CHAPTER 1

INTRODUCTION

This chapter includes the aim and approaches of this study and an abbreviated literature review of the evolution, diversity and systematics of the Eriophyoidea as background for the research presented in this dissertation.

1.1 AIM AND APPROACHES OF THIS STUDY

1.1.1 Topic

Systematics of the superfamily Eriophyoidea (see classification of the Eriophyoidea in Table 1.1).

1.1.2 Taxa and classification of the Eriophyoidea

The Eriophyoidea are considered to belong to the acariform Prostigmata or Trombidiformes (= Sphaerolichida + Prostigmata *sensu* Lindquist, 1998) (Table 1.1). The Trombidiformes are a large and diverse group of mites, mainly characterized by the lack of character states found in other major groups of acariform mites than by synapomorphies of their own (Lindquist, 1998). Within Trombidiformes, the Prostigmata are united by having the stigmatal openings to the tracheal system located anteriorly (mostly on the prodorsum or near the base of the mouthparts), and this was indicated as a synapomorphy of this group in a cladistic analysis by O'Connor (1984). More recent cladograms of relationships of taxa within Trombidiformes (or Prostigmata) were presented by Norton *et al.* (1993) and Lindquist (1998) but these were based on unpublished analyses. According to Lindquist (1998), Prostigmata constitute a group within Trombidiformes, but confusingly, Prostigmata is frequently used as an alternative name of Trombidiformes and *vice versa* (e.g., Baker, 1999). In this dissertation, I follow the names and groups as shown in a cladogram by Lindquist (1998), but refer to Prostigmata (since this group name is generally used in recent publications) as the major group including Eriophyoidea (also refer to the title of the dissertation). Prostigmata in this dissertation, however, refers to the group within Trombidiformes *sensu* Lindquist (1998), and not as an implied alternative name of Trombidiformes.

The relationship of the Eriophyoidea with other groups of prostigmatid mites will be dealt with in more detail in Chapter 4.

Table 1.1. The classification of Acari and Eriophyoidea within Animalia (including some sister groups) [according to Weygoldt & Paulus (1979) and Lindquist (1984, 1996b)], and the classification of suprageneric groups within Eriophyoidea (following Amrine *et al*., 2003).

Kingdom: Animalia
Phylum: Arthropoda
Subphylum: Chelicerata
Class: Arachnida
Subclass: Acari (sister group: Ricinulei)
Order: Acariformes (Actinotrichida)
Suborder: Trombidiformes (= Sphaerolichida + Prostigmata)
Cohort: Prostigmata: Eupodina

Superfamily: **Eriophyoidea** Nalepa, 1898 (sister group: Tydeoidea)

- **Family:** **Phytoptidae** Murray, 1877
  - Subfamily: Prothricinae Amrine, 1996
  - Subfamily: Novophytoptinae Roivainen, 1953
  - Subfamily: Nalepellinae Roivainen, 1953
    - Tribe: Pentasetacini Shevchenko, 1989 (*in* Boczek *et al*., 1989)
    - Tribe: Trisetacini Farkas, 1968
    - Tribe: Nalepellini Roivainen, 1953
  - Subfamily: Phytoptinae Murray, 1877
  - Subfamily: Sierraphytoptinae Keifer, 1944
    - Tribe: Sierraphytoptini Keifer, 1944
    - Tribe: Mackiellini Newkirk & Keifer, 1971

- **Family:** **Eriophyidae** Nalepa, 1898
  - Subfamily: Aberoptinae Keifer, 1966
  - Subfamily: Nothopodinae Keifer, 1956
    - Tribe: Colopodacini Mohanasundaram, 1984
    - Tribe: Nothopodini Keifer, 1956
  - Subfamily: Ashieldophyinae Mohanasundaram, 1984
  - Subfamily: Cecidophyinae Keifer, 1966
    - Tribe: Cecidophyini Keifer, 1966
    - Tribe: Colomerini Newkirk & Keifer, 1975
  - Subfamily: Eriophyinae Nalepa, 1898
    - Tribe: Diphytoptini Amrine & Stasny, 1994
    - Tribe: Eriophyini Nalepa, 1898
    - Tribe: Aceriini Amrine & Stasny, 1994
  - Subfamily: Phyllocoptinae Nalepa, 1892
    - Tribe: Acaricalini Amrine & Stasny, 1994
    - Tribe: Calacarini Amrine & Stasny, 1994
    - Tribe: Tegonotini Bagdasarian, 1978
    - Tribe: Phyllocoptini Nalepa, 1892
    - Tribe: Anthocoptini Amrine & Stasny, 1994

- **Family:** **Diptilomiopidae** Keifer, 1944
  - Subfamily: Diptilomiopinae Keifer, 1944
  - Subfamily: Rhyncaphytoptinae Roivainen, 1953

The Eriophyoidea had about 3 500 recognized species of about 300 genera in three families: Phytoptidae, Eriophyidae and Diptilomiopidae (with 21, 227 and 53 genera, respectively) in 2003 (Amrine *et al*., 2003). The suprageneric classification within Eriophyoidea will be treated in more detail in Chapter 4.

1.1.3 Problems with eriophyoid systematics

Many problems are experienced with the systematics of the Eriophyoidea, including:

1) the knowledge on the biodiversity of Eriophyoidea is particularly scant, probably only 1 to 20% or less of extant taxa are known (see later in this chapter);
2) practical difficulties are experienced in the classification and description of eriophyoid taxa, which lead to problems with the identification and differentiation of possibly new taxa, of which some are economically important;
3) few, particularly comprehensive, keys to species are available;
4) relatively little is known about intra-specific variation, and recognition of species is in many regards still uncertain;
5) character, character state and species descriptions are not always adequately precise and thorough, particularly for their utilization in phylogenetic studies;
6) when using phase contrast light microscopy to study slide-mounted specimens, few additional characters, apart from those already used for taxonomy, are available for systematics;
7) the phylogeny of the Eriophyoidea has hardly been studied, especially using new techniques, such as cladistic analyses, and the existing classification seems to be artificial; and
8) there are so many pressing needs, particularly for studying economically important species, and description of new species (alpha taxonomy), that it is difficult to prioritize systematic research for Eriophyoidea.

1.1.4 Primary aim, scope and objectives of this study

The primary aim of this study is to investigate, appraise and propose improvements for some aspects of the systematics of the Eriophyoidea. The study is based on: a) assessing and studying the phylogeny using current systematic techniques and b) improved morphological studies, incorporating scanning electron microscopy (SEM). The study focuses on southern hemisphere taxa in order to provide a systematic framework for future research on the biodiversity of Eriophyoidea in South Africa and beyond. An alpha taxonomic study – description of three new *Diptilomiopus* spp. from South Africa – is included to address the need for the description of unknown taxa.

1.1.5 Relevance of study

Any systematic study on Eriophyoidea will be a valuable contribution to all aspects of research and management of the group. Many eriophyoid species are potential or known economic plant pests, some are important in the quarantine of plant material exported and imported globally, while others are useful as biological control agents of weeds. The current state and lack of knowledge on the systematics of these species, frequently pose major restrictions to their applied research. The Eriophyoidea also constitute a cosmopolitan part of plant ecology and occurs as part of all plant ecosystems, yet less than 1% of this diversity might be known. The taxonomic shortfall for this group is massive. In order to contribute towards improving the systematics of the group, this study includes the evaluation and critical appraisal of some of the techniques and processes used in eriophyoid systematics.

