CHAPTER 1: GENERAL INTRODUCTION

1.1 *Placement of* Loudetia *and* Loudetiopsis

The family Poaceae is currently subdivided into five to seven subfamilies based on anatomical features (Davis & Soreng). Major subfamilies are defined by shared features, but there are some small groups which exhibit unstable relationships with one or more genus. Although the Panicoideae, Andropogoneae, Chloridoideae and Centrothecoideae (PACC) clade has been recovered in many phylogenetic hypotheses, indicating that together they form a monophyletic group, relationships among members of each subfamily are not well understood (Clayton & Renvoize, 1986; Davis & Soreng, 1993; Spangler *et al.*, 1999; GPWG, 2001). Also not fully-resolved is the placement of the rest of the subfamilies of the Poaceae (Clayton & Renvoize, 1986; Davis & Soreng, 1993). Within the tribe Arundinelleae, there are two main evolutionary groups, with *Garnotia* and *Arundinella* on one hand and *Loudetia* Hochst. ex Steud. / *Loudetiopsis* Conert with the rest of the genera on the other (Clayton & Renvoize, 1986). However, relationships among the genera of the Arundinelleae remain unresolved, mainly because of the lack of synapomorphies blamed on reticulate character distributions.

Loudetia and *Loudetiopsis* are predominantly tropical species distributed in Africa, Madagascar and South America (Table 1.2). These genera belong in the tribe Arundinelleae Raddi within the subfamily Panicoideae. Panicoideae is subdivided into seven tribes based on spikelet characters (Table 1.1). Of these, the only well-delimited tribes to date are Pooideae, Bambusoideae, Chloridoideae and Paniceae (Clayton & Renvoize, 1986; Davis & Soreng, 1993). Panicoideae is morphologically highly variable and therefore its monophyletic status is uncertain (Clayton & Renvoize, 1986; Davis & Soreng, 1993; GPWG, 2001). On the other hand, the Arundinelleae forms a monophyletic group of 12 genera (Table 1.2). Within the subfamily, the Arundinelleae can be distinguished by deciduous spikelets with dimorphic florets and geniculate awns of the upper lemma, with connate pedicels in more advanced forms and the panicle forming before spikelets are mature (Clayton & Renvoize, 1986). The tendency of spikelets clustering in threes has been mentioned as another diagnostic feature, but diads are also common in some genera, including *Trichopteryx*, while *Loudetia* exhibits both forms. The possession of a pair consisting of a male or sterile lower and hermaphrodite upper floret places *Loudetia* and *Loudetiopsis* in the Arundinelleae. *Loudetia* and *Loudetiopsis* can further be distinguished by persistent glumes with subterete spikelets that have a tendency to fall entire (Hubbard, 1934; Conert, 1957; Clayton & Renvoize, 1993).

Table 1.1. Genera of the tribe Arundinelleae. After Clayton & Renvoize (1986).

Genus	Total number of species	General geographical distribution
Arundinella	±50	Tropics & subtropics, mainly in Asia
Garnotia	29	Tropical Asia
Loudetia	26	Tropical & South Africa, Madagascar & South America
Tristachya	±22	Central & South Africa, Madagascar & Central & South America
Danthoniopsis	±20	West, Central & South Africa and Pakistan
Loudetiopsis	11	West tropical Africa & South America
Trichopterix	5	Western, central & southern Africa & Madagascar
Dilophotriche	3	Senegal to Ivory Coast
Zonotriche	3	Central Africa
Chandrasekharania	1	India
Gilgiochloa	1	Central Africa
Jansenella	1	India

Table 1.2. Recognized tribes of the subfamily Panicoideae. After Clayton & Renvoize (1986).

Tribe	Number of genera
Paniceae	101
Arundinelleae	12
Isachneae	5
Neurachneae	3
Eriachneae	2
Hubbardieae	1
Steyermarkochloeae	1

1.2 Taxonomic problems in the Arundinelleae

Circumscribing genera and their constituent species in the Arundinelleae has been problematic, partly because of disagreement on what should constitute a genus, but chiefly due to the limited number of group-defining characters in general. In this tribe, many potentially diagnostic characters occur in combinations shared by different genera (Phipps, 1964). This trend gives no clear diagnostic traits and also presents chaotic character state distributions.

