


Vegetation survey of the Khomas Hochland in central-western Namibia: syntaxonomical descriptions

Authors

¹Prof. Ben Strohbach 

Affiliations

¹Biodiversity Research Centre,
Namibia University of Science
and Technology, Private Bag
13388, Windhoek, Namibia.

Corresponding Author

Prof. Ben Strohbach, e-mail:
bstrohbach@nust.na

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Background: The Great Escarpment of southern Africa takes the form of an extended mountainous highland in central-western Namibia, commonly referred to as the 'Khomas Hochland'. It is regarded as an area of high botanical diversity. Yet only few localised studies on the vegetation composition are available. The Khomas Hochland is formed on the southern part of the Damara Orogen and dominated by metamorphosed sediments. Climatically it forms a transition between the hot desert of the Namib and the slightly cooler hot steppe in the inland.

Objectives: To classify and provide syntaxonomical descriptions of the vegetation of the Khomas Hochland.

Methods: A dataset comprising 1151 relevés and 914 species was compiled from various surveys, mostly collected under, and to the standards of, the umbrella project 'Vegetation Survey of Namibia'. For first classifications, the data set was reduced to a synusial set consisting of trees, shrubs, dwarf shrubs and grasses only.

Results: The classification resulted in four major landscape units, being the Pre-Namib and Escarpment zone, the Khomas Hochland proper, riverine habitats as well as surrounding lowlands. The classification was further refined using Cocktail procedures to produce 30 associations, one with four sub-associations. These are described in this paper.

Conclusion: A classification of synoptic data grouped the associations into five orders and one undefined cluster of associations on specialised desert habitats. Four of these orders correspond to the habitat types identified in the first classification. The fifth order, the *Senegalia hereroensis*–*Tarchonanthoetalia camphorathi*, represents high mountains of the central Khomas Hochland, which link biogeographically to the grassland biome in South Africa.

Keywords: Damara Orogen; Great Escarpment; highland savanna; modified TWINSPAN; Namib; phytosociology.

Introduction

The Great Escarpment is a \pm 5000 km long geomorphological feature along the rim of the southern African subcontinent. It is regarded as a zone of high biological diversity, containing numerous Centres of Endemism (Clark et al. 2011). Whereas most of the Great Escarpment forms a narrow divide between the coastal lowlands and the inland plateaux, in central Namibia the Damara Orogen created a mountainous landscape nearly 200 km wide from west to east. This mountainous landscape is commonly referred to as the Khomas Hochland (or Khomas highlands) (Schneider 2004; Swart & Marais 2009; Goudie & Viles

2014). Giess (1998) broadly describes the vegetation as 'highland savanna', without providing any details on composition or diversity.

Although the Khomas Hochland has been identified as an area of high botanical diversity (Hofmeyr 2004; Craven & Vorster 2006), only a few localised descriptions of the vegetation of this landscape exists. Of note here are a study by Volk and Leippert (1971) on a few farms southeast of Windhoek, using data from the 1950s and 1960s; an unpublished study by Kellner (1986) focusing on the Daan Viljoen Game Reserve west of Windhoek as well as portions of two farms southwest and east of Windhoek; a preliminary description of the vegetation of the Auas Mountain Range south of Windhoek (Burke & Wittneben 2007); as well as an account of the vegetation of the Auas-Oanob Conservancy southwest of Windhoek (Strohbach 2017). None of these studies provide a comprehensive overview of the entire landscape. In contrast, a fairly comprehensive description of the adjacent central Namib desert is available (Jürgens et al. 2013).

The Vegetation Survey of Namibia project has been initiated to fill this, and similar data gaps, at a national level (Burke & Strohbach 2000; Strohbach 2001). The project is aimed at providing data about the resource 'natural vegetation' to allow for sustainable planning and management of this renewable resource (Strohbach 2018). Due to the sheer size of the country, however, a strong emphasis is placed on utilising existing reliable data sources in addition to collecting, over a number of

seasons, additional, gap-filling data. At the same time, due to the lack of necessary data density for a detailed study, the result will be at a regional overview level (often referred to as 'reconnaissance level') (Küchler & Zonneveld 1988; Strohbach 2001). This paper aims to contribute a first formal classification and description at this level of the vegetation found in the Khomas Hochland in central-western Namibia.

Methods

Study area

The study area is a block of roughly 31 000 km² in central western Namibia, between the coastal Namib desert lowlands and the inland plateaux (Figure 1). It stretches from the border of the Namib-Naukluft Park in the west to about 17° 30'E, and from the B6 trunk road between Okahandja and Karibib in the north to about the Gaub Valley in the south. Administratively, it covers the western half of the Khomas Region, but also reaches into the Erongo and Otjozondjupa regions of Namibia.

The Khomas Hochland had its origin some 900 Ma ago as a sea between two tectonic plates, the Kalahari- and Congo cratons. Sediments deposited in this sea solidified and were metamorphised during the formation of the Gondwana supercontinent \pm 650 to 450 Ma ago. At that stage, uplift also happened, resulting in the Damara Orogen (Schneider 2004; Swart & Marais