1.1.6 The rationale behind the aim, scope and research order

Lindquist & Amrine (1996) noted that the need for alpha taxonomic research on the Eriophyoidea must be supported and it should not be viewed as a simpler or lesser science. The classification and systematic knowledge (particularly phylogeny) on the Eriophyoidea pose numerous problems, though. This should ideally be addressed simultaneously while documenting the fauna, which will improve the framework for description of yet more new taxa and other alpha taxonomic endeavours.

Some apprehension exists that phylogenetic studies may be premature, seen in the light of the shortfall of basic descriptive data, and urgency to describe existing diversity. It may be detrimental to the future knowledge and further research on the diversity and phylogeny of the Eriophyoidea, however, if taxon descriptions are not improved. Identifying specific improvements needed, can be obtained by formatting and coding descriptive data in comprehensive data matrices, continuously subjecting the data to phylogenetic analyses, and using the data in tools such as multi-access (interactive) keys (see Chapters 2 and 4).

Descriptive data (including definition of characters and character states) has to improve from current norms or at least adhere to an acceptable standard, if it is to be useful or sufficient for analyses (e.g., cladistic analyses) of the group. If this is not done, the description of these taxa will have to be repeated or improved in future. Although re-descriptions will necessarily always remain a part of the systematic study of a group, especially in the Eriophyoidea it should be minimized as far as possible. It is a huge and time-consuming task in this group, because slide-mounted type material is lost over time and the pressing need for describing new species will remain for a long time to come.

The supraspecific classification of the Eriophyoidea is for now relatively stable and accepted by leading eriophyoidologists globally, but it is most likely artificial (Lindquist & Amrine, 1996), at least in part, and thus has most likely little predictive power and may become unstable and problematic with the addition of new species. To base the classification on natural relationships between taxa is a further reason for continuously analyzing descriptive data, even if the resulting phylogenetic hypotheses may change radically over time. New phylogenetic hypotheses don't necessarily need to be translated into classifications for practical use until they are relatively "stable" and reliable, especially if such new hypotheses may cause confusion in the taxonomy of the Eriophyoidea.

When studying the phylogeny of a group, it can be done from top down or bottom up (of smaller groups). The monophyly of the Eriophyoidea as a group amongst other mites is virtually uncontested (Lindquist, 1996b). However, the monophyly of most supraspecific groups within Eriophyoidea is suspect (Lindquist, 1996b; Lindquist & Amrine, 1996). It was therefore decided to commence this study with preliminary and exploratory analyses of the relationships between type species of selected genera across a large part of the diversity of the superfamily. This analysis will test the monophyly of families, subfamilies and tribes. It also has the purpose to identify smaller hypothetically monophyletic groups for further phylogenetic analyses of relationships between species in these smaller groups. For the current study, the aim was to discover such a small hypothetically monophyletic clade within the Eriophyoidea that contains undescribed species and genera occurring in South Africa that have already been collected, and are ready for description. The aim was to describe these new taxa to include alpha taxonomy as part of the study, and at the same time contribute towards describing new taxa from South Africa. The phylogenetic analysis of the type species of the genera across the Eriophyoidea also tests the results and conclusions of another study (Hong & Zhang, 1996a) published in this regard.

A SEM study of the morphology of selected eriophyoid species was included because it became clear that the characters and character states were not well-defined and described in enough detail to be optimally useful for phylogenetic analyses (see Chapters 3 and 4). Many current descriptions are generally vague and characters carelessly defined in some instances. While capturing data for phylogenetic analyses, it was observed that many of the characteristics of slide-mounted specimens are either obscured and distorted, or not clearly visible using light microscopy. Due to the extremely small size of Eriophyoidea mites and the problems associated with and limitations of conventional phase contrast light microscopic study of their morphology, an appraisal of the systematics of the group can not be complete without an appraisal of the techniques used to study the group, and an investigation into improved ways of studying these tiny organisms. It was decided to at least investigate and evaluate the potential, usefulness and current use of SEM in the systematics of the Eriophyoidea.

The primary aim of the SEM study was to investigate the morphology in as natural and "true" life state and condition as possible, and also to further investigate the influence and importance of artefacts caused by preparation and slide-mounting on morphological data used for the systematics of the Eriophyoidea. The morphology from SEM images was compared with some slide-mounted specimens and published descriptions to investigate whether more potential systematically informative characters can be identified using SEM studies.

1.1.7 Study material and area

The data sets for the phylogenetic analyses of the Eriophyoidea (including all *Diptilomiopus* spp.) mainly include published descriptive data, and of species worldwide. The study of morphology using SEM, and description of new species, were done on specimens collected in South Africa.

1.1.8 Some published hypotheses and problems regarding the Eriophyoidea prior to and applicable to this study

1) The Eriophyoidea are a natural, morphologically distinct, monophyletic group of phytophagous mites [hypothesized by authors throughout the systematic research history of the group; comprehensively summarized, reviewed and extrapolated on by Lindquist (1996a, b) (see later)].
2) Eriophyoid mites are generally highly host specific or with narrow host ranges (Lindquist & Oldfield, 1996), and it seems that most angiosperm plants will host at least one species (S. Neser, *unpubl. data*, 2003).
3) A tiny proportion of extant eriophyoids are known globally (Farkas, 1969; Amrine *et al*., 2003). In South Africa, and Africa, in particular, the diversity is essentially unknown.
4) General evolution – it is proposed that they originated on gymnosperms, radiated on all plants including angiosperms (Lindquist & Oldfield, 1996).
5) Higher classification is artificial, and not a reflection of phylogenetic relationships (Lindquist & Amrine, 1996).
6) In some groups, problems are experienced with identifying species and assigning species to genera, because generic concepts, diagnoses and delimitations are problematic (Amrine *et al*., 2003). Very few comprehensive species identification keys are available, and some

genera without comprehensive species keys are very large, such as *Aceria* which has more than 900 species worldwide (Amrine *et al*., 2003).

1.1.9 Hypotheses tested and presumptions investigated in this study

1) Study of slide-mounted specimens contributes to errors incorporated in eriophyoid descriptions and classification.
2) Additional useful morphological characters are available for description, classification and study of phylogeny than are currently available or studied.
3) The definition of characters and character states and the description of these for Eriophyoidea are not optimal and should be improved.
4) Families, subfamilies and tribes of the Eriophyoidea are not monophyletic, with the possible exception of the Diptilomiopidae.
5) Phylogenetic analyses of a comprehensive sample of variation at the generic level of the Eriophyoidea will find useful, potentially monophyletic suprageneric groups for further study alternative and additionally to the suprageneric taxa presented in Amrine *et al*. (2003).
6) Phylogenetic studies can be incorporated parallel to pure descriptive work without detriment to the productivity and quality of alpha taxonomy.
7) The more extensive incorporation of new technologies will improve the systematics of the Eriophyoidea.

