i.e. Thoracostachyum, Capitularina, etc.). On the basis of my analyses, it seems more reasonable (though equivocal) to place Chorizandra, Chrysitrix, and Lepironia in the Hypolytreae. Indeed, the position of these three genera within the Hypolytreae was the tribe’s most stable feature.

Another constant feature of these analyses in relation to the Hypolytreae was that Scirpodendron never constituted the basal member of the tribe; i.e. there was no support here for postulating this monotypic genus as the ‘ancestral sedge’ (contrast with Holttum 1948; Kern 1974; Goetghebeur 1986). The relationships of Scirpodendron and the other
genera of the Hypolytraeae whose placement was unstable in these analyses seem to require further investigation.

Eighteen features characterize *Hellmuthia* as a terminal taxon in analysis #19: habit ‘long-rhizomatous’ (3,1), leaf sheaths open to the base (40,1), leaf sheaths with overlapping margins distally (41,1), culm intercostal cells regular and rectangular (59,1), culm epidermal cells in transverse section noticeably ‘radially elongated’ (62,1), culm trans-section circular (76,5), primary inflorescence bracts foliose (186,1), subtending bracts imbricate (197,2), terminal spikelets absent (199,2), spikelet prophylls lateral (205,1), the spikelet prophyll keels indumented (214,1), rachillae vestigial (216,1), floral bracts absent (231,2), terminal flower present (250,1), style-base ‘not enlarged’ (295,3), stigmatic papillae ‘foot-like’ (299,2), fruit epidermal cells ‘constituting hairs’ (314,2), and cotyledon not markedly widened (323,2). Examination of them revealed that all but three (#62, 299, and 314) are congruent with the Hypolytraeae, though the first of these (culm epidermal cells in transverse section noticeably ‘radially elongated’) is not listed for the Hypolytraeae as it was scored as variable for *Chorizandra*, *Chrysitrix*, and *Lepironia*, and thus treated as unknown in the cladistic analyses. Two of the attributes equally support *Hellmuthia* and the base of the Hypolytraeae clade (#199, 205), while cross-referencing with the synapomorphic attributes for the Hypolytraeae in analysis #24 with *Hellmuthia* in #19 reveals that four attributes support both groups, i.e. #197, 199, 205, 214, and most of the others are consistent with the recognition of one group including both *Hellmuthia* and the remainder of the Hypolytraeae.

Discrepancies between the original description of *Hellmuthia* (Haines and Lye 1976) and my observations are highlighted be these analyses, as well as difficulties which arise from different interpretations of floral and inflorescence morphology. My observations on the fruit of *Hellmuthia* (all apparently sterile) corroborate that the exocarp comprises the outer pericarp epidermis, that the mesocarp is fibrous and the endocarp thin. However, I found the exocarp to be papillose and thin-walled (see Chapter 3 Pl. 32.2), rather than "marked by hollows and undulating ridges" and "with a thick cuticula" (Haines and Lye 1976 p.65). These differences should be investigated further to ascertain whether there is variation in these attributes in relation to maturity and/or fertility of the fruits. Of more concern is the Haines and Lye illustration of homology between the layers in *Hellmuthia* and various mapanioids. In both cases they depict a thick inner hatched zone equivalent to the endocarp, and a thin outer stippled ‘mesocarp’. This conforms with the situation in most mapanioids but is inconsistent with their own description of *Hellmuthia*, and with my observation that it has a thin endocarp. The deciding factor, which appears to provide a marker for the interpretation of the
pericarp layers, is the location of the pericarp vascular bundles. These are located in
the mesocarp, irrespective of whether the mesocarp constitutes fibres, as in *Hellmuthia*
(and *Cyperus* etc.) or parenchyma, as in *Thoracostachyum* (Chapter 3 Pls 32.2-3).

Flattened, winged styles are not common among the mapanioids. *Lepironia* exhibits
these features but styles of *Hellmuthia* are much more like those of *Desmoschoenus*; in
both *Hellmuthia* and *Desmoschoenus* the base is not enlarged and there are three style
branches. Nor is the embryo of *Hellmuthia* typical of most mapanioids: it most closely
matches that of *Lepironia*, but differs in that the germination pore is oriented parallel
to the first embryonic leaf primordium, and the second embryonic leaf primordium is
not detectable (by contrast with the perpendicular germ pore and presence of the second
embryonic leaf primordium in *Lepironia*). Comparing the embryo characters (and
ignoring loose categorization of ‘embryo-type’), the embryo of *Hellmuthia* is most
similar to those of *Cyperus* subgenus *Cyperus* and *Pycnostachys* and *Eriophorum*
(Appendix 1b).