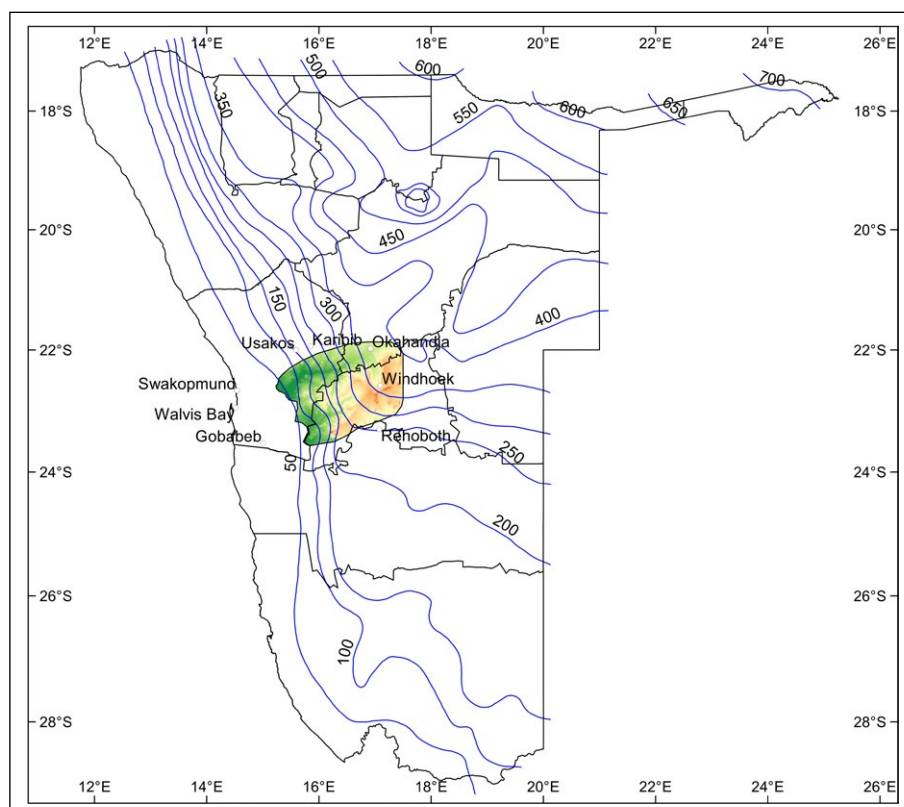


Figure 1. The study area in western central Namibia. Mean Annual Rainfall is indicated as blue isohyets. Data source: NARIS (2001).

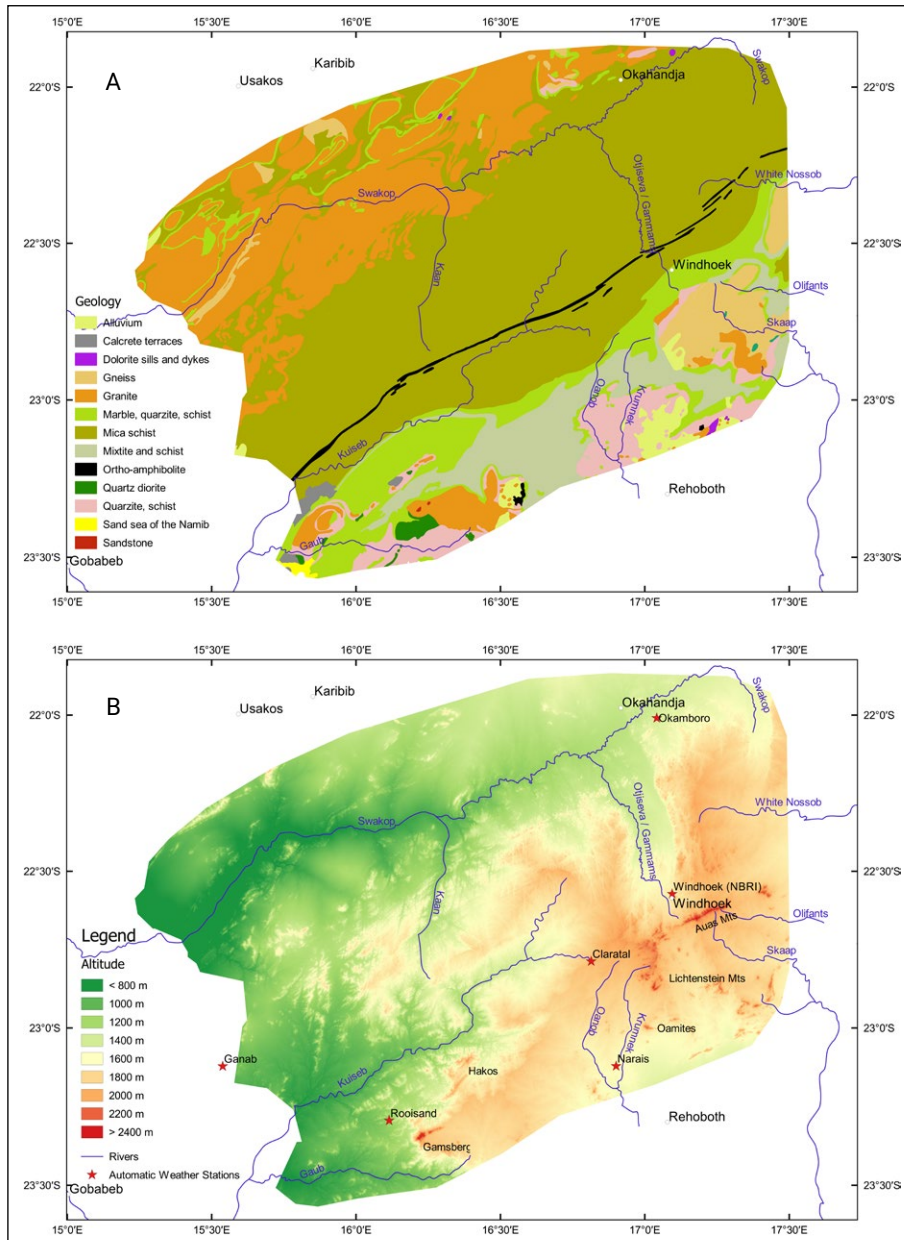


Figure 2. A, Simplified geological map of the study area, indicating the major lithological substrates; B, Topography of the study area, indicating several landmarks and major rivers draining the Khomas Hochland. Data sources: Geological map adapted from Namibia Geological Map (Geological Survey 1980); topography derived from SRTM image (Jarvis et al. 2008).

2009). The main body of the Khomas Hochland consists of mica schists of the Kuiseb and schists and mixtites of the Chuos Formation (Figure 2A). The mica schists of the Kuiseb Formation are dissected by a narrow band of ortho-amphibolites of the Matchless Member. The southern rim is formed by hardened quartzites of the Auas Formation, before merging with older rocks (granites and metamorphites of the Rehoboth Sequence) of the Kalahari Craton. To the north of the Kuiseb formation, intrusive granites resulted also in the formation of several marble ridges (Figure 2A) (Geological Survey 1980; South African Committee for Stratigraphy 1980; Schneider 2004).

The escarpment of the Khomas Hochland raises from the Namib desert plains at about 900 m above sea level (asl) to well over 1 400 m asl. The central Khomas Hochland forms a deeply dissected, steep mountainous

highland, raising to over 2 000 m asl in places (Figure 2B) (Swart & Marais 2009). This is only topped by the mountain ranges Auas, Lichtenstein, Hakos and Gamsberg, which reach altitudes of over 2 400 m asl (Schalk 1983; Swart & Marais 2009). The study area is drained through a dense system of ephemeral rivers, forming tributaries to the Swakop and Kuiseb rivers to the west, Oanaob and Skaap rivers to the southeast, and White Nossob as well as Olifants rivers to the east (Figure 2b) (Strohbach 2008).