1.2 EVOLUTION, DIVERSITY AND SYSTEMATICS OF THE ERIOPHYOIDEA

1.2.1 Evolution

- Palaeontology and origin

A fossil rust mite (*Aculops keiferi* Southcott & Lange, 1971) was found in 37 million year old (Lower Middle Eocene) North Maslin Sands in South Australia (Southcott & Lange, 1971). The characteristics of this fossil mite are essentially the same as extant leaf vagrant eriophyoids (Keifer, 1975a) that are hypothetically more derived among Eriophyoidea (Smith, 1984), and it was thus extrapolated that the Eriophyoidea may have originated as long ago as the Early Tertiary, 50 million years ago (Keifer, 1975a), or even earlier (Smith, 1984).

Distribution patterns of species of the Phytoptidae (hypothetically early derived taxa) may indicate an ancestral lineage of eriophyoid mites that arose in association with ancient gymnospermous plants in the Pangaean supercontinent during the Triassic and Jurassic (about 140 - 225 million years ago) (Lindquist & Oldfield, 1996) when coniferous plants dominated plant diversity due to drier climates. Later, this distribution split into Gondwanian and Laurasian elements during the Early Cretaceous (140 million or fewer years ago) (Lindquist & Oldfield, 1996). Shevchenko *et al.* (1991) proposed that eriophyoids may have originated even earlier based on possible irreversible evolution in setal patterns following the divergence of gymnosperm- and angiosperm plants during the Late Carboniferous (about 270 - 280 million years ago). Care should, however, be taken with evolutionary extrapolations from present, probably artificial classifications of the Eriophyoidea. Be as it may, Eriophyoidea are probably a very old lineage and their biological and morphological homogeneity suggest they originated from a single primordial ancestral lineage (Keifer, 1975a).

- General evolution

General eriophyoid evolutionary trends as first presented by Farkas (1966, 1969) and Shevchenko (1970, 1976), and later compiled by Lindquist & Oldfield (1996) are presented in the introduction of Chapter 4.

- Eriophyoid-host plant co-evolution and species radiation

It is generally assumed, because of their close and frequently unique ecological relationships with their host plants by being very host specific, and causing very specific growth reactions on particular hosts, that eriophyoid mites co-evolved and co-speciated closely with the host plant taxa. Sabelis & Bruin (1996) argued that co-evolution itself might be the driving force for the evolution of the high host specificity observed in Eriophyoidea, and that this offers the most important alternative to the predation *versus* competition explanation they favour. They further speculated that the role eriophyoids play in virus transmission is the most promising area for revealing close co-evolution between eriophyoids and their hosts.

In their treatise of eriophyoid species occurring on Gymnospermae, Boczek & Shevchenko (1996) argued, based on distribution patterns of eriophyoid taxa on different extant gymnosperm and angiosperm taxa, that eriophyoid taxa co-speciated with their host taxa. Smith (1984) presented some examples of co-evolution between Nearctic and Palaearctic *Trisetacus* spp. and their host plants. He found that morphologically similar species utilize similar sites on closely related host species. According to Sukhareva (1994), ancient members of the Poaceae are inhabited by more specialized species (and thus presumably species that co-evolved with their plant hosts the longest) of eriophyoid mites. Boczek & Shevchenko (1996) postulated that the same situation exists on gymnosperm plants where the hypothetically oldest eriophyoid genus, *Pentasetacus*, occurs on a member of the Araucariaceae, the oldest gymnosperm taxon with extant representatives.

On the other hand, Fenton *et al.* (2000) found that the molecular phylogenetic tree structure of seven morphologically closely related *Cecidophyopsis* spp. and that of their *Ribes* host species differed significantly. This implies that in this group of species (colonizing species of one host genus), mite speciation did not closely follow the speciation events in the plant hosts (no strict co-speciation took place) on this level, despite a long co-existence between these hosts and eriophyoid mites. However, the *Ribes* infesting *Cecidophyopsis* spp. in his study included gall-formers and open-living vagrants not inducing distorted plant growth, and these grouped together and not with another gall-forming *Cecidophyopsis* sp. from a gymnosperm host, and a gall-forming *Phyllocoptes* sp. from a *Rubus* sp. in the analysis. At the level of the gymnosperm-infesting *Cecidophyopsis* sp. not grouping with the *Ribes*-infesting *Cecidophyopsis* spp., the molecular phylogenies of the plant hosts and mite species are in concordance (Fenton *et al.*, 2000). The results also indicate that the species grouped together due to their colonization of a specific host genus, and not due to their gall-forming ability (Fenton *et al.*, 2000). Further, it seemed the *Ribes* infesting mites evolved and speciated much more recently and for a shorter time than their hosts, similarly it seemed that *Ribes*-infesting *Cecidophyopsis* spp. and the *Cecidophyopsis* sp. living on the gymnosperm separated much more recently than the separation of Gymnospermae and Angiospermae (Fenton *et al.*, 2000).

In their analysis of Eriophyoidea collected in northeast India, among which no Phytoptidae occurred, apparently because their “probable” hosts were not surveyed, Das & Chakrabarti (1989) did not find any indication of co-evolution between the 94 species in 38 genera and their hosts from this region. They discussed these findings in view of the hypothesized co-evolution between eriophyoids and their hosts based on the close associations between eriophyoids and their host plants, and the occurrence of intra-generic complexes of morphologically very similar species occurring on particular plant families (closely related host species). They considered that both environmental (e.g., pressure by predators, availability of plant species-rich environments, difference in speciation rate between mites and their hosts and changes between sheltered and exposed life-styles) and factors favouring co-evolution (e.g., intimate associations with their hosts, possibly lack in successful colonization of potentially new host species), are equally important in determining the evolution of the Eriophyoidea.

The distribution of known eriophyoid species on host plant taxa (presumably the earlier derived members of the Phytoptidae largely occur on Gymnospermae, and most members of the presumably more recently derived Eriophyidae and Diptilomiopidae occur on Angiospermae) seems to indicate that co-speciation may occur in the case of the higher taxa of the mites and plants. These arguments are partly based on the assumption that the families within Eriophyoidea are monophyletic and that the polarization from early to more recently derived families are true, and the same for plants.

1.2.2 Extant and described diversity and biogeography

- Number of species

Recently the count of known eriophyoid species worldwide was 4 000 species (De Lillo & Skoracka, 2010). This probably represents only a tiny proportion of extant species. Several new genera and nearly 100 new species are described annually despite relatively limited systematic studies in the Eriophyoidea (Amrine *et al*., 2003). Conservatively, it is estimated that the world extant eriophyoid fauna may range from 35 000 to 50 000 species (Amrine *et al*., 2003). Based on the experience with collecting eriophyoids, including a fairly comprehensive survey of all eriophyoids to be found on the indigenous trees in the Magaliesberg region in South Africa, the number of eriophyoid species extrapolates to as many as 250 000 species worldwide, using the numbers per plant species[1] (S. Neser, *pers. comm.* & *unpubl. data*, 2003). These extrapolations indicate that less than 1% to possibly about 20%, depending on the country and area, may be known.