Taxonomic decisions regarding *Hellmuthia* have generally been largely based on
floral characters. Those authors who lay emphasis on androecia and gynoecia which
appear to constitute trimerous bisexual flowers relegate *Hellmuthia* to or near *Scirpus*
(e.g. Nees 1835; Kunth 1837; Clarke 1909; Schoenland 1922; Mattfeld 1938). By
contrast Haines and Lye (1976), and Goetghebeur (1986) emphasize the presence of
spikelet prophylls (which are present in only some of the proximal spikelets of each
lateral branch inflorescences), and which are represented by two lateral, keeled and
ciliate bracts, and thus place *Hellmuthia* with the mapanioids. Mattfeld (1938), Holttum
(1948) and Schultzze-Motel (1959) interpreted the ‘flower’ here as derived from the
bisexual mapanioid spikelet composed of a number of unisexual flowers. Goetghebeur
(1986) proposes a similar phyletic line, but his theoretical interpretation and terminology
are different (Chapter 4). Haines and Lye (1976) refer to the floral structure in
*Hellmuthia* as a "'flower'". To avoid prejudging the issue for the present purpose these
characters were left unscored rather than scoring the floral units in terms of bisexual or
unisexual. Of course, this in itself constitutes a form of character weighting by
emphasizing the importance of the remaining characters scored for *Hellmuthia*, and also
denies the omitted characters a chance to indicate a relationship. The fact that
*Hellmuthia* does not join the Hypolytreae clade in any of the cladistic analyses suggests
that floral characters are important in deciding upon its relationships, and that many of
the other features (e.g. fruit anatomy, embryo morphology and style) are not congruent
with this hypothesis. Put another way, there is abundant homoplasy in the data, and no
definitive judgment should be made on its taxonomic position on such evidence (except in so far as it vindicates recognition of a monotypic genus).

There remain two conservative options, viz., the inclusion of *Hellmuthia* in the Hypolytreae group, or its association with *Desmoschoenus* in the Scirpeae group. A third option would be to include it in a group with the Arthrostylideae. The last option would markedly increase the heterogeneity of a small group without obvious resolution of the apparent conflicts. Given this uncertainty, opting for the grouping most congruent with the phenetic analyses should at least maximize the utility of any grouping, while awaiting further evidence on this aberrant genus. *Hellmuthia* is, therefore, included in the Hypolytreae (Table 9.5).

Goetghebeur (1986) recognizes the Mapanioideae as comprising two tribes, Hypolytreae (*Capitularina, Diplasia, Exocarya, Hypolytrum, Mapania, Mapaniopsis, Paramapania, Principina, Scirpodendron, Thoracostachyum*) and Chrysitriceae (*Chorizandra, Chrysitrix, Hellmuthia, Lepironia*; see also Table 9.5). Comparisons are constrained by differences in interpretation of some features, particularly floral and inflorescence. He presented 'one character' supporting the subfamily (i.e. the tribe Hypolytreae as considered here): whether the "glumellae" are of two sorts, with the lateral bracts bigger/stronger and usually keeled (as opposed to being alike and in groups of 3+3). He defines "glumellae" (= 'perianth members') very broadly; including some structures which are interpreted in the current study as spikelet prophylls, floral bracts and perianth members. In terms of my character list, his character corresponds with whether the spikelet prophylls are lateral (rather than dorsiventral) and whether a perianth is present or absent. By contrast, I consider the occurrence of spikelet prophylls and of a perianth to be separate features. As seen above, lateral spikelet prophylls are a typical, but not universal feature of the mapanioids. None has a perianth, and not all of them possess floral bracts. Goetghebeur's cladogram of the two tribes of the Mapanioideae has no synapomorphs for the Hypolytreae and three for the Chrysitriceae: 1) inflorescence with few "spikelets" (or spikes in the current treatment) and limited "flowering" (i.e. spikelets with definite growth), 2) embryo of the "Schoenus-or more differentiated types", and 3) elaminate or laminae very weakly developed. The first attribute occurs in the Hypolytreae, e.g. in *Paramapania* and *Mapania*, and the second involves the use of an *a priori* transformation series resulting in the application of inadequately defined character states. The third is a reasonable generalization, though several genera of the Hypolytreae show differentiation into separate sterile (laminate) and fertile (elaminate) shoots, while some species of *Chorizandra* and *Chrysitrix* have well-developed but not very broad leaves. These
features provide little support for the distinction between Goetghebeur's "Hypolytreae" and "Chrysitricheae". Judging from my analyses the "Chrysitricheae" minus *Hellmuthia* have good credentials as a robust clade, but it was always highly nested when associated with the remainder of the Hypolytreae, rendering the latter paraphyletic (Table 9.4). Further, the addition of *Capitularina* to the Chrysitricheae could also be justified (see above). In view of these discrepancies, I recommend a single tribe including all fourteen genera (Table 9.5).

**The Subfamilies**

Higher level groups, each encompassing more than one of the clades or groups described above, are generally apparent in the analyses (see Appendix 4), though in some of the cladograms (e.g. #13 and 24) highly chained trees are apparent with less obvious major groupings. Three groups were moderately robust: 1) the cyperoid group or clade, including the Cypereae, Scirpeae, Abildgaardieae, and Arthrostylideae; 2) the schoenoid group, including the Rhynchosporeae and Schoeneae; and 3) sclerioid group, composed of the Sclerieae, Cryptangieae, Trilepideae, Cariceae, Bisboeckelereae, and Hypolytreae (mostly ignoring *Hellmuthia*, see above). Three combinations of these groups predominated, with more than one of them acceptable in a number of cases: 1) all three appearing as more or less discrete groups (#6, 15, 19 and 21); 2) the cyperoid-schoenoid group, and the sclerioid group (#7, 8, 13-16, 21, and 23-24); and 3) the cyperoid group, and the schoenoid-sclerioid group (#1-6, 9-12, 14, 16-20, 22, 25-30). More often than not, even ignoring minor exceptions, these groups constitute paraphyletic/paraphenetic rather than monophyletic/monophenetic groups (Table 9.3).