The climate can be described as a hot desert in the western half to a hot steppe in the eastern half, following Köppen (1936). The mean annual precipitation (MAP) ranges from ± 50 mm in the west to about 350 mm in the east (Figures 1 and 3), with a high degree of variation between seasons. Along the western edge of the study area, the coefficient of variation (CV)

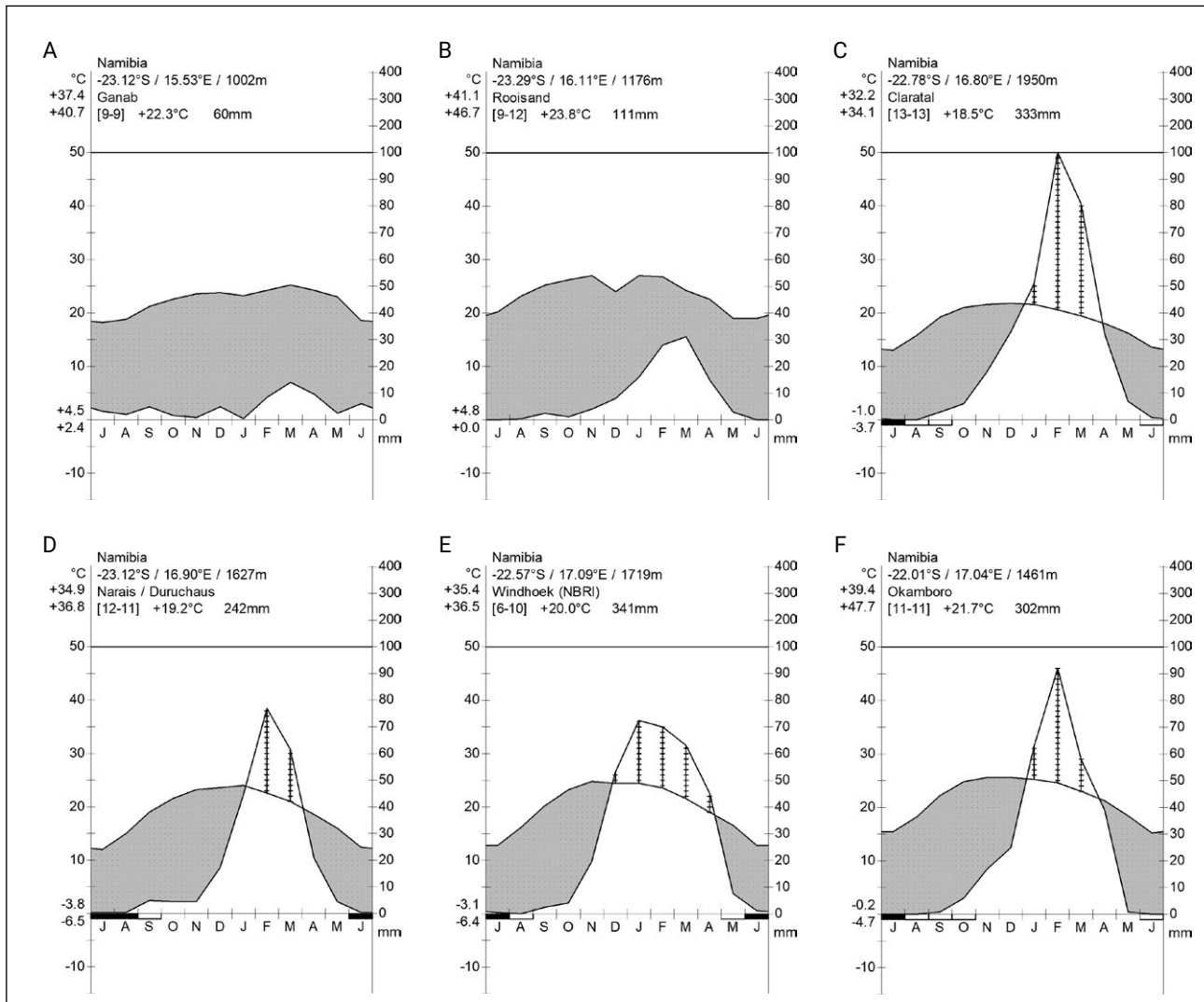


Figure 3. Climate diagrams after Walter et al. (1975) of available automatic weather stations within the study area: Ganab, Rooisand, Claratal, Narais, Windhoek (NBRI) and Okamboro. Data sources: SASSCAL (2020) and BIOTA AFRICA (2009).

of MAP is as high as 90%, in the east around Windhoek the CV of MAP is about 40% (Mendelsohn et al. 2002). The orographic effect of the escarpment and high mountains in the study area are not known. The desert margins below the escarpment become relatively hot, with maximum temperatures measured well over 40°C. Frost is also rare or absent here. In contrast, the central highlands are cooler, with maximum temperatures around 36°C. Frost regularly occurs in the highlands in the winter months between May and August, at places as late as October (Figure 3).

Data sources

A data set of 1 151 relevés with 914 species was selected from the phytosociological database of Namibia (GVID ID AF-NA-001) (Strohbach & Kangombe 2012). Details of the selected data subsets are listed in Table 1.

The quality of the rainy season, which has an influence on the growth of the vegetation, was derived according

to the criteria of Botha (1998). Normal years had an annual precipitation of between the 40th and 70th percentile of long-term precipitation records, whilst extreme years had below the 10th (extreme dry) or above the 90th percentile (extreme wet) annual precipitation.