In comparison with Europe and North America, very few Eriophyoidea have been described from Africa. In South Africa, for example, Tucker (1926) was the first to describe five new species, and only 13 species, mostly cosmopolitan economically important pest species, were reported in 1960 (Ryke & Meyer, 1960). Since then, M.K.P. Smith Meyer and/or E.A. Ueckermann have described more than 190 new species and nine new genera from South Africa, from the *ad hoc* collections of mainly one collector, S. Neser (almost 100% of collected eriophyoid mites were new). Another *ca*. 200 unknown species (mostly *Aceria* spp.) have already been collected and are awaiting description and S. Neser from his collecting experience regards this as only the “tip of the iceberg” (S. Neser, *pers. comm*., 2008). It is unlikely that all eriophyoid species will be described before they are lost, and it is thus important to plan surveys and studies in order to gather data that will be useful to extrapolate on the shortfall.

- Biogeography of eriophyoids

During the evolution of life on earth, habitat occupation, niches, movement and evolution of plants and animals were not universally dispersed throughout the earth’s environment, but were

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[1] It should be noted that when eriophyoids were collected for the SEM study reported on in this dissertation, even more species per plant species were found than originally discovered by S. Neser. These additional new species usually were vagrant mites not causing any visible symptoms.

"restricted" by barriers to different and changing geographical areas over time. Today, spatial boundaries of biogeographical regions can be clearly- or less clearly-defined on biological similarity, and biological differences between the areas.

The morphology and diversity of living organisms coincide with biogeographical regions and biomes. Biogeographical areas and biomes for plants and animals are not exactly the same. Eriophyoid mites are obligatory plant-feeders, closely associated with their host plants, and may have originated as early as the Late Carboniferous when all land was part of the Pangaean supercontinent. On some classification levels, eriophyoid mites probably followed the divergence of the angiosperms and conifers. It thus seems feasible to presume that extant eriophyoid diversity may resemble extant plant diversity and biogeographical distribution more closely than that of other animals that are not closely associated with plants.

Eriophyoids occur widely on ferns, coniferous plants, monocots and dicots worldwide. They occur in the Arctic regions and at altitudes as high as 3 300 m (Oldfield, 1996). The distribution of many eriophyoid species on crops and exotic plants was probably expanded with them being transported with their host plants to other countries than their native areas. In his treatise of the diversity and host plant specificity of Eriophyoidea, Oldfield (1996) also listed and particularly presented the geographical ranges of eriophyoid genera and suprageneric groups. He, however, didn't come to any conclusions about the geographic distribution of Eriophyoidea.

- Future surveys and identification of eriophyoids

In practice when revising a higher taxon, or having to identify whether a species is new or previously described, comparing with all species of, for example, a specific genus on a global scale may be too laborious and impracticable. This is particularly so when no comprehensive and global keys for a group are available (this is particularly a problem in some of the larger genera, such as the genus *Aceria*, with a worldwide distribution and with more than 900 described species). It seems sensible in such studies to compare specimens or species in "similar" biotas. Additionally, one should also compare new material with phylogenetically closely related species, if it can not be compared with all species within a genus, or morphologically similar genera. This is not possible in the Eriophyoidea, however, because the classification is most probably still very artificial and not based on phylogenetic relationships (see Chapter 4).

In previous taxonomic studies of Eriophyoidea in South Africa, comparisons with described species were restricted to other species occurring in Africa (the Afrotropical Region) and occurring on the same host species, or host genus if it was not practical to compare such new material with all species described in the particular genus under study (E.A. Ueckermann, *pers. comm.*, 2008). For species comparisons with new material, the larger floral geographical areas and similar biomes should rather be chosen for restriction of study, and not, as it has been traditionally done, to the Afrotropical Region, which is essentially an animal geographical area. In addition, eriophyoid mites mainly disperse with wind, and wind currents (Zhao & Amrine, 1997), and this may artificially enlarge the distribution area of species, particularly when only single specimens are collected, that may be "accidentals".

Several major biomes are defined in South Africa with reasonably sharp transitions between them (Mucina & Rutherford, 2006). These biomes and their constituent vegetation types are regularly used as a framework for the ecology and biogeography of the flora, and as a foundation for conservation assessments and actions (Van Rensburg *et al.*, 2004). They may also serve as an appropriate framework for planning future surveys of Eriophyoidea in South Africa. In addition, the role physical aspects of the environment play, such as altitude, climate, relative humidity, and temperature should be taken into account. A further indicator could be the biogeographical patterns in phytophagous insects that have been studied more comprehensively. Whatever plan for surveying is drawn up, biodiversity sampling should lend itself to extrapolation of the data.

1.2.3 Systematics

- History of eriophyoid taxonomy

Lindquist & Amrine (1996) included the most recent comprehensive review of the taxonomic history of the Eriophyoidea. An abbreviated rendition is presented here.

Early descriptive work (1737-1885): The first published descriptions of eriophyoid mites described the symptoms caused by the mites on their plant hosts, and not the mites themselves (Keifer, 1975a; Lindquist & Amrine, 1996). Réaumur (1737), 273 years ago, appears to be the first author that commented on some of these growth abnormalities, mistaking the eriophyoid mites for tiny maggots (Keifer, 1975a; Lindquist & Amrine, 1996). Afterwards, early post-Linnaean taxonomists proposed the first generic names for the symptoms caused by the mites, but mistook them for fungi, such as *Erineum* and *Phyllerium* (Persoon, 1797). During the next century, the mites themselves were named according to taxonomic convention, such as *Eriophyes* von Siebold, 1850 and *Phytoptus* Dujardin, 1851.

Nalepa Period (1886-1929): Alfred Nalepa, working in Vienna, Austria, published the first adequate eriophyoid descriptions and was the prominent taxonomist on these mites during his career, setting the standard followed by his European counterparts. He described some 479 species, and 12 genera, and presented the first classificatory schemes for them. His last work was a catalogue of the then-described eriophyoid mites, their symptoms and host plants (Nalepa, 1929). This remained a standard work used worldwide for information on names, hosts and references until the next catalogue published by Davis *et al*. (1982). Nalepa published in "old" German, and unfortunately, his work is somewhat difficult to access and comprehend by non-German-speaking researchers, and even difficult to translate by modern German-speaking translators (one translator commented that she suspect that Nalepa's native language might not have been German). Detailed information on the "Nalepa Period" is provided by Keifer (1975a), Newkirk (1984), and Lindquist & Amrine (1996). The bulk of eriophyoid systematic literature from the work of Nalepa up to the present includes alpha taxonomic publications on descriptions of new genera and species.

Keifer Period (1938-1982): Another major contributor to the taxonomy and biology of the Eriophyoidea was H. H. Keifer working in California, the United States of America. He was author or co-author of 711 species and 113 generic descriptions, most still recognized today (Amrine & Stasny, 1994). Keifer established a standard of illustrative and descriptive format which is in essence presently followed by most eriophyoid taxonomists. He also developed the classification of the Eriophyoidea to almost that widely accepted today. He further contributed a comprehensive review and compilation of systematic and other information on Eriophyoidea of the world in two chapters on Eriophyoidea and injurious eriophyoid mites (Keifer, 1975a, b in Jeppson *et al*., 1975), and an appendix to the book: *Synoptic keys to the groups and genera of Eriophyoidea* (Newkirk & Keifer, 1975).