The recognition of two groups, viz. the cyperoid group (the Cyperoideae) and the schoenoid-sclerioid group (the Caricoideae) is consistent with more of the analyses than the recognition of other combinations of the three major groups present above. That is, the two-group solution minimizes the number of polyphyletic/polyphenetic and paraphyletic/paraphenetic groups. Indeed, this solution is a more effective explanation of the pattern of variation (i.e. it reduces the number of relationships which would have to be considered to be a result of homoplasy) than is total abandonment of groupings above the tribal level (the solution adopted by Hooper, 1973).

Capricious treatment of *Dulichium* and the Cariceae was generally associated with the defective earlier analyses, and is therefore largely discounted. The relationships of the Rhynchosporeae and Arthrostylideae to the cyperoid and schoenoid groups was also
equivocal, but cannot similarly be dismissed. Here the Arthrostylideae are included in the Cyperoideae while the Rhynchosporeae are referred to the Caricoideae. By contrast, Goetghebeur (1986; as many before him, Table 9.1) includes the three tribes in the Cyperoideae, with the Schoeneae and Rhynchosporeae forming a sister group, and Arthrostylideae constituting basal clade (cf. Table 9.4). Collectively the three tribes constitute a basal or outlying group in his cladogram of the subfamily. In fact, two of the nodes in his cladograms of these tribes are unsupported by shared derived features and the three tribe statement can be reduced to an unresolved trichotomy.

In line with a general trend, Goetghebeur’s solution here accords better with my phenetic than with my cladistic analyses. Regarding these three tribes, my results to date agree with Goetghebeur’s in the recognition of the sister group relationship between the Schoeneae and the Rhynchosporeae. However, the existence of a number of undescribed species, putative members of the Arthrostylideae (unpublished data), may have a significant bearing on resolving the relationships of these groups. Meanwhile, the characters supporting the Cyperoideae and Caricoideae of the present study will be set out, with reference to those cladograms which portray them as monophyletic groups.

The Cyperoideae (Appendix 1, pp 406-412)

Four tribes are included in this subfamily, namely the Cypereae (with 17 genera), Scirpeae (27 genera), Abildgaardieae (seven genera) and Arthrostylideae (four genera; see above and Table 9.5).

In analysis #17 the Cyperoideae are supported by eleven attributes: viz. habit ‘long-rhizomatous’ (3,1), leaf bases not breaking down into fibres (39,2), ligules present (49,1), culm sclerenchyma comprising peripheral strands (100,1), culm palisade mesophyll present (106,1), leaf blade sclerenchyma forming strands (154,1), inflorescence primary axis contracted (175,2), rachillae of indefinite growth (217,1), proximal sterile bracts 0 (232,1), each flower enclosed directly by its subtending floral bract (249,1), and fruit epidermal cells ‘constituting hairs’ (314,2). By comparison in #18 five features unite the subfamily: viz. habit ‘long-rhizomatous’ (3:1), leaf bases not breaking down into fibres (39,2), proximal sterile bracts 1 or more (232,2), perianth indumentum retrorse (267,1), and fruit dorsiventrally compressed (304,2). Characters #3 and 39 are common to both sets, but none of them are constant for all the genera, nor are any of them unique to the group, though attributes #217,1 and 267,2 are possessed by only two genera of the Caricoideae. The character state trends evident in
the subfamilial descriptions (Appendix 1), however, provide some support for this group.

The recognition of the Cypereae, Scirpeae, Abildgaardieae and Arthrostylideae as constituents of the Cyperoideae is in broad agreement with Raynal’s (1973) partitioning of the subfamily, and as far as it goes, is congruent with Goetghebeur’s treatment. The broad circumscription of the Scirpeae will no doubt be reduced with further study into a number of components, however, the groups of genera that formed within this tribe were generally labile, and neither reliable limits nor substantial agreement with Goetghebeur’s Fuireneae, Ficinieae and Scirpeae could be established, while his Eleocharideae and Dulichieae may well prove to be but part of somewhat larger clades (see Table 9.4).

The Caricoideae (Appendix 1, pp 412-418)

The remaining eight tribes are included in the second subfamily, the Caricoideae. These are the Rhynchosporeae (with four genera), Schoeneae (27 genera), Cryptangieae (five genera), Trilepideae (four genera), Cariceae (six genera), Sclerieae (two genera), Bisboeckelereae (four genera) and the Hypolytreae (14 genera; see above and Table 9.5).

The Caricoideae in analysis #17 are supported by ten attributes: culm mesophyll ‘translucent tissue’ absent (83,2), culm boundary layer cells forming a ‘complete’ sheath (94,1), culm sclerenchyma coalescing to form a ‘ring’ (102,1), female-fertile spikelets androgynous (200,2), the spikelet prophyll keels indumented (214,1), floral bracts increasing in absolute length acropetally (241,3), functionally male-only flowers 1 per spikelet or more (254,2), style-base sharply differentiated from the fruit apex (294,2), style-base ‘enlarged-pyramidal’ (295,2), and cotyledon ‘markedly widened’ (323,1); and eleven attributes in analysis #18: ligules absent (49,2), culm sclerenchyma coalescing to form a ‘ring’ (102,1), lateral branch inflorescences ‘planipanicle’ to anthelate (184,2), lateral inflorescence branch bases enclosed (185,1), female-fertile spikelets androgynous (200,2), female-fertile spikelets laterally compressed (202,1), rachillae of definite growth (217,2), floral bracts persistent (235,1), floral bracts increasing in length acropetally (241,3), each flower enclosed by a distal floral bract (249,2), functionally male-only flowers 1 or more per spikelet (254,2). Attributes #102,1 and 200,2 appear in both cases. Whilst none of these are unique to the schoenoid-sclerioid clade, several occur only in a few genera of the cyperoid clade. Thus, Actinoschoenus, and Ficinia and Scirpus, are variable for character #102; Crosslandia and Ficinia are variable for #200; members of the Arthrostylideae share the attribute of 249,2 with the schoenoid-
sclerioids; and Abildgaardia, Ficinia, Kyllinga and Scirpoides are variable for #254. The C_3 Thoracostachyum was the only genus of the Caricoideae to be scored #94,1, however, this attribute may be a red-herring in the context of C_3 species, in any case the attribute hardly defines the group. The overlap apparent here between features of the Caricoideae and the Arthrostylideae can be interpreted either as providing support for the inclusion of the latter in this group, or as evidence of homoplasy explaining the occasional inclusion in phenetic analysis or ordering of clades in a few cladistic analyses such that the Arthrostylideae appeared between the Schoeneae and Rhynchosporeae. The exclusion of the Arthrostylideae from the schoenoid-scleroid group is generally supported by the analyses discussed above. It remains, however, one of the most contentious decisions.