Due to this chaotic distribution of attributes, workers have resorted to defining taxonomic groups in the Arundinelleae by a suite of character states shared by members of a particular taxon even if taken individually; each character state is also shared with members of other genera (Phipps, 1964). However, circumscribing taxonomic groups with few or no unique traits can present difficulties when determining boundaries based on attributes assignable to a taxonomic group and is thus prone to error. Consequently, there have been two schools of thought. Some workers preferring broadly- and others narrowly-defined genera (Phipps, 1964; Clayton, 1967). Broadly defined genera became extremely heterogeneous whereas narrowly defined ones lacked distinctive boundaries. Each school of thought necessitated rearrangement of genera and their constituent species. As a result, inconsistencies and instabilities of taxonomy and circumscription of some of the genera in the Arundinelleae (including *Loudetia* Hochst. ex Steud.) have been common (Hubbard, 1936; Phipps, 1966a, 1972a; Clayton, 1967, 1972b; Renvoize, 1987). Eighteen narrowly-defined genera, with less intraspecific variations were recognized in the Arundinelleae (Phipps, 1964). However, workers disagreed with some of the genera because they were based on few or unreliable separating characters (Clayton, 1967, 1972a). Among the genera that are no longer recognized are *Rattraya* Phipps, *Muantijanvella* Phipps and *Jacques-Felixia* Phipps and were sunk by Clayton (1967). Changes in the circumscription of genera caused movement of their constituent species from one genus to another. As a result, different authors have reported varying numbers of species. Therefore determining the number of species in the genus *Loudetia* has been extremely difficult.

Recent work in the Arundinelleae concentrated on resolving generic circumscriptions (Phipps, 1964, 1972b to 1972e) while defining species limits in highly variable taxa, such as *Loudetia simplex* (Nees) C.E. Hubb. was largely neglected. Also neglected was the elucidation of phylogenetic hypotheses in *Loudetia*, with the only attempt, based on intuition published in 1967 (Phipps, 1967). Since then, knowledge of the genus and cladistic methods have changed, necessitating testing the monophyly of *Loudetia* based on modern cladistic methods. This thesis therefore presents an attempt to clarify the *L. simplex* complex, test the circumscription of *Loudetia* and *Loudetiopsis*, provide an updated enumeration of species in *Loudetia*.

1.3 *Species clarification in the* <u>Loudetia</u> simplex *complex*

Many attempts have been made to subdivide members of the *L. simplex* complex into varieties, subspecies and separate species. The species, when treated under *Trichopteryx simplex* Nees was divided into var. *minor* Stapf, var. *crinita* Stapf (Stapf, 1898); var. *sericea* Rendle and var. *gracilis* Rendle (in Cat. Afr. Pl. Welw. **2**: 214 (1899)). Then, the complex was divided into subspecific ranks (*L. simplex* Nees ssp. *stipoides*) and later as distinct species, *Loudetia simplex, L. camerunensis* (Stapf) C.E. Hubb. and *L. stipoides* (Hack.) Conert (Stapf, 1898; Conert, 1957). Establishing boundaries between these varieties, subspecies and the closely related species (*L. camerunensis* and *L. stipoides*) became extremely difficult because of character intergradation when the entire population was examined (Clayton, 1974). Because of this continuous variation, the closely related forms were treated under *L. simplex* (Clayton, 1974), resulting in an extremely variable group, the *Loudetia simplex* complex. The heterogeneity within this complex indicates that cluster analysis and ordination techniques of morphometric methods might provide classification. An attempt has therefore been made to clarify the delimitation of the *Loudetia simplex* complex (see Chapter 2).