During this period, European authors also contributed significantly to the systematics of the Eriophyoidea, including descriptions of 64 species by Farkas, 83 species by Liro and Roivainen, and 91 species by Boczek (Lindquist & Amrine, 1996). Other more comprehensive works, including catalogues, were published for Finland (Liro & Roivainen, 1951), central Europe (Farkas, 1965b), North America (Keifer *et al*., 1982), California (Keifer, 1952b), Kansas (Hall, 1967), South Dakota (Briones & McDaniel, 1976) and India (Channabasavanna, 1966).

1982-present: The post-Keifer period saw an increase in alpha taxonomic studies on Eriophyoidea from areas outside North America and Europe. These include descriptions of some new genera, and major contributions of newly described species (in brackets) among others from India (*ca*. 240), South Africa (*ca*. 190), New Zealand (*ca*. 55), Brazil (*ca*. 200), China (*ca*. 280), Thailand (*ca*. 130), Taiwan (*ca*. 170), and Yugoslavia (*ca*. 50).

- Morphology used in systematics

Characteristics from the entire body and all appendages are already used in the description of taxa, and the character list largely follows the descriptions done by Keifer during his career. Amrine & Manson (1996) reviewed taxonomic characters and their use, and proposed what should be included in a description of an eriophyoid species. Eriophyoid morphology and its application in systematics of the group are dealt with in Chapters 3 and 4.

- Morphometric studies

Linear measurements of setal lengths and of other morphological structures form an integral and large part (more than half of the descriptive information) of a "standard" eriophyoid species description. Additionally, some structures are also counted (meristic data). Unfortunately, these measurements and counts are frequently presented vaguely and inaccurately and without proper statistical structure. For example, frequently single measurements are not defined, and can either be random single or holotype measurements or means; ranges are not always included with means; or ranges are recorded without the means and number of specimens measured. This carelessness renders the published data almost useless, other than when the gap between two measurements being compared is robust and large enough to differentiate between taxa.

In a landmark study, Amrine, Fenton and co-workers (Fenton *et al*., 1993; Amrine *et al*., 1994; Kumar *et al*., 1999; Fenton *et al*., 2000) studied a complex of five morphologically very similar *Cecidophyopsis* spp. on *Ribes* spp. (currants and gooseberries). Some of these species could not be distinguished morphologically from each other in earlier studies, and were regarded as physiological strains based on their apparent host specificity to different plant species. Amrine *et al.* (1994) statistically separated the five species using one-way analysis of variance (ANOVA) and the Least Significant Difference (LSD) test based on careful and accurate measurements of some morphological features. Their findings were supported by biological and molecular studies.

Geometric morphometric analyses are a relatively recent method that can be utilized to quantify and visualize shape variation and change (eliminating the effect of size, position and orientation). Shape variation may provide information that may be used in order to obtain evidence of similarity among taxa/populations and may be useful in testing hypotheses related to ecology and systematics. The first geometric morphometric analysis of eriophyoids was undertaken by Navia *et al*. (2006) in which they investigated the morphological variation between populations of *Aceria guerreronis* (the coconut mite) across its almost cosmopolitan distribution wherever coconuts occur, and to relate this variation with the geographic distribution of the studied populations. They found significant correlation between shape variation in the coxigenital and ventral mite body regions and the geographic origin of the populations sampled. These results agreed with results obtained in a similar study by Navia *et al*. (2005) using mitochondrial (16S) and nuclear (ITS) sequences. Both these studies corroborated the hypothesis that the species originates from America. Navia *et al*. (2006) proposed that multivariate and geometric morphometry may contribute to improving systematic studies of eriophyoid mites, if good and standardized preserved specimens are available.

- Molecular studies

It is evident from the first phylogenetic studies based on morphological characters (Hong & Zhang, 1996a, b, 1997; this study), that many problems are associated with studying relationships using morphological data. Currently, there are too few phylogenetically-informative morphological characters available or known for analyses. This is probably due to the difficulty in studying such microscopic animals, the relative simplification of the eriophyoid body and the seemingly high incidence of homoplasy in the morphological structures of Eriophyoidea. There is also a problem with separating particularly sibling eriophyoid species, or determining whether observed variation can be attributed to intra-specific variation, or whether it defines separate species.

By studying mite DNA one may circumvent many of the problems with morphological characters. The results can also be used to estimate the approximate timescale for the evolution of speciation (Fenton *et al*., 2000). The first studies on the chromosomes of Eriophyoidea for systematic use, were done by Huang & Huang (1990), Kuang *et al*. (1992) and Kuang *et al.* (1995). The first molecular study on Eriophyoidea was undertaken by Fenton and co-workers (Fenton *et al*., 1993, 1995, 1996; Kumar *et al*., 1999; Fenton *et al*., 2000; Jones, 2000). They studied a complex of morphologically closely related *Cecidophyopsis* spp. living on *Ribes* spp. Fenton *et al*. (1993) used polymerase chain reaction (PCR) amplification of ribosomal DNA (rDNA) and restriction fragment length polymorphism (RFLP) analyses to show that three of the then five *Cecidophyopsis* spp. found in the complex are probably valid species. The host species, distribution (Fenton *et al*., 1995) and niches (Fenton *et al*., 1996) of the different *Cecidophyopsis* spp. on *Ribes* spp. were also determined from the series of molecular studies. Jones (2000) reported that the three known *Cecidophyopsis* spp. on *Ribes* could be rapidly identified unambiguously, and that additionally four new species were identified, using rDNA data of the mites. The systematic process of one of the four new species specified by the molecular analyses (Kumar *et al*., 1999) was not completed, and the species is yet to be described morphologically and named. Fenton *et al.* (2000) analysed the phylogeny of the seven known *Cecidophyopsis* spp. on *Ribes* hosts, as well as a *Cecidophyopsis* sp. from a gymnosperm host, and a *Phyllocoptes* sp. from a *Rubus* sp. using equivalent rDNA sequences. Three groups of closely related mite species were found: two groups of gall-forming species, and one group with the non gall-forming species. This is an example of an excellent holistic systematic study including not only molecular studies, but also careful and comprehensive morphological studies (including morphometric analyses, see above) (Amrine *et al*., 1994) and biological studies (Easterbrook, 1980).

Carew *et al*. (2004) showed with PCR-RFLP analyses that the bud and leaf gall mites on grapevine, previously believed to be morphologically identical strains of the grapevine eriophyid pest, *Colomerus vitis* (Pagenstecher, 1857), (Smith & Stafford, 1948), are two closely related but distinct species. The two species were not morphologically described and named. Navia *et al*. (2005) used analyses of mitochondrial ribosomal (16S) and nuclear ribosomal internal transcribed spacer (ITS) sequence data to study the geographical origin, ancestral host associations and invasion history and routes of the invasive coconut eriophyid mite pest, *Aceria guerreronis* Keifer, 1965. The results suggested that it originates from America, and the original host of the mite is a non-coconut palm. Goolsby *et al*. (2006) identified the haplotype and location of an eriophyid species, *Floracarus perrepae* Knihinicki & Boczek, 2002, which offers the most potential for control of its fern host, *Lygodium microphyllum* (Cav.) R. Br. which became an exotic weed in Florida, USA, by matching the overlapping geographical relationships between the fern and mite haplotypes and match it with the haplotype and origin of the plants which invaded Florida. They determined the mite haplotypes with parsimony and maximum-likelihood analyses of sequence data from the domain 2 gene region (D2) of the 28s rDNA gene and a portion of the mitochondrial CO1 region. Navajas & Fenton (2000) reviewed the used of molecular markers in the study of diversity in acarology, including molecular studies of the Eriophyidae.