The compositions of the tribes within the Caricoideae are generally uncontentious. The Hypolytreae and Cariceae are recognized almost universally in other treatments. Both have also often been ascribed subfamilial status. Judging from both the phenetic and cladistic analyses this is unwarranted in the case of the Cariceae and equivocal for the Hypolytreae. Perhaps the general uniformity of the spikelet prophyll characters have been responsible for the common elevation of the caricoids to subfamilial rank. The enormous size of Carex (with about 2000 species it is one of the largest genera of flowering plants; see Standley 1985) and its ubiquity in the Northern Hemisphere environments has almost certainly influenced Northern Hemisphere cyperologists’ impressions of the taxonomic significance of this group.

The remaining tribes of this subfamily as delimited in the present study match Goetghebeur’s (1986) four tribes of his Sclerioideae (the Trilepideae, Cryptangieae, Sclerieae and Bisboeckelereae – i.e. the sclerioids *sensu traditus*). These tribes are also recognized by Eiten (1976a-b) in her work on inflorescence structure, and resolve more finely the Sclerieae *sensu lato* and the Cryptangieae *sensu lato* (or Lagenocarpeae) recognized in earlier treatments (Table 9.1).

The recognition of the subfamily Caricoideae including the Rhynchosporeae, Schoeneae, Sclerieae, Cryptangieae, Trilepideae, Bisboeckelereae, Cariceae, and Hypolytreae is new, though various overlapping components of this subfamily have previously been formally recognized. The Cariceae and sclerioids *sensu traditus* were placed in one subfamily by Bentham (1843), Kern (1974) and Schultze-Motel (1964, largely on the basis of sexuality. Koyama (1969 and 1971) joined the Hypolytreae and sclerioids *sensu traditus*, while Pfeiffer (1925) included all three tribes in his Caricoideae. The union of the Schoeneae (including the Rhynchosporeae) and the sclerioids *sensu traditus* was made by Koyama (1961). The similarity between the
groupings of Pfeiffer (1925), Koyama and the present study is partly explained by
common use of vegetative anatomical characters, though Koyama’s interpretation of
fruit anatomy (largely rejected by Goetghebeur, 1986, and in the present study, see
Chapter 3 and Appendix 1) also greatly influenced his more recent decisions. While my
analyses included many vegetative anatomical characters, they were ‘balanced’ by the
inclusion of a broad spectrum of characters from other features, including those of the
fruit, embryo, flowers, inflorescence and general morphology, and the pattern of
relationships observed was not solely dependent on these anatomical characters.

By contrast with the two subfamily solution proposed here, Goetghebeur (1986
p.154) adopts four (Table 9.5). On his cladogram of subfamilies the Mapanioidae are
supported by a single attribute, which in terms of my character list is equivalent to
whether the spikelet prophylls are lateral (and paired, see above and Chapter 3), a feature
also found in Schoenoides). The clade including his Cyperoideae, Sclerioideae and
Caricoideae has two synapomorphs: trimerous floral pattern, a feature shared with the
mapanioids Hellmuthia and Principina as he defines it. The other feature, of the
"glumellae differentiated", is peculiar to his interpretation of floral morphology, and is
considered a non-comparison in the present study. His subfamily Cyperoideae is
unsupported and forms the sister group of the Mapanioidae and Caricoideae, which are
supported by the attribute of unisexual flowers. According to my interpretation the
mapanioids generally possess unisexual flowers, but even disregarding them to avoid
differences attributable to different interpretations, genera/species with strictly
unisexual flowers occur in the Schoeneae and the Rhynchosporeae. Goetghebeur’s
Sclerioideae are also unsupported. His Caricoideae are supported by three features, and
this clade is not the subject of controversy (though the rank should be, see above).
Nevertheless one of them, susceptibility to Anthracoidea, is paralleled in Baeothryon.
Unequivocal attributes are uncommon at the subfamilial rank, however these comments
serve to highlight the effect of character interpretation and the equivocal nature of the
few features substantiating his rather conventional subfamilial classification of the
Cyperaceae.