1.4 *The formulation of characters and coding of character states*

Cladistic analyses based on erroneously defined character states may not reflect the phylogeny of the group and are likely to produce long tree lengths and low internal branch support, consistency index and retention index. Thus, erroneously defined character states may affect the results of a classification (Bisby & Nicholls, 1977). The low internal branch support, retention and consistency indices and long tree length have been noted in a preliminary cladistic analysis of the Arundinelleae (see chapter 3, section 3.1). Similar results have been reported in previous publications (Phipps, 1967; Clayton, 1967, 1972b). The lack of characters unique to a particular taxonomic group could be due to several phenomena. There is the possibility of a rapid evolutionary divergence with low rates of extinction to eliminate the intermediate morphotypes and hybridization may occur (Clayton, 1967). Rapid divergence of grasses is believed to have occurred between late Oligocene and Pliocene when the persistence of glaciation caused widespread dry weather conditions (Raven & Axelrod, 1974). Rapid evolution and hybridisation may have contributed towards causing large numbers of morphologically unspecialised characteristics in the Arundinoideae (Phipps, 1966b, 1967; Clayton, 1967; Li & Phipps, 1973; Stebbins, 1981).

In addition to the evolutionary history, error in formulating characters and defining character states may also contribute to the levels of homoplasy observed in cladistic analyses based on morphological data sets in the Arundinelleae. However, it is unclear whether taxonomic problems in the Arundinelleae can be attributable to error in the formulation and definitions of characters and character states. Nevertheless, it was felt to be necessary to investigate whether character state definitions are part of the taxonomic problems in the Arundinelleae by defining character states quantitatively (see Chapter 3).

1.5 *Phylogenetic hypothesis*

The creation of the genus *Loudetiopsis* Conert from parts of *Loudetia* and *Tristachya* was meant to reduce the morphological heterogeneity in *Loudetia* (Conert, 1957). However, *Loudetiopsis* has become a controversial genus because of the lack of diagnostic characters. A phylogenetic analysis based on intuition and a morphometric study of the Arundinelleae indicated that there are no morphological distinctions between *Loudetia* and *Loudetiopsis* to warrant recognition at generic level (Phipps, 1967; Clayton, 1967, 1972b). In the phylogenetic hypothesis based on intuition, *Loudetiopsis* forms a grade within the *Loudetia* clade, results which have been mirrored in this study by a cladistic analysis based on the morphological and anatomical data set. It was therefore doubtful that *Loudetia* and *Loudetiopsis* were monophyletic genera. Therefore the circumscriptions of these genera were tested phylogenetically using a combined anatomical and morphological data set (see Chapter 3).

1.6 *Enumeration of species in Loudetia*

The genus *Loudetia* is currently known from several piecemeal studies scattered in regional and other accounts such as Hubbard, 1934, 1936, 1937, 1949, 1957; Hutchinson & Dalziel, 1936; Chippindall, 1955; Conert, 1957; Jackson & Wiehe, 1958, Jacques-Félix, 1960; Metcalfe, 1960; Chapman, 1962; Phipps, 1964, 1966a, 1966b, 1967, 1970, 1972a to 1972d; Astle, 1965; Li *et al.*, 1966; Clayton, 1967, 1968, 1970, 1972a, 1972b, 1974, 1978; Lubke, 1969; Phipps & Mahon, 1970; Tadros, 1971; Lubke & Phipps, 1973; Renvoize, 1980; Clayton & Renvoize, 1989; Anderson, 1990; Watson & Dallwitz, 1994; van Oudtshoorn 1999 and others. Therefore obtaining useful information about the genus as a whole from these scattered publications can be difficult.

Wide coverage of the genus may be found in Hubbard's (1936, 1937) treatments, Conert's (1957) monograph and Lubke's (1969) and Lubke & Phipps' (1973) revision of the Arundinelleae, but some species have since been excluded from the genus and additional species have been included in recent publications (Chippindal, 1955; Conert, 1957; Phipps, 1964; Clayton, 1967, 1972b). None of the existing publications contain a list of species that incorporates all of the recent taxonomic changes in the genus. This emphasizes the need to provide an updated species enumeration.