A molecular study is currently underway studying the phylogeny of the Eriophyoidea (M. Lekveishvili, *pers. comm*., 2008). See Chapter 4 for more detail about this study.

- <u>Species descriptions, concepts and delimitation</u>

There are uncertainties about the species-level systematics of Eriophyoidea. The description and differentiation of many species in essence rely heavily on the assumption that species of particularly some groups generally tend to be extremely host specific (specific to one host plant species, or sometimes even specific to bio- or ecotypes of one plant species). Very few studies have been undertaken to actually study host specificity and inter- and intra-species variation.

On the one hand, it seems as if some species may have extensive intra-specific variation in some characters, especially when the populations occur on different host plants. For example, significant morphological differences and variation between populations of *Aculus fockeui* (Nalepa & Trouessart, 1891) occurring on different host plants were found, or even between populations collected from the same host species (Boczek *et al*., 1984). This variation included differences in the shape and ornamentation of the prodorsal shield.

On the other hand, only slight morphological differences were found between morphologically very similar *Cecidophyopsis* spp. occurring on *Ribes* spp. (Amrine *et al*., 1994). Only after studying thousands of specimens (J.W. Amrine Jr., *pers. comm*., 1995) could Amrine finally find very slight differences in their very similar dorsal shield patterns, together with mainly slight morphometric differences, to separate and identify the different species morphologically (Amrine *et al*., 1994). Amrine *et al*. (1994) mentioned that this study indicates that with careful biological, morphological and molecular studies we may discover complexes of sibling species occurring on several different host species. Some species complexes may already be lumped under present day species names, for example, among many others, *Calacarus citrifolii* Keifer, 1955 and *Diptacus gigantorhynchus* (Nalepa, 1892).

These occurrences of morphologically similar groups of species are a recurrent theme in Eriophyoidea, including the following studies: When describing *Epitrimerus rumicis*, Farkas (1968a) noted the extraordinary similarity between some *Epitrimerus* spp. These species could practically not be distinguished from each other, at least not morphologically. Published observed differences used to differentiate species were from intra-specific variation between individuals of the same colonies, and errors resulting from faulty measurements. He suggested two explanations. There is a single, polyphagous species occurring on various host species, or there are ecologically distinct, but morphologically identical species living on different kinds of plants. In his opinion, the latter possibility is the more probable. Das & Chakrabarti (1989) mentioned that within some eriophyoid genera, complexes of morphologically very similar species occur on specific host families (closely related host species). Skoracka *et al*. (2002) found discontinuous variation among populations of *Abacarus hystrix* on different hosts during their research on grass-feeding eriophyoid mites. Skoracka (2009) described a cryptic new species from *A. hystrix* populations using molecular studies, careful morphological, including morphometric study, and information about the host specificity of the populations. Huang (2001c) studied eriophyoid mites from the Tengchih area in Taiwan. He found several incidences of intra-specific morphological variation. Some species varied in the shape of their microtubercles (e.g., *Trisetacus taiwanensis* Huang, 2001), some in the shield design (e.g., *Abacarus bambusae* Channabasavanna, 1966), and some in the number of empodial rays in specimens from different localities, or between legs I and II. He commented that in future we may find that the range of morphological features used to delimit a species of eriophyoid mites is too broad, and may overlap in morphologically similar species.

The practice of identifying or even describing new species, based mainly on the host plant and the symptoms and niche thereon, is problematic. It has, for instance, been demonstrated that two or more species of *Trisetacus* exploit the same feeding sites and host species (Smith, 1984). In the present study, the same was found for two *Diptilomiopus* spp. on *Apodytes dimidiata* E. Mey ex Arn. (Appendix M).

- Genera, suprageneric groupings and phylogeny

This aspect is dealt with in Chapter 4.

CHAPTER 2

GENERAL MATERIAL AND METHODS

2.1 INTRODUCTION

Methods used for collecting, preparation, study and eventual description in alpha-taxonomic studies are particularly crucial for the Eriophyoidea, which are microscopically tiny, fragile and delicate, and easily distort during preparation. They are slide-mounted to facilitate morphological study, but type material is lost over time, because permanent slides with specimens cannot be prepared. Therefore, the quality, exactness and comprehensiveness of taxon descriptions are extremely important and can not be stressed enough (De Lillo *et al*., 2010). Morphological descriptions are further complicated because some of the detailed morphology is so minute that it doesn't fall within the resolution range of light microscopy. Knowing and using the correct and most appropriate and technologically advanced techniques and apparatus are crucial in securing the highest integrity and quality of data as is practicably possible. Even the improvement of studying of mites (including Eriophyoidea) over time is closely associated with the development and improvement of apparatus including different kinds of microscopes and microscopic techniques. A basic knowledge of the strengths and weaknesses of each technique and the resulting data are in some regards fundamental to presenting and analyzing systematic data of the Eriophyoidea. Although the current study at first largely concerned the appraisal and study of existing systematic data, it soon became apparent that such a study is essentially incomplete if the material and methods used in obtaining published data are not taken into account as well.

2.2 DATA SOURCES USED FOR THE PRESENT STUDY INCLUDING DISCUSSION THEREOF

2.2.1 <u>Mite specimens included and collection methods</u>

Mite specimens representing a wide variety of eriophyoid taxa from South African indigenous plants were collected particularly for the SEM study (Chapter 3). Collecting efforts were designed to focus on re-collecting described species, and particularly genera described from South Africa. Slide-mounted specimens were prepared when enough material was available, both in the SEM study (Chapter 3), and the phylogenetic study of the Eriophyoidea (Chapter 4). Specimens already collected and slide-mounted before the present study were available to it, and were studied if they were suitable. Preferably, live specimens from freshly collected plant material were used for the SEM study (see "Material and methods" in Chapter 3). Slide-mounted specimens and SEM studies were used for the description of three new *Diptilomiopus* spp. from South Africa (Appendix M). In a few instances, mite material from other countries was also available, for example, a *Trisetacus* sp. collected from pines in France, and these were included in the present study.