Goetghebeur (1986) also presented the relationships of the Cyperaceae in the form
of a ‘cross-section through a phylogenetic tree’. Such pictorial presentations are difficult
to test and are essentially phenetic (see Abbott et al. 1985). It is not surprising, therefore,
that the pattern he presents compares better with the phenograms than with the
cladograms of the present study.
Proposed Classification of the Cyperaceae

The Cyperaceae are assigned here to ten tribes and two subfamilies (Table 9.1; Appendix 4: see also Subfamilial and Tribal descriptions), with ranking and nomenclature chosen pragmatically to avoid adding unnecessarily to the already weighty synonymy of the family (see Goetghebeur 1985). The most striking innovation of this classification is the composition of the two subfamilies. Traditionally (see Table 9.1) the Schoeneae and Rhynchosporeae (usually treated as one tribe) have been included in the Cyperoideae (or the equivalent Scirpoideae) or less often in the Rhynchosporoideae (or ‘Schoenoideae’). Here they are included in the Caricoideae.

The classification presented here is based on the cladistic and phenetic analyses listed in Table 9.2, concentrating on analyses #17, 24 and 30 (see also Tables 9.3 and 9.4; Appendix 4). Only a few of the tribes (the Cariceae, Sclerieae, Trilepideae, and possibly the Rhynchosporeae) have the credentials of monophyletic groups. The other tribes, and the subfamilies are scarcely convincing in that respect (Table 9.3), but they are taxonomically defensible in practical terms, providing reasonable predictive generalization about the characters employed and constituting a working basis for further sampling.

Small data sets with little intra-taxon variability and few unknown or inapplicable values, resulting in a single or strictly limited number of models/hypotheses are largely restricted to the idealized examples typically provided by taxonomic theoreticians and purveyors of classificatory programs. These are not characteristics shared with the present data. The methodological and interpretive problems posed by a relatively large data set dictated my resorting to heuristic means of appraising the results. The degree of consensus between the phenograms and the cladograms, and the relative stability of the latter in the face of experimental changes in the data matrices, contrasts with high levels of homoplasy (cf. the low consistency indices: Table 9.2) and the discrepancies between the synapomorphs and the data. If the worth of the cladograms as hypothetical phylogenies is debatable, their poor capabilities in connection with the information retrieval component of taxonomy is apparent, at least in the present context. The same examples demonstrate that cladograms are not necessarily "more informative than the phenetic analyses with regard to characters" (see Kitching 1985). As regards retrieval of recorded, hard data, possession of automated descriptions supersedes generalization from classifications (cf. Appendix 3).
These analyses represent a preliminary appraisal of the data available from a database which forms the nucleus of an ongoing investigation of the Cyperaceae, and it would be premature to formalize the proposed classification. It has been successful in providing comparisons with previous classifications, in highlighting conflicts in the data and areas in need of more intensive study, and in the recognition of stable groups. The areas of conflict and the groups recognized provide a clear guide to facilitate future sampling of the family for new features, e.g. molecular, and provide a basis for future analyses addressing questions of biogeography. *Oreobolus* and *Scirpodendron* are not supported here as ‘ancestral sedges’ (Hutchinson 1973; and Kern 1974; Goetghebeur 1986). Rather, a variety of relatively distantly related genera and groups of genera constituted the basal ingroup from one cladistic analysis to another (Table 9.2). It is not clear whether this inconclusive result stems primarily from heterogeneity/homoplasy of outgroup, ingroup or both, or from the large numbers of unknowns, inapplicables and variables in the data. Future experiments should include additional or alternative outgroups which may stabilize (or undermine) the proposed classification. A worthy longer term objective on the road to finally resolving taxonomic relationships in Cyperaceae would be a comprehensive species-level database.
### Table 9.1. Comparison of important suprageneric classifications of the Cyperaceae

The subfamilies (in bold) and the tribes are listed in the order that they appear in the respective treatments. The code to the left of the names in columns 2-8 cross-reference them with the proposed new classification in the first column. Fractions indicate number of genera and species respectively. ~ = chospor.

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* allocation of *Remirea* to other than the Cypereae.
† allocation of *Hellmuthia* to other than the Hypolytreae/Chrysisitriceae, see also Haines and Lye 1976.
Table 9.2. Summary of parameters and results for the cladistic and phenetic analyses


- = WEIGHTS SCALE not applied, + = WEIGHTS SCALE applied. G = most grade or quantitative characters, minimum = inappropriate and linked characters, pp = photosynthetic pathway. Length = number of character state changes, CI = consistency index. Bis = Bisboeckeleraeae, Car = Cariceae, Cry = Cryptangieae, Scl = Sclerieae, Tri = Trilepideae. See text for discussion of deleted taxa and characters. * = delete bundle sheath and ‘minimum cells-distant count’ characters for culm and leaf blades; include photosynthetic pathway, and C₄ anatomical and biochemical type. S = Acriulus, Scleria, Diplacrum and Becquerleria: hypogynium scored as present, perianth scored as absent, in all other runs the cupule was treated as a perianth. ξ = except for Helmmuthia.

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Table 9.3. Emergence of mono-, para-, and poly-phyletic/phenetic groups in the analyses relative to the proposed classification


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Table 9.4. Emergence of mono-, para-, and poly-phyletic/phenetic groups in the analyses relative to Goetghebeur's 1986 classification

Analyses 1-24 cladistic using PAUP, 25-30 phenetic using flexible clustering. Run = analysis, cross-references with Table 9.2; M = mono-phyletic/phenetic; P = para-phyletic/phenetic; na = not applicable, monotypic taxon. M' = Mapanioideae, C = Cyperoideae, S = Scleroideae, K = Caricoideae, Hy = Hypolytreae, Ch = Chrystrichae, Si = Scirpeae, Fu = Fuireneae, El = Eleocharideae, Ab = Abildgaardieae, Fi = Ficinieae, Cp = Cypereae, Du = Dulichieae, Ar = Arthrostylideae, Rh = Rhynchosporeae, Sh = Schoeneae, Cy = Cryptangieae, Tr = Trilepideae, SI = Sclerieae, Bi = Bisboeckelereae, Ca = Cariceae. *=disregarding Hellmuthia.