Data collected by Kellner (1986) was captured from tables in his thesis as the original relevé data (field sheets) were no longer available. These relevés were also collected from 25 × 25 m (i.e. 625 m²) plots. No accurate position data, nor habitat data, are available for these relevés. Data collected by Burke, Wittneben and Mannheimer (Auas Mountains and Windhoek Townlands) were in the form of species lists on specific sites rather than regular survey plots. Position data are available in most cases, but the habitat data are incomplete. These data were however included, as the sites were limited to specific habitats and limited in sizes (no longer than 100 m, no wider than 10 m), i.e. comparable to regular survey sites used for the Vegetation Survey of Namibia project. Especially the data by Burke and Wittneben

Table 1. Overview of data used for this study. All data form part of GVID ID AF-NA-001 (Strohbach & Kangombe 2012)

Relevés	Dataset name	Number	Year	Season quality	Surveyor	Area of interest	Reference (if any)
937–1165	BS_Auas-Oanob	229	2000 & 2002	Extreme wet Normal	B. Strohbach	Auas-Oanob Conservancy	(Strohbach 2017)
1833–2180	Khomas_2004	204	2004	Normal	B. Strohbach	Khomas Hochland (Kuseb valley)	
2212–2258	Khomas_2005	124	2005	Dry	B. Strohbach	Khomas Hochland (Kuseb valley)	
2797–2977	Kellner_1985	181	1985	Normal	K. Kellner	Daan Viljoen, Claratal, Bergvlyg	(Kellner 1986)
5798–5854 and 5900–5914 and 5980–5987	Zuna_2005	80 of 204	2005	Dry	Z. September	Biota transect Aris to Witvlei (limited to 17°30' East)	
7114–7140	BS-SK_Khomas_2007	27	2007	Normal	B. Strohbach & S. Kruger	Windhoek area	
9438–9564	BS_Khomas_2009	127	2009	Wet	B. Strohbach	Northern and western Khomas	
9565–9598	Auas_W+B_2004	34	2004	Normal	A. Burke & M. Wittneben	Auas Mountain Range	(Burke & Wittneben 2007; Strohbach 2017)
10192–10221	CM_Windhoek-townlands	30	2009	Wet	C. Mannheimer	Windhoek Townlands	
10612–10632	BS_Narais_2011	21	2011	Wet	B. Strohbach	Narais observatory	BIOTA observatory (Jürgens et al. 2010)
11475–11540	BS_Midgard-2014	66	2014	Extreme wet	B. Strohbach	Midgard Country Estate (south)	
70001–70028	Ovitoto_2001	28	2001	Normal	T. Sheuyange	Ovitoto Observatory	BIOTA observatory (Jürgens et al. 2010)

(2007) covered extreme, inaccessible habitats, making the data invaluable for the completeness of this study.

All other surveys followed the guidelines of the Vegetation Survey of Namibia project, i.e. were surveyed on a 20 × 50 m (1 000 m²) plot, whilst plot layout was restricted to a specific habitat. In cases where the nature of the habitat did not allow a 20 m × 50 m sized plot (e.g. riverine habitats, rock outcrops), the plot shape was adapted to fit the habitat, without reducing the size, nor moving into a different habitat. The size of 20 × 50 m was chosen as suitable for an arid savanna and conforms to size criteria proposed by Brown et al. (2013). For these relevés, the position as determined by GPS, as well as habitat descriptors related to landscape, topography, lithology and stone cover have been noted.

Unknown species were collected for identification in the National Herbarium of Namibia (WIND). Species' nomenclature follows Klaassen and Kwembeya (2013), with the exception of the genus *Acacia s.l.*, for which Kyalangalilwa et al. (2013) was followed.

Classification procedures

An initial classification was done using modified TWINSPAN (Roleček et al. 2009), with average Sørensen as distance measure, and utilising pseudospecies cut levels at 0 and 5% cover to differentiate between low-cover desert margin vegetation and inland vegetation at higher cover values. This classification was based on synusial data (i.e. trees, shrubs, dwarf shrubs and grasses

only) (Gillet & Julve 2018), and resulted in three clusters. These clusters were interpreted as representing the Pre-Namib and Escarpment zone, the central Khomas Hochland as well as a third group comprising riverine habitats and lowlands surrounding the Khomas Hochland. This classification result was used to split the data set into three subsets for further analysis.

The three clusters were further classified using the modified TWINSPAN classification algorithm, always using average Sørensen as distance measure, and utilising pseudospecies. For the Pre-Namib/Escarpment zone cluster, these were kept at 0 and 5%; for the other clusters cut levels were set at 0 and 10%. This difference in pseudospecies cut levels was necessary because the Pre-Namib has an inherent lower vegetation cover than the inland vegetation. In the case of Cluster 3 (riverine and lowland habitats), the data set was again split into two subsets after an initial classification using synusial data. The level of splitting was determined using peaks in crispness values (Botta-Dukát et al. 2005).

The classification of the clusters using synusial data was transferred to the full data set. Analysis of the resulting clusters revealed partial mixing of relevés between associations, or in several cases, known units to be included in other associations. This prompted a refinement of the classification results using Cocktail procedures (Bruehlheide & Flintrip 1994; Bruehlheide 1997), based on existing descriptions (e.g. Kellner 1986; Strohsbach 2017), or on field observations. A detailed account of these Cocktail refinements is presented in the Results section of this paper.

Once an ecologically interpretable result was achieved, phytosociological tables were compiled and the synopsis for various associations extracted. Diagnostic species were determined using the phi coefficient of association (Chytrý et al. 2002). For this calculation the numbers of relevés were standardised following Tichý and Chytrý (2006). Species with $\phi \geq 40$ were considered as diagnostic and with $\phi \geq 60$ as highly diagnostic; however, species with a non-significant fidelity at $\alpha = 0.05$ using Fisher's exact test were omitted. Species occurring with at least a 60% frequency were regarded as constant and with at least an 80% frequency as highly constant.

Further descriptors of the associations

The average structure for each grouping (i.e. average tree, shrub, dwarf shrub, perennial grass, annual grass and herb cover) was calculated using the available growth form data. Descriptions follow Edwards (1983). For the species density (number of species per 1 000 m²), the relevé data from Kellner (1986) were excluded, as these were sampled on 625 m² plots (25 × 25 m), not 1 000 m² plots as for all other relevés. In addition, an estimate of potential species richness for

the association has been calculated with a first order Jackknife as proposed by Heltshel and Forrester (1983) as well as Palmer (1990).

Higher syntaxonomy

Due to the extensive refining of clusters with Cocktail, partially resulting in splitting of clusters or the definition of new clusters, the initial classification dendrograms could not be used as an indication of higher-order syntaxonomy as is customary (e.g. Luther-Mosebach et al. 2012). Instead, synoptic tables of the associations were prepared using percentage frequency for all four classifications. The synopsis of each association was taken as a pseudo-relevé, and these were combined into a single data set for classification with modified TWINSPAN (Roleček et al. 2009). No pseudospecies were used for this classification. This approach follows broadly the approach used by Winterbach et al. (2000).