Eriophyoid mites require special collection methods. They are frequently excluded from biodiversity surveys, even when other mites are included, because they cannot be collected by general methods, such as beating. Collection methods of Eriophyoidea are reviewed by Amrine & Manson (1996) and De Lillo *et al.* (2010). Plant material of the known host plants of eriophyoid species selected for the study were hand-collected in the field from localities where they were collected before. The material included the structures on or within which the species normally live, which are frequently symptoms caused by their feeding. In many cases, the particular host on which they were collected before was surveyed. It was sometimes necessary to continuously re-sample a particular plant species to find the targeted eriophyoid species, especially when it was a vagrant causing no detectable symptoms. Three or four non-target species were frequently found on the same sampled plant material (Table 3.1). Many of these were undescribed species. After being collected, the plant material was kept as fresh as possible, and brought into the laboratory for further preparation as soon as possible. The collected material was kept fresh by first wrapping it in damp paper towel, and then putting it into a plastic bag. The bags with material were kept in a cooler box at the collection site, and if the material could not be used immediately on arrival at the laboratory, it was stored in a fridge at about 4 °C, usually not longer than a week, until it could be processed (see collecting and SEM processing dates in Table 3.1). In this way mite colonies can be kept alive for a month or longer (De Lillo *et al*., 2010). Field collected plant material was searched for eriophyoid mites *in situ* with the aid of a high end quality dissecting stereo microscope with a cold light source, at magnifications ranging from 20–80x.

Mites were collected from the plant material by hand, using a minuten pin or hair lash mounted on a stick or other appropriate holder (De Lillo *et al*., 2010), with the aid of a stereo microscope. Whenever possible, large samples were collected, trying to include entire colonies with both females and males and all developmental stages.

In my experience even when plant material is searched thoroughly with the aid of a dissecting microscope, some species that are sparsely distributed on the plant material, may be missed. To alleviate this limitation, parts of the infested plant material can additionally be washed with a solution containing bleach and detergent. The mites in the solution can be concentrated by sieving through fine mesh screens or with centrifugation (Monfreda *et al*., 2007). This method could be at least twice as effective and time-saving as *in situ* inspection of plants and their parts (Monfreda *et al*., 2007), and should be seriously considered for biodiversity surveys. Because the specimens in the present study were largely collected for SEM study, and had to be kept as natural and alive as possible, they were not washed from the plant material.

2.2.2 Physical preparation and study of specimens

- Light microscopy

The mites destined for slide-mounting were collected into an isopropanol-sorbitol solution (Keifer, 1975a; De Lillo *et al*., 2010). They were subsequently cleared and mounted in batches of about 100 specimens at a time, using the three media, "F-medium", "HCl-solution" and "Phenol-solution" developed and recipes provided by Keifer (1975a). Specimens were transferred from the collecting liquid into a solution in a depression slide, made up of a droplet of each of the three mentioned media of Keifer (1975a) which are kept in separate holders. The depression slide with solution and mites was briefly heated over an open flame, without boiling the solution, to clear the specimens. After clearing the specimens, and removing them from the heat, the clearing solution was diluted with two to three drops of F-medium to stop the clearing process and render the solution more fluid. The specimens were then mounted in a droplet of "F-medium" on a microscope slide (five specimens per slide), and covered with a cover slip. The slides with mounted specimens were left at room temperature for about two days for the fluid to "settle" and become more viscous. The cover slip was sealed ("ringed") afterwards with Glyptal®, a special moisture resistant paint (Amrine & Manson, 1996). See Keifer (1975a), Amrine & Manson (1996) and De Lillo *et al*. (2010) for alternative methods.

Slide-mounted specimens were studied with a Zeiss Axioskop microscope using phase contrast and Achroplan quality objectives. Drawings of the mites were made with a drawing tube (camera lucida) and the final realistic drawings were not modified to be semi-schematic. Digital images of some specimens studied with the said light research microscope were captured with a Wirsam Olympus CC12 digital camera and the analySIS® LifeScience ©2005 imaging system series by Soft Imaging System GmbH, an Olympus Company (http://www.soft-imaging.net).

- Scanning electron microscopy (SEM) (see Chapter 3)

2.2.3 Data from published descriptions

The goal of the present study was a broad appraisal and therefore published morphological descriptive data were used, rather than studying specimens, particularly for the explorative phylogenetic analyses of the Eriophyoidea (see "Material and methods" of Chapter 4). Published descriptions are the most reliable and available data, because it is almost impossible to obtain specimens, and particularly type specimens, of most taxa described worldwide, primarily because slide-mounted specimens frequently deteriorate over time until they are insufficient for studying (De Lillo *et al*., 2010). For example, Smith (1984), in his study on *Trisetacus* spp. of North America found that much of the type material of the large and important Keifer collection at the USDA in Beltsville, was in poor condition and that detailed study of specimens is difficult and re-illustration impossible. Some slide-mounted material in the South African National Collection of Arachnida–Acari was already badly deteriorated after five years.

Published eriophyoid species descriptions of acceptable standard are largely standardized, and they include morphological descriptive and morphometric data of a comprehensive range of the characters used in eriophyoid taxonomy. Additionally, descriptions should be, and are usually, accompanied by detailed descriptive line drawings. It is thus in theory possible to practice most taxonomy (comparing and identifying species, differentiating new species, and constructing identification keys), and to score a reasonably comprehensive descriptive data base from published descriptions. In taxonomic practice, it is further accepted, and is supported by surveys, that most eriophyoid species, particularly non-vagrants, are host-specific to a plant species, or at least a few closely related species within the same genus, and rarely have an extended host range across more than one plant family. The host plant information thus also aids in general taxonomic practices on these mites.

It is quite common practice, but not always defendable, to study published descriptions of those taxa for which specimens are not readily available, rather than the specimens themselves during taxonomic studies of the Eriophyoidea. This practice is not restricted to the Eriophyoidea; relatively few authors describing mites in general take time to study type material of previously described species (Lindquist, 2001).

The problems with obtaining type specimens of the Eriophyoidea are not an excuse for totally excluding the study of type specimens of described species in all systematic endeavours in this group. In practice, however, it is often unproductive to incorporate type material or try to collect additional specimens of a previously described species before proceeding with the taxonomic study at hand, especially in the light of the huge shortfall in description of extant diversity. With the goal of describing the diversity as soon as possible, the quality of taxonomic studies of eriophyoids, in which study of type material was not included, is reasonable. However, whenever possible the study of specimens should be incorporated, and obviously particularly in cases of uncertainty. Using published descriptive data for the phylogenetic study in the present study was the optimal option, but restricted the character sample, and potentially incorporated many errors in the data sets of which the significance in influencing the results can not be measured.

2.3 DATA FROM SPECIMENS AND PUBLISHED DESCRIPTIONS: CAPTURE AND MANAGEMENT

Data capture formed a significant and problematic part of the present study mostly caused by the bulk of partly inconsistent and unstructured information to be captured for analyses. I attempted to capture descriptive data only once, and subsequently use the structured data set for taxon descriptions, keys (printed dichotomous keys and electronic interactive keys), and monographs and as data for phylogenetic analyses. This attempt was only partly successful (see discussion further on).

2.3.1 Software and protocol used

Descriptive data from published descriptions, and observations of slide-mounted specimens and SEM images were digitally captured and managed with *DeltaAccess*[1] (Hagedorn, 2007a).