Tribes underlined are equivalent to those of the same name in the proposed classification. Mapanioideae is equivalent to Hypolytreae in the proposed classification. Data from Appendix 4.

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Table 9.5. Allocation of the genera of the Cyperaceae to the proposed classification.

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<td>Cyperae</td>
<td>Alinula, Ascolepis, Ascopolysis, Courtoisina, Cyperus, Hemicarpha, Kyllinga, Lipocarpha, Mariscus, Monandrus, Pycreus, Queensandiella, Remirea, Rikliella, Sphaerocyperus, Torulinium, Volkiella</td>
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| Scirpeae             | Androtrichum, Anosphor, Baeothryon, Blysmsopsis, Blysmus, Bolboschoenus, Desmoschoenus, Dulichium, Egleria, Eleocharis, Eleogiton, Eriophoropsis, Eriophorum, Eriochirpus, Ficinia, Furiensa, Hymenochaeta, Isopleis, Kyllingiella, Oreobolopsis, Oxycaryum, Phylloclirpus, Pseudoschoenus, Schoenoplectus, Scirpoideae, Scirpus, Sumatrosicirpus, Websterea |

| Abildgaardieae       | Abildgaardia, Bulbostylis, Crosslandia, Fimbriystylis, Nemum, Nelmesia, Tylocarya |

| Arthrostyleae        | Actinoschoenus, Arthrostylis, Trachystylis, Trichoschoenus |

<table>
<thead>
<tr>
<th>CARICOIDEAE</th>
<th>Rhynchosporeae</th>
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<td>Cypereae</td>
<td>Micropapyrus, Pleurostachys, Rhynchospora, Syntrinema</td>
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<td>Schoeneae</td>
<td>Baumea, Carpha, Caustis, Cladium, Costularia, Cyathochaeta, Cyathocoma, Epischoenus, Evandra, Gahnia, Gymnoschoenus, Lepidosperma, Lophoschoenus, Machaerina, Mesomelaena, Moreloia, Neesenbeckia, Oreobolus, Pitlanthelium, Reedia, Rhynchloradium, Schoenoides, Schoenus, Tetraria, Tetratopsis, Trianopile, Tricoscularia</td>
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| Cryptangiellae       | Cephalocarpus, Didymiandrum, Everardia, Esochogyne, Lagenocarpus |

| Trilepeideae         | Afrotrilepis, Coleochloa, Microdracoides, Trilepis       |

| Cariceae             | Carex, Cymophyllus, Kobresia, Schoenoxiphium, Uncinia, Vescicarex |

| Sclerieae            | Acriulus, Scleria                                         |

| Bisboeckleriaceae    | Becquerelia, Bisboecklera, Calyptocarya, Diplacrum       |

| Hypolytrae           | Capitalularina, Chorizandra, Chrysitrix, Diplasia, Exocarya, Hellmuthia, Hypolytrum, Lepironia, Mapania, Mapaniopsis, Paramapania, Principina, Scirpodendron, Thoracostachyum |
Figure 9.1. Part of tree 1 from analysis #24 showing the Cypereae
Names are abbreviated to the first eight letters except for Cyp Pyc = *Cyperus* subgen. *Pycnostachys*, and Cyp Cyp = *Cyperus* subgen. *Cyperus*. See see text for discussion and Appendix 4 for the complete cladogram.
Figure 9.2. Part of tree 1 from analysis #24 showing the Scirpeae
Names are abbreviated to the first eight letters. The descriptions for *Blysmopsis* and *Blysmus*; the C₃ species and C₄ species of *Eleocharis*; *Eriophoropsis*, *Eriophorum*, *Erioscirpus*; and *Ficinia* and *Ficinia* subgen. *Sickmannia* have been amalgamated. See see text for discussion and Appendix 4 for the complete cladogram.
Figures 9.3A-B. Parts of tree 1 from analyses #24 and #19 showing the Arthrostylideae and Abildgaardieae

Names are abbreviated to the first eight letters except for Abild C3 = Abildgaardia (the C3 species). See see text for discussion and Appendix 4 for the complete cladogram.

Figure 3A: #24, the descriptions of the photosynthetic pathway variants of Abildgaardia have been amalgamated and that the description of Trichoschoenus has been omitted from the analysis. The bald extensions at node 226 and 230 represent the location of branches including the Rhynchosporaeae, and the Scirpeae and Cyperaeae respectively.

```
  ***** 1 Abildgaa
  **232 *** 29 Crosslan
  * * 132
  * 145 ******** 106 Tylocary
  ***231 *
  * * ** 52 Fimbrist
  * *
  * ***** 15 Bulbosty
  *

  **230
  *

  *226 *
  * *
  * *

  *****225
  *

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  *

  **** 2 Actinosc
  *118
  ********121 ******** 102 Trachyst

  ***** 6 Arthrost
```