Results

First classification results and Cocktail refinements

The first classification resulted in three major vegetation zones, namely the Pre-Namib and Escarpment zone, the Khomas Hochland proper and the riverine habitats and lowlands vegetation surrounding the Khomas Hochland. The latter was further subdivided into two subsets for further classification. Cocktail refinements were necessary on all four clusters. Details of these refinements are provided in Table 2.

Pre-Namib and Escarpment zone

The vegetation of the Pre-Namib (*Vornamib sensu* Giess (1962, 1998) and Escarpment zone is dominated by the plant families Poaceae, Fabaceae, Bignoniaceae and Burseraceae, in descending order of importance. The classification resulted in seven associations, which are formally described according to the International Code of Phytosociological Nomenclature (Weber et al. 2000). The synoptic table for these is presented in Appendix 1, and the phytosociological table in Appendix 2, available online only (DOI: XXXXXX, DOI: XXXXXX).

Within the synopsis, basic statistics on the association (or other syntaxa) are given, as derived from the analysis of clusters in Juice. Highly diagnostic species (with phi coefficient >60) and highly constant species (occurring in more than 80% of relevés) are indicated in **bold**. All structural descriptions follow Edwards (1983). Landscape descriptors follow conventions of the Digital

Table 2. Refinements necessary to the classification results for improved ecological interpretability

Unit changed	Selection based on following criteria	Relevés involved	Based on
Cluster 1: Pre-Namib and Escarpment zone:			
This data cluster consisted of 279 relevés and 329 species. The synusial data had only 121 species. Classification of this subset resulted in five clusters, which were refined as follows:			
Karpfenkliffs (Association 1.1)	<i>Adenolobus pechuelii</i> , <i>Enneapogon desvauxii</i> , <i>Fagonia isotricha</i>	8 relevés from Cluster 1	Field observations
Rostock sand drift plains (Association 1.3)	<i>Crotalaria podocarpa</i> , <i>Sesuvium sesuvioides</i> , <i>Crinum macowani</i> , <i>Kohautia caespitosa</i> , <i>Stipagrostis obtusa</i> , <i>Grielum sinuatum</i>	7 relevés from Cluster 1	Field observations
Gravel plains of Pre-Namib (Association 1.2)		Remainder of Cluster 1	
Cluster 2: Khomas Hochland proper:			
This data cluster consisted of 350 relevés with 588 species. The synusial data set had only 198 species. Classification of this subset resulted in five clusters. Refinements were done as follows:			
Steep cliff faces (Association 2.2)	<i>Ficus ilicina</i> , <i>Pennisetum foermeranum</i> , <i>Steganothaenia araliacea</i> . A minimum of two of these species had to be present	5 relevés from Cluster 4 (rock outcrops)	Kellner 1986
Cluster 3 <i>sensu lato</i>	<i>Osyris lanceolata</i> , <i>Hypoestes forskoolii</i> , <i>Danthoniopsis ramosa</i>	13 relevés from Cluster 5	Strohbach 2017
High altitude mountain veld of the south-facing slopes (Association 2.3)	<i>Jamesbrittenia pallida</i> , <i>Selago alopecurooides</i> , <i>Frankenia pomonensis</i> , <i>Eriocephalus dinteri</i>	Split from Cluster 3 (8 relevés)	Strohbach 2017
High altitude mountain veld of the north-facing slopes (Association 2.4)	<i>Selago angustibractea</i> , <i>Lopholaena cneorifolia</i> , <i>Cheilanthes multifida</i> , <i>Babiana hypogaea</i> , <i>Eriocephalus scariosus</i> and <i>Adromischus</i> species	Split from Cluster 3 (8 relevés)	Strohbach 2017
Mid-altitude mountain veld (Association 2.5)		Remainder of Cluster 3	
Oamites mountain veld (Association 2.7)	<i>Ornithoglossum calcicola</i> and <i>Melhania damarana</i>	Split from Cluster 5 (9 relevés)	Strohbach 2017
Khomas Hochland mountain veld (Association 2.8)		Remainder of Cluster 5	
Cluster 3: Riverine habitats:			
This data cluster consisted of 59 relevés and 304 species. The synusial data contained only 114 species. Classification of this subset resulted in eight clusters. Due to high intrinsic variation however, not all associations were ecological interpretable, and extensive refinement, including partial recombination of relevés into associations was necessary.			
Dry riverbeds (Association 3.2)		Recombined clusters 2, 3 and 4 as one	
Cluster 5 <i>sensu lato</i>	High abundance of <i>Stipagrostis namaquensis</i>	Split into two	
Riverine sand banks (Association 3.3)	High abundance of <i>Stipagrostis namaquensis</i>	Cluster 5A (3 relevés), as well as 1 relevé from Cluster 7 and 1 relevé from Cluster 8	Strohbach 2017
Inland riparian woodlands (Association 3.5)	High abundance of <i>Vachellia karroo</i>	Clusters 5B and 6, as well as several relevés from the surrounding lowlands (Cluster 4, mostly relevés sampled by Kellner (1986)) found to fit into this group. These were manually moved here.	Strohbach 2017; Kellner 1986

Table 2. Refinements necessary to the classification results for improved ecological interpretability (continued)