DeltaAccess (a relational data base application) is a SQL interface to DELTA (the Description Language for Taxonomy) implemented in *Microsoft® Office Access* operating in *Microsoft® Windows* environment. During this study *DeltaAccess* was upgraded through several versions (Hagedorn, 1999, 2007a), and the final version used for the present study was *DeltaAccess* 1.9 for *Microsoft® Office Access* 2000 and 2002/XP (Hagedorn, 2007a). *DeltaAccess* will be renamed to *DiversityDescriptions* and a new version of *DiversityDescriptions* (= *DeltaAccess* 2.0) is currently being tested. With its release, the information of *DiversityDescriptions* (*DeltaAccess*) (also that at http://www.diversityworkbench.net/OldModels/Descriptions/index.html) will all be moved to Wiki at http://www.diversityworkbench.net/Portal/wiki/DiversityDescriptions (Hagedorn, 2007b). *DiversityDescriptions* will eventually form part of the *Diversity Workbench* –

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Software Components for Building and Accessing Biodiversity Information (Hagedorn, 2010). The advantages of capturing and managing data as structured data are given and discussed by Hagedorn *et al*. (2005).

Among the other positive attributes of relational data bases, *DeltaAccess* (a data base with a standard industry software interface) makes it possible to link data from other sources (such as nomenclatorial, specimen, or literature reference data bases) with DELTA data. It thus makes data in DELTA format accessible to relational data bases, which is not possible with data exclusively in DELTA format. Data in relational data base structures can be imported to or exported from *DeltaAccess*, as well as from or into DELTA coded text files through *DeltaAccess*.

DELTA is a descriptive data exchange format (Dallwitz, 1980; Dallwitz & Paine, 1999) and the basic directives of DELTA are endorsed by the International Taxonomic Database Working Group (TDWG) (TDWG, 2009), a section of the International Union of Biological Sciences (IUBS). DELTA as an international taxonomic data standard is currently being enhanced and extrapolated with the development of the SDD (Structure of Descriptive Data) standard (Hagedorn *et al*., 2005a). DELTA is a standard for formatting descriptive data and not a computer program. It can be used by several major taxonomic software packages (including the DELTA program packages) that can be used to analyze taxonomic data, generate natural language descriptions, or produce printed keys as well as interactive keys. Some of the DELTA software sources on the internet have been listed and hyperlinked by Hagedorn (2005b).

DeltaAccess can be used in several ways, but for this study it was primarily used as the central data repository and management system around which this and future systematic work will be organized. The Access Basic source code of *DeltaAccess* is included with the application and its information model and documentation thereof is available (Hagedorn, 2005a). This aspect was of particular importance to this study, since particularly the numeric (real and discrete) fields had to be modified to accommodate morphometric data in published eriophyoid descriptions, which were frequently not defined and structured statistically. This necessitated additional official definitions (for example "single value, not defined") of a particular numeric entered into the data base that was not provided for in the data base. Additional data extraction queries and reports were also created for the data base as needed.

2.3.2 Problems

The terminology, definition and delimitation of many characters and character states are not standardized in eriophyoid descriptions. I decided not to subjectively standardize and reinterpret the data while capturing it in the descriptive data base, particularly because the type specimens were not studied concurrently, and standardization will be more advantageous when a large data bank of descriptive data has been compiled for comparison. This caused a problem for the exact definition and delimitation of character and character state data base fields, leading to, among other shortcomings, redundant data in the data base. Redundancy was caused by duplication of character state fields, because some descriptive data did not clearly fit into already defined and named character state fields at that stage of capturing the data. Most morphometric data from the descriptions did not fit into statistically defined fields, and this is another weak point of the data base data. The data base is essentially still a working data base and the captured data and character and character state fields need to be redefined and reinterpreted, before it can be exported and used unmodified in other applications, including natural language descriptions, interactive keys, and data sets for phylogenetic analyses.

In classical taxonomy, apart from a core set of characters described for an entire larger group, for example the Eriophyoidea, many characters of the group are only recorded for smaller subgroups in which they are taxonomically applicable. In a comprehensive descriptive data set destined for applications like phylogenetic analyses and interactive keys, all systematically informative characters used in the larger group must be scored for all species in it.

In theory it is already possible to structure and enter descriptive data only once and use data exported from this single data base, with minimal modification, in other applications, and this was the goal in the present study. Standards for structuring descriptive data (TDWG, 2009), and programs for using such structured data (see for example Hagedorn, 2005b) are available. In practice, though, such holistic integration between currently available software programs is not fully functional at all levels yet, to my experience. There is also not one total user friendly software package available for capturing and managing structured descriptive data at the functionality possible in *DeltaAccess*, as well as application modules for utilizing the data in all systematic applications, including the export of data matrices for phylogenetic analyses. Some software companies, however, for instance the Centre for Biological Information Technology (CBIT) developing the Lucid programs (CBIT, 2010a), are progressing towards developing more comprehensive software packages for managing and using descriptive data. In the present study descriptive data in *DeltaAccess* exported to DELTA formatted text documents, could not be utilized directly (without modification) in developing an interactive key (CBIT, 2010b) in Lucid v3.3 (CBIT, 2010c), although this Lucid version was reportedly able to use data in DELTA format. The developers of Lucid attempted to import the data, and worked on the problem, but could not solve the importation totally, and most of the data will probably have to be recaptured in Lucid. This is unnecessary duplication of effort, and hopefully capturing and utilizing descriptive data will become more integrated and functional in future.

2.3.3 Data captured in *DeltaAccess*

The character definition consists of 462 characters with a total of more than 2 000 character states (including numeric fields). The maximum number of states for a single character is 82. The descriptive data of 317 species (items) were captured. The characters include text, ordered and unordered discrete multistate and discrete and real numeric data.

2.4 PHYLOGENETIC STUDIES (SEE CHAPTER 4)

The taxon and character samples and construction and management of the data matrices for the phylogenetic studies, and the protocols and programs used for phylogenetic parsimony analyses are given and discussed in the “Material and methods” section of Chapter 4.

2.5 DISCUSSION

The electronic capturing and structuring of descriptive data of eriophyoid taxa and eventual use of the data for generating natural descriptions, developing identification keys and spawning data matrices for phylogenetic studies were only partly successful, and required intensive and time consuming set up time. The problems and eventual inability to capture the descriptive data once and use it with minimal modification for other applications, were partly caused by problems with integration between available software, but also by the inadequacies of the published descriptive data of eriophyoid mites, of which the most important were incomplete descriptions, lack of detail, precision and standardization, and sometimes pure mistakes. Despite these problems, I am still convinced that enough progress was made with compiling, structuring and managing descriptive data and identifying weak points in the description and taxonomy of eriophyoid mites to pursue these methods further. It is important in systematic studies to continuously search for better and more holistic electronic procedures for capturing and utilizing data, because one of the major requirements of systematics is to gather and manage descriptive data of taxa which will also be used as primary homologies for phylogenetic studies. In the Eriophyoidea it is of particular importance, because of numerous new taxa being described. The most pressing immediate need, however, is to standardize and improve the descriptions of the Eriophyoidea (also see Appendix L – article of De Lillo *et al*., 2010). Close cooperation and a team effort from all scientists with a good knowledge of the group currently actively describing new eriophyoid taxa will enhance their quality and accuracy.