Figure 3B: #19.

```
  ***** 2 Abild C3
  ***133
  ***137 ******** 67 Hellmuth
  *

  ***199 *** 8 Arthrost
  *

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  *

  *200 **135

  **** 116 Trachyst

  **201 *

  *

  *** 90 Phyllosc
  *

  *

  * ** 61 Ficinia
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Figures 9.4A-B. Parts of tree 1 from analyses #18 and #24 showing the Rhynchosporeae
Names are abbreviated to the first eight letters except for the following: Rhyn C4R = *Rhynchospora* (the C₄ rhynchosporeoid species), Rhyn C4C = *Rhynchospora* (the C₄ chorocypereoid species), Rhyn C3 = *Rhynchospora* (the C₃ species). See text for discussion and Appendix 4 for the complete cladogram.

**Figure 4A: #18**

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267
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* ****** 85 Micropap 
**  
** 194 ** 105 Rhyn C4R
**  
** 192
** 193 ****** 118 Syntrine
** 195
**  
**  
** 106 Rhyn C4C
**  
**  
** 104 Rhync C3
**  
**  
*** 95 Pleurost
```

**Figure 4B: #24**, the descriptions of the three photosynthetic pathway variants of *Rhynchospora* have been amalgamated and that the description of *Pleurostachys* has been omitted from the analysis.