Species inventories provide baseline data for monitoring of ecosystem dynamics, or implementing the ecosystem approach to conservation and management strategies, documenting patterns of diversity and supporting tourism (Cracraft, 2002: 132). Knowledge of species distributions can guide the search for new products, or promote trade in natural resources, ecotourism, control of pests or invasive species, crop improvement or monitoring of the effects of climate change on ecosystems (Cracraft, 2002). Plotting the spatial distribution of species depends on availability of comprehensive inventories. Whereas the temperate flora is well known, the tropics, although they support relatively higher botanical diversities, are poorly inventorized, therefore the need to compile species inventories is greater in tropical than in temperate regions (Prance, 1984). The present study provides an enumeration of *Loudetia* species, which may contribute towards the compilation of local, regional and global inventories (see Chapter 4).

1.7 *Method of predicting the risk of extinction using herbarium specimens*

Herbarium specimens have been recommended and even used for determining the conservation status of species (Prance, 1984; MacDougall *et al.,* 1998; Willis *et al.,* 2003). The number of specimens gathered per species over a given period of time and the number of localities from where specimens have been collected have been processed to yield the degree of threat. Species represented by few collections and / or exhibiting restricted distributions in herbaria are considered to be at a higher risk of extinction than well-represented and widespread species (MacDougall *et al.,* 1998). However, herbarium collections are unsystematic (Rhoads & Thompson, 1992). Thus, rare and / or endangered species may be over- represented in herbaria - giving a false indication that they are at a lower risk of extinction than well represented and widespread species that are poorly collected and vice versa. Besides, there are no indications about changes in population and / or range sizes because once collected, herbarium records represent fixed historic records which are not sensitive to any degree of subsequent change. Changes to the size of a population and / or its range are important indicators of the degree of threat for a particular species (Pimm, 1988; IUCN SSC, 2001). The absence of indications of the expansion and / or shrinkage of the population and / or range size may therefore lead to the placement of an endangered species in the lower risk category or vice versa, which may have serious implications for conservation and management efforts. Because of this information deficiency, it was felt that herbarium records may be used only in predicting species which may require a detailed conservation status assessment. Therefore an attempt to devise a standard method of predicting which species requires detailed conservation status assessment has been made (see Chapter 5).

1.8 *Motivations for the study*

The existence of a highly variable entity in *Loudetia,* the *L. simplex* complex, is an indication that species delimitations in the genus are not complete. Insufficiently known taxa present problems when assessing biodiversity (Phipps, 1964; Cracraft, 2002). This study aims to update knowledge of the genus, demonstrate the need to clarify species delimitations within the Arundinelleae for the remaining variable species and motivate similar analyses in other tribes of the Poaceae.

Workers have doubted if the separation of *Loudetiopsis* from *Loudetia* is warranted; hence the circumscriptions of these genera needed to be tested. As circumscribed, it is doubtful if *Loudetia* and *Loudetiopsis* are monophyletic. Knowledge of *Loudetia* has changed during the past 70 years. Changes in the number of species may have altered species relationships (Sanderson & Donoughue, 1984). The circumscription of *Loudetia* and species relationships in the genus may be resolved using modern phylogenetic methods. The cladogram has then been used to infer a classification of the genus.

Species enumerations, inventories and distributions are important in the formulation of conservation strategies and future biodiversity monitoring activities on predicted effects of global warming on biodiversity (Cracraft, 2002). The varying numbers of species reported in different publications makes the determination of the number of species in the genus impossible. Compilation of an updated enumeration of species of *Loudetia* is intended to contribute towards the global and local inventory of species.

It has been widely reported that human driven habitat modification and direct use of plant resources are threatening species survival and ecosystem dynamics in the southern African region (White, 1983; Pimm, 1988); Vane-Wright *et al.*, 1991; Golding, 2002). However, scientific knowledge of the current or future probability of species extinction due to environmental degradation in the region is scanty. Conducting conservation status assessment studies for all species can be time demanding and expensive. Investigating whether species are likely to be threatened using herbarium specimens and thus require detailed conservation status assessment studies may reduce time and expenses by concentrating efforts on species that have already been prioritized. A standard method for prioritizing species as requiring detailed conservation status assessments will ensure comparability of results while accelerating the acquisition of knowledge of species that might be at risk of extinction.