Unit changed	Selection based on following criteria	Relevés involved	Based on
Cluster 3: Riverine habitats (continued)			
Omirimbi vegetation (Association 3.4)	Manual selection according to habitat description, verified with Cocktail based on <i>Tragus berteronianus</i> , <i>Schmidtia pappophoroides</i> , <i>Themeda triandra</i> , <i>Talinum cafferum</i> , <i>Platycarphella carlinoides</i> , <i>Monsonia angustifolia</i> , <i>Microchloa caffra</i> , <i>Chloris virgata</i>	Remainder of clusters 5 and 6, but weakly defined	Volk & Leippert 1971; Strohbach 2017
Riparian woodlands of the westerly rivers (Association 3.6)	<i>Tamarix usneoides</i> , <i>Salvadora persica</i> , <i>Euclea pseudebenus</i> , <i>Stipagrostis hochstetteriana</i> and <i>Faidherbia albida</i>	Cluster 7 (remainder) and 1 relevé from Cluster 6	Field observations
Big inland rivers (Association 3.8) and Omeya plains vegetation (Association 4.7)	Geographical location and habitat	Several relevés grouped into Cluster 8 (big inland rivers) were found to belong to the Omeya plains according to their location. These were manually moved to the data subset of Cluster 4, Association 4.7	
Cluster 4: Lowlands surrounding the Khomas Hochland:			
This data cluster consisted of 462 relevés and 688 species. The synusial data set contained only 227 species. Classification of this data set resulted in ten clusters. On closer inspection, these were found to be fairly mixed due to the synusial data reduction, requiring extensive refinement through Cocktail procedures as follows:			
Oanob Plateau (Association 4.2)	<i>Panicum lanipes</i> , <i>Plinthus sericeus</i> , <i>Pteronia eenii</i> , <i>Pentzia incana</i> and <i>Blepharis integrifolia</i>	Clusters 2 and 3	Strohbach 2017
Cluster 3 <i>sensu lato</i> (weakly defined)		Remainder of clusters 2 and 3	
Gölschau plains (Association 4.3)	<i>Aptosimum spinescens</i> , <i>Eriocephalus ericoides</i> , <i>Geigeria pectidea</i> and <i>Galenia africana</i>	From Cluster 3 <i>sensu lato</i>	Field observations
Southern Khomas (Association 4.4)	<i>Aizoon schellenbergii</i> , <i>Panicum arbusculum</i> , <i>Hibiscus discophorus</i> , <i>Kohautia cynanchica</i> and <i>Aptosimum albomarginatum</i>	From Cluster 3 <i>sensu lato</i>	Strohbach 2017
Degraded/bush encroached vegetation of the Khomas Hochland (Sub-association 4.8.1)		Remainder of Cluster 3 <i>sensu lato</i> , combined with Cluster 9	Strohbach 2017
Khomas Hochland lowlands (Association 4.6)	<i>Senegalia erubescens</i> , <i>Combretum apiculatum</i> , <i>Grewia flavescens</i> and <i>Dichrostachys cinerea</i> (minimum of two species, with high abundance of <i>Senegalia erubescens</i>)	Cluster 5, with extra relevés from Cluster 10	Field observations
Khomas Hochland lowlands (Sub-association 4.8.1)	<i>Vachellia reficiens</i> at high abundance	Remainder of Cluster 10, excluding clusters 8 and 9	Field observations
Khomas Hochland lowlands (Association 4.8)		The recombined Clusters 7 and 10, as well as the original Clusters 8 and 9 were recognised as sub-associations of association 4.8.	

Soil and Terrain Database (SOTER) of FAO (FAO 1993). Specifically, the following slope classes apply:

- Flat: 0–1° / 0–2%
- Gently undulating: 1–3° / 2–5%
- Undulating: 3–6° / 5–10%
- Rolling: 6–9° / 10–15%
- Moderately steep: 9–17° / 15–30%
- Steep: 17–30° / 30–60%
- Very steep: >30° / >60%

This format is also followed for all further descriptions in this paper.

1.1 *Enneapogono desvauxii*– *Adenoloboetum pechuelii* ass. nov.

Synopsis:

Number of relevés: 8
Type relevé: 2065 (holotype), sampled on 15 March 2005 at 23°28'01"S, 16°05'22"E
Number of species observed: 27
Estimated number of species: 46
Average species density per 1 000 m²: 14

Diagnostic species: *Adenolobus pechuelii*, *Fagonia isotricha* var. *isotricha*, *Enneapogon desvauxii*, *Indigofera auricoma*

Constant species: *Euphorbia glanduligera*, *Eragrostis nindensis*, *Stipagrostis hirtigluma*, *Tribulus zeyheri*

These low desert herblands (Figures 4A and 5B) are dominated by *Eragrostis nindensis* and *Enneapogon desvauxii*. This association occurs on old eroded fluvial deposits commonly referred to as 'Karpfenkliff Conglomerate' (Ward 1987) along the upper reaches of the Kuiseb and Gaub canyons, with altitudinal ranges between 800 and 1 100 m asl. The substrate consists of carbonate-cemented conglomerates, which are between 40 and 60 m deep. The erosion of these conglomerates results in a steeply dissected hill landscape. Low rainfall (between 100 and 150 mm Mean Annual Precipitation – MAP), high runoff and a compact substrate allowing little infiltration result in this depauperated form (diversity- and cover-wise) of the *Enneapogono desvauxii*–*Eragrostietum nindensis*. Because of its unique habitat, it is recognised as an association.

1.2 *Enneapogono desvauxii*– *Eragrostietum nindensis* ass. nov.

Synopsis:

Number of relevés: 82
Type relevé: 9439 (holotype), sampled on 10 March 2009 at 22°54'06"S, 16°37'36"E
Number of species observed: 64
Estimated number of species: 111
Average species density per 1 000 m²: 16

Diagnostic species: *Enneapogon desvauxii*

Constant species: *Eragrostis nindensis*, *Tribulus zeyheri*, *Euphorbia glanduligera*, *Stipagrostis ciliata*, *Stipagrostis hirtigluma*

These low desert grasslands (sometimes rather desert shrublands) are dominated by *Eragrostis nindensis* and various other grass, herb and dwarfshrub species (Figures 4B and 5B). This association occurs on the expansive calcrete gravel plains of the Pre-Namib and has been described by Jürgens et al. (2013) as 'eastern calcrete plains grasslands'. The altitude ranges between 780 and 1 300 m asl, and the landscape is generally flat. MAP ranges between 50 and 150 mm, but because of the reduced run-off and looser substrate, this association is far more species rich compared to the *Enneapogono desvauxii*–*Adenoloboetum pechuelii* (depending on the quality of the rainfall season).

1.3 *Crotalario podocarpae*– *Stipagrostioetum obtusae* ass. nov.