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166
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*  
**  
*** 72 Micropap
* 158
*176 ** 86 Rhynchos
*  
********** 97 Syntrine
```
Figure 9.5. Part of tree 1 from analysis #24 showing the Schoeneae

_Evandra_ is not included in this Schoeneae grade (cf. Figs 9.7 and 9.6). Names are abbreviated to the first eight letters. See text for discussion and Appendix 4 for the complete cladogram.

* 224
  ** 19 Carpha
  * 168
  * 81 Ptilanth
  * 167
**223 205 103 Trianopt
  * 75 Oreobolu
  * 162
  * 90 Schoenoi
  * 26 Costular
  * 130
  * 31 Cyathoco
  * 192
  * 27 Lophosch
  * 160
  ** 73 Moreloti
  * 193 159
**222 99 Tetrario
  * 10 Baumea
  * 150
  * 64 Lepidosp
  * 149
  * 67 Machaeri
  * 151
  ** 20 Caustis
  * 133
****221 45 Epischoe
  ** 140
  * 91 Schoenus
  * 70 Mesomela
  * 146
  * 55 Gymnosch
  * 161
**220 84 Reedia
  * 177 74 Neesenbe
  * 98 Tetraria
  * 104 Tricostu
  * 24 Cladium


Figure 9.6. Part of tree 1 from analysis #15 showing the Schoeneae
Names are abbreviated to the first eight letters, except for Cost bre = Costularia brevicaulis.
See text for discussion and Appendix 4 for the complete cladogram.
Figure 9.7. Part of tree 1 from analysis #24 showing the Bisboeckelereae, Cryptangieae, Trilepideae, Sclerieae, and Cariceae

Evandra is included in the clade with the Cryptangieae (cf. Fig. 9.4). Names are abbreviated to the first eight letters, except in the case of Car+Ves which represents the amalgamated descriptions of the four subgenera of Carex and Vesicarex. See text for discussion and Appendix 4 for the complete cladogram.
Figure 9.8. Part of tree 1 from analysis #24 showing the Hypolytreae and Juncaceae. Helmutia does not appear in the clade. Names are abbreviated to the first eight letters. See see text for discussion and Appendix 4 for the complete cladogram.

*215
**    **** 17 Capitula
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**    ***153 *** 22 Chorizan
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**    **         129
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**    **         152**** 23 Chrysitr
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**    ***172
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**    **         65 Lepironi
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**    173
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**    **         92 Scirpode
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**    *174
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**    * *       49 Exocarya
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**    * **** 79 Principi
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****214
**** 40 Diplasia
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*** 77 Paramapa
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**** 58 Hypolytr
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** 110 Andesia
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179**** 116 Oxychloe
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180** 111 Distichl
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181** 112 Juncus
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183 *** 114 Marsippo
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****184 *** 113 Luzula
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**** 115 Prionium
Chapter 10

Concluding Remarks

Defining operational taxon limits (Chapter 2), primarily genera, for the purpose of inclusion in an automated database proved to be a challenge, as may be appreciated from a consideration of the extensive generic synonymy (Appendix 1), and it was fortunate that a thorough nomenclatural treatment of the family at this level became available at an opportune time (Goetghebeur 1986). Whilst convenience dictated acceptance of relatively narrow generic concepts for purposes of the database (see Chapters 8-9), several of those used should be merged in the interests of acquiring satisfactory generic circumscriptions. (e.g. Costularia brevicaulis with Costularia: the ambiguity of its relationship with Tetraria or Costularia having being resolved, Chapter 9; and the descriptions of genera segregated on the basis of photosynthetic pathway type, Chapters 5 and 9).

Development of the generic character list (Chapter 3) revealed many questions of homology in need of resolution. In a study such as this, with a broad scope, not every character can receive the sort of attention one may wish. Some moderately detailed studies were, however, possible (Chapters 4, and 6-8). An SEM investigation of floral morphology at different developmental stages in five sedges representing both subfamilies (Chapter 9) affords support for interpreting their floral morphology along traditional lines (Chapter 4; contrast Goetghebeur 1986). The generality of this interpretation, however, needs testing with resort to extended sampling across the family. Such investigation should clarify the taxonomically unsatisfactory situation regarding the mapanioids (Hypolytreae; Chapter 4). Another approach to the mapanioid genera (Chapter 9) would be to extend the preliminary studies on anthers and pollen in the Cyperaceae (Appendix 1), which are a source of taxonomic data independent of interpretation of floral morphology.

The broad survey of C₃ and C₄ photosynthetic pathways in the Cyperaceae (Chapter 5) confirmed Cyperus and Rhynchospora as variable. Hitherto unknown variation in photosynthetic pathway was found in Abildgaardia and Eleocharis (Chapters 5-7). Coincidentally, the ‘one cell distant criterion’ was found to accurately predict C₄ pathway in sedges, with the exception of Eleocharis. The checklist presented as Appendix 2 provides a guide for future sampling requirements. Much of the information is available interactively in the INTKEY set (Appendix 3) which will be maintained and
updated. Sampling has been very thorough at the generic level, but future effort could be directed towards extending the species coverage of genera (and their closest relatives) exhibiting variation. Taxonomic revisions of photosynthetically variable genera now seem to merit high priority: e.g. *Eleocharis* (especially *E. series Tenuissimae*), *Abildgaardia* and *Fimbristylis* section *Fuscae*.

*C₄* acid decarboxylation assays undertaken in the course of this study confirmed earlier findings (Jones *et al.* 1981; Chen *et al.* 1974; Ueno *et al.* 1986) and extended the range of variation known for photosynthetic pathways in the Cyperaceae with the discovery of NAD-ME *Eleocharis* species (Bruhl *et al.* 1987; Chapter 6). No PCK species are known in the Cyperaceae, but the sample biochemically assayed remains relatively small (Chapter 7). The relatives of the NAD-ME sedges may be the best candidates for PCK photosynthesis (cf. Burnell and Hatch 1988). Of particular interest will be the anatomically anomalous species (Chapter 5) for which unavailability of fresh material has so far precluded biochemical analysis.

The variation in photosynthetic pathways within *Eleocharis*, including the recently reported intraspecific variation in *E. vivipara* (Ueno *et al.* 1988), is leading to increased interest in this group of helophytic to hydrophytic sedges, and the work should be extended to include the submerged aquatic relatives, *Egleria* and *Websteria*. These are currently designated *C₃* (Chapter 5), but it would be interesting to test their response to terrestrial conditions. Given the anatomical variation within *Eleocharis* (the breakdown of the 'one cell distant' criterion in the *C₄* species generally and the apparent plasticity within *E. vivipara*) further work in this circle of affinity should include screening for CAM photosynthesis. Ecophysiological experiments might profitably explore the relationship of *C₄* sedges with nitrogen use efficiency.

Ultrastructural characteristics previously reported (Black and Mollenhauer 1971; Laetsch 1971; Carolin *et al.* 1977; Gilliland and Gordon-Gray 1978; Jones *et al.* 1981; Ueno *et al.* 1988) for the then known (chlorocyperoid, fimbristyloid and rhynchosporoid) anatomical types were largely confirmed (Chapter 8), though some evidence of poorly developed peripheral reticulum (PR) in *C₄* rhynchosporoid sedges was presented. As one might have predicted from correlations established for NAD-ME species in other families, the NAD-ME *Eleocharis* species (cf. Hatch and Mau 1973; Hatch and Kagawa 1974a-b; Kagawa and Hatch 1975; Hattersley 1987) and the *C₃*-like *C₃*-*C₄* intermediate *E. pusilla* (cf. Holaday *et al.* 1984; Hylton *et al.* 1988; Rawsthorne *et al.* 1988) possess abundant mitochondria and chloroplasts with well stacked grana in the PCR/bundle sheath cells: an intriguing convergence in form.
The ultrastructural features of the photosynthetic tissue in the Cyperaceae are sufficiently distinct and well enough preserved in dried material to allow biochemical typing of sedges from herbarium material (Chapter 6). C₄ typing of taxonomically interesting species which are rare and/or relatively inaccessible is therefore feasible.

The extensive development of PR in the PCR chloroplasts of the NAD-ME *Eleocharis* is in line with the supposition that it is involved in rapid metabolite transport (Ueno *et al.* 1988). Application of ultra-fine SEM techniques employing freeze-fracture, developed by Barnes and Blackmore (1986) for studies of pollen development, may provide both a clearer picture of the structural differences between the chloroplasts of sedges of different photosynthetic pathway types, and further insight into their functional significance.

I regard Appendix 3 (i.e. the interactive version of my data bank, for use on MS-DOS microcomputers) as a major achievement of this project (Chapter 8). More than a third of the descriptions are of monotypics, and extension of the whole data set to species level is a worthwhile goal, requiring international collaboration. Meanwhile, continuing development and refinement of the generic data should provide a useful tool for systematic studies, as well as providing non-taxonomists access to upgraded facilities for identification and data retrieval.

Use of the DELTA system has facilitated a more thorough and experimental approach to classificatory analyses than would have been possible by other means, and the database remains available for continuing efforts towards improving the classification. Critically selected subsets of the characters and the taxa have been analyzed phenetically and cladistically, resulting in a comprehensive (albeit tentative) classification (Chapter 9). This conforms in many respects with past classifications (e.g. regarding tribal delimitations; cf. Goetghebeur 1986 and Chapter 9, Table 9.1), but the subfamilial limits are new. My work has highlighted areas especially in need of further research, in particular the composition and relationships of the Arthrostylideae and the Hypolytreae and the interpretation of flowers and inflorescences for comparative purposes. Other outstanding problems and uncertainties in the classification of the Cyperaceae concern the detection tribal delimitation around the Scirpeae and the recognition of convincing subfamilies. Resolution of these may have to await a world-wide species treatment of the family combined with nucleic acid sequencing of appropriate samples.


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