1.9 *Aims and objectives of this thesis*

The aims and objectives of the present study including major questions to be answered are outlined in Table 1.3.

1.10 *An overview of themes and questions addressed in this thesis*

Four distinct themes have been studied in this thesis. The first concerns the taxonomic clarification of the *Loudetia simplex* complex (Questions 1.1 and 1.2; Chapter 2). The second theme relates to the circumscription and species relationships to accommodate recent knowledge about the genus (Questions 2.1 – 2.4; Chapter 3). The third theme is an attempt to provide an updated species list (Questions 3.1 – 3.4; Chapter 4) and the fourth theme is the development of a standard method for using herbarium specimens in predicting the risk of extinction (Question 4.1; Chapter 5). These themes have been dealt with using morphometric and phylogenetic methods to investigate whether taxonomic groups can be identified within the *Loudetia simplex* complex and test the circumscriptions of *Loudetia* and *Loudetiopsis,* respectively and an assessment of herbarium data that might indicate whether species are at risk of extinction, thereby helping to predict the conservation status. The major questions this study attempts to answer are presented in Table 1.3).

Table 1.3. Aims, objectives and questions of the present study.

NO.	AIM	OBJECTIVES	QUESTIONS
1	Providing a classification of *Loudetia* through: phenetically appraising the *Loudetia simplex* complex	Providing a taxonomic clarification of the *Loudetia simplex* complex	1.1 Can distinct taxonomic groups be identified within the *Loudetia simplex* complex? 1.2 At what taxonomic level is it appropriate to recognize such groups, if they exist?
2	Phylogenetically evaluating the generic circumscription of *Loudetia* and *Loudetiopsis*	Providing a hypothesis of species relationships based on the combined morphological and anatomical data set	2.1 Are the genera *Loudetia* and *Loudetiopsis* monophyletic? 2.2 What are the species relationships as elucidated by anatomical and morphological characters? 2.3 Do morphological data give the same species relationships as anatomical data? 2.4 How does a classification inferred from the cladogram compare with previous classification schemes?

NO.	AIM	OBJECTIVES	QUESTIONS
3	Investigating the value of quantitative morphological and anatomical characters in the elucidation of phylogenetic relationships of species of *Loudetia* and *Loudetiopsis*	3.1 Determining the phylogenetic contribution of quantitative characters in *Loudetia* 3.2 Determining if morphological and anatomical data sets give similar or aberrant phylogenetic relationships 3.3 Investigating the effect of omitting one character at a time from the data matrix on species relationships	3.1 Are quantitative characters valuable in the cladistic analysis of species of *Loudetia* and *Loudetiopsis*? 3.2 Can determining character boundaries quantitatively shade light on whether homoplasy in *Loudetia* is due to error in character formulation and coding or the evolutionary history of the group? 3.3 Do morphological data give the same species relationships as anatomical data? 3.4 Are trees stable when the combined morphological and anatomical data set is altered by excluding one character at a time?
4	Evaluating biogeographical information in the light of the estimated age of the genus and homoplasy	Estimating the age of the genus and its chaotic character state distributions from the inferred biogeographical evidence	4.1 Can biogeography offer clues about the estimated age of the genus *Loudetia* and its chaotic character distributions?
5	Providing an updated enumeration of species of *Loudetia*	5.1 Inferring a classification from the cladogram 5.2 Determining the	5.1 How many species

NO.	AIM	OBJECTIVES	QUESTIONS
		number of species in *Loudetia*	are there in the genus?
6	Developing a standard method for predicting species which require detailed conservation status assessments using herbarium specimens of species of *Loudetia*	Determining useful parameters for predicting the risk of extinction using herbarium specimens	6.1 What parameters are useful in predicting the risk of extinction using herbarium records?

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