Synopsis:

Number of relevés: 7
Type relevé: 1997 (holotype), sampled on 19 February 2004 at 23°20'49"S, 15°56'58"E
Number of species observed: 23
Estimated number of species: 34
Average species density per 1 000 m²: 11

Diagnostic species: *Crotalaria podocarpa*, *Stipagrostis obtusa*, *Sesuvium sesuvioides*, *Grielum sinuatum*, *Crinum macowanii*, *Kohautia caespitosa* subsp. *brachyloba*, *Limeum myosotis*, *Stipagrostis ciliata*

These short open grasslands are dominated by *Stipagrostis ciliata* and *Stipagrostis obtusa* (Figures 4C and 5C), occurring on sand drift plains in the Pre-Namib. Striking examples are found along the western end of the C26 main road before joining the C14. The topography is an undulating sand drift plain, ranging between 1 050 and 1 100 m asl. This area receives between 50 and 100 mm MAP.

1.4 *Tribulocarpo dimorphantho*– *Vachellietum eriolobae* ass. nov.

Synopsis:

Number of relevés: 4
Type relevé: 2013 (holotype), sampled on 20 February 2004 at 23°15'57"S, 16°07'28"E
Number of species observed: 22
Estimated number of species: 26
Average species density per 1 000 m²: 15

Diagnostic species: *Xenostegia tridentata* subsp. *angustifolia*, *Requienia sphaerosperma*, *Harpagophytum*

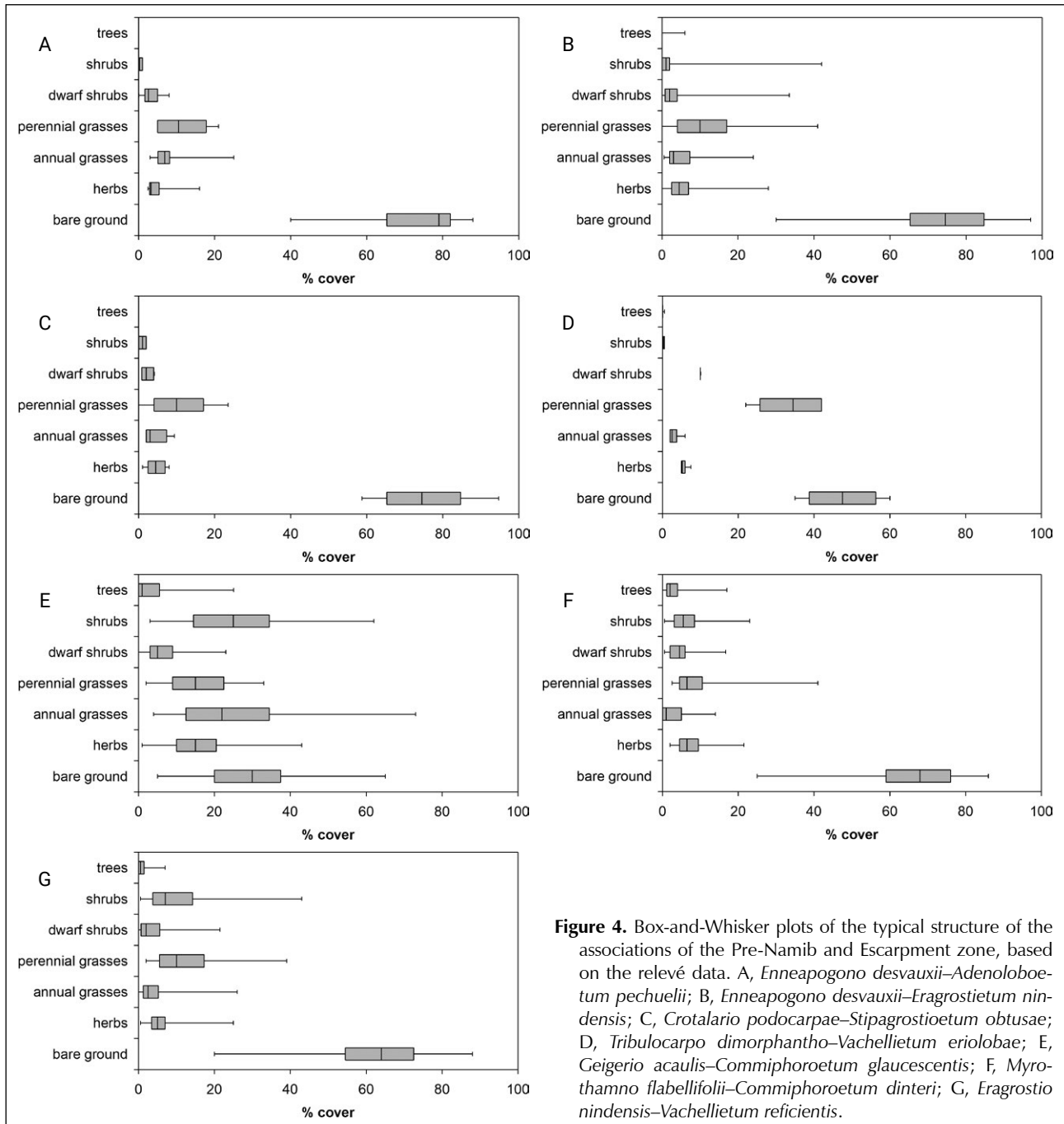


Figure 4. Box-and-Whisker plots of the typical structure of the associations of the Pre-Namib and Escarpment zone, based on the relevé data. A, *Enneapogono desvauxii*–*Adenoloboeum pechuelii*; B, *Enneapogono desvauxii*–*Eragrostietum nindensis*; C, *Crotalaria podocarpae*–*Stipagrostioetum obtusae*; D, *Tribulocarpus dimorphanthus*–*Vachellietum erioloabae*; E, *Geigerio acaulis*–*Commiphoroetum glaucescentis*; F, *Myrothamno flabellifolii*–*Commiphoroetum dinteri*; G, *Eragrostio nindensis*–*Vachellietum reficientis*.

procumbens, *Hermannia guerkeana*, *Oxygonum alatum*, *Tribulocarpus dimorphanthus*, *Brachiaria glomerata*, *Ipomoea magnusiana*, *Vachellia erioloaba*, *Gisekia africana*, *Centropodia glauca*, *Stipagrostis hochstetteriana*, *Dicoma capensis*, *Stipagrostis ciliata*, *Heliotropium nelsonii*

Constant species: *Stipagrostis uniplumis* var. *uniplumis*

This short desert woodland is dominated by *Stipagrostis uniplumis* var. *uniplumis* and *Stipagrostis ciliata* with a scattered cover of *Vachellia erioloaba* trees (Figures 4D and 5D). It is situated further inland from the *Crotalaria podocarpae*–*Stipagrostioetum obtusae* in the valleys below the escarpment at an altitudinal range of

between 1 200 and 1 250 m. The substrate is aeolian Kalahari sands, thus supporting typical Kalahari elements like *Vachellia erioloaba*, *Brachiaria glomerata*, *Requienia sphaerosperma* and *Harpagophytum procumbens*. MAP ranges between 100 and 150 mm.

1.5 *Geigerio acaulis*–*Commiphoroetum glaucescentis* ass. nov.

Synopsis:

Number of relevés: 59

Type relevé: 9467 (holotype), sampled on 12 March 2009 at 22°21'16"S, 15°49'55"E

Number of species observed: 165

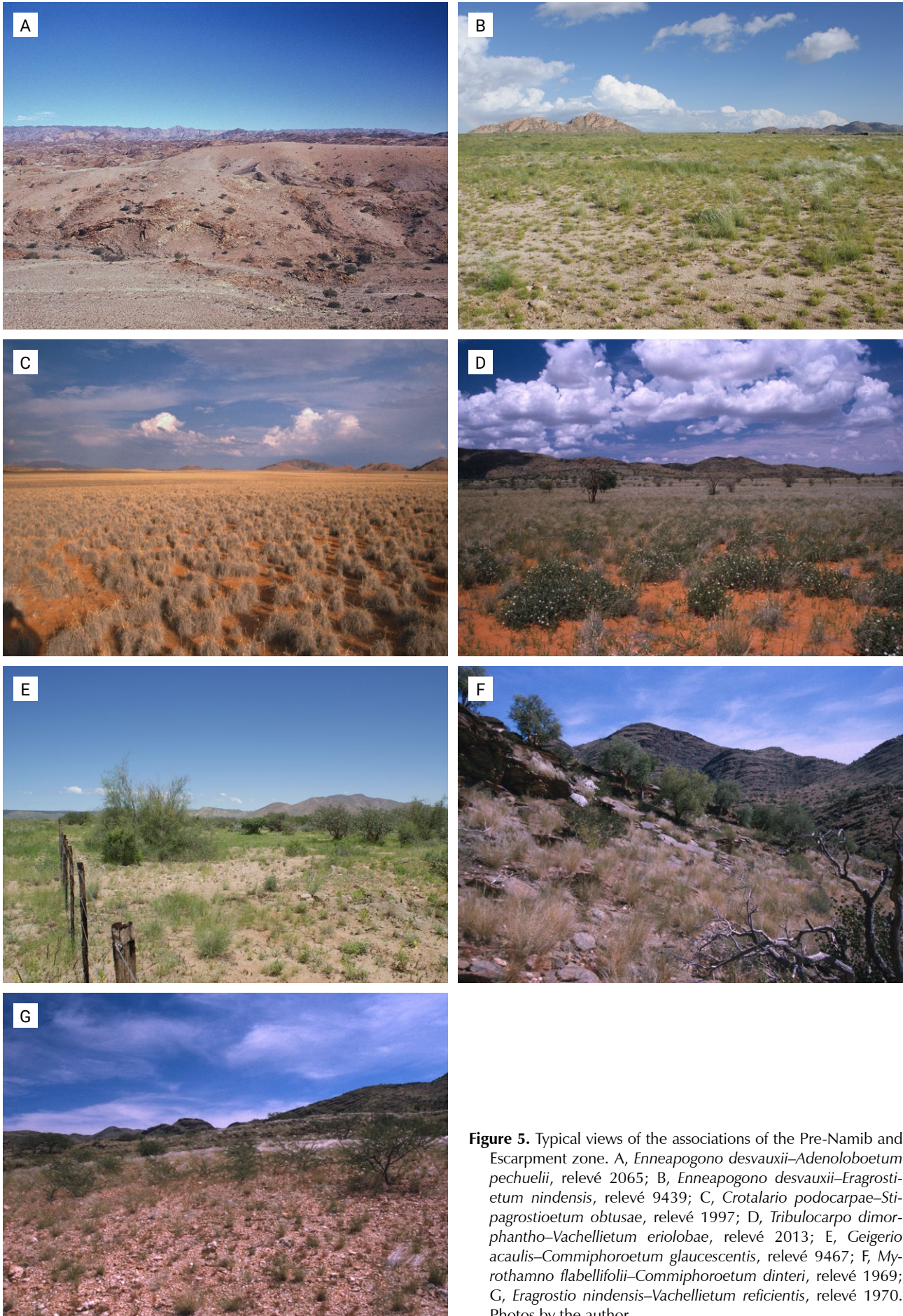


Figure 5. Typical views of the associations of the Pre-Namib and Escarpment zone. A, *Enneapogono desvauxii*–*Adenoloboaetum pechuelii*, relevé 2065; B, *Enneapogono desvauxii*–*Eragrostietum nindensis*, relevé 9439; C, *Crotalario podocarpae*–*Stipagrostioetum obtusae*, relevé 1997; D, *Tribulocarpo dimorphantho*–*Vachellietum eriobae*, relevé 2013; E, *Geigerio acaulis*–*Commiphoroetum glaucescentis*, relevé 9467; F, *Myrothamno flabellifolii*–*Commiphoroetum dinteri*, relevé 1969; G, *Eragrostio nindensis*–*Vachellietum reficientis*, relevé 1970. Photos by the author.

Estimated number of species: 214
Average species density per 1 000 m²: 33

Diagnostic species: *Schmidtia kalahariensis*, *Aristida adscensionis*, *Melinis repens* subsp. *grandiflora*, *Lycium bosciifolium*, *Aristida effusa*, *Eragrostis porosa*, *Enneapogon cenchroides*, *Geigeria acaulis*, *Albizia anthelmintica*, *Aptosimum arenarium*, *Merremia bipinnatipartita*, *Senegalia erubescens*, *Grewia tenax*, *Kyphocarpa angustifolia*

Constant species: *Stipagrostis uniplumis* var. *uniplumis*, *Eragrostis nindensis*, *Stipagrostis hochstetteriana*, *Boscia foetida*, *Vachellia reficiens*

These semi-open high shrublands are strikingly characterised by scattered trees of *Commiphora glaucescens* (Figures 4E and 5E). They occur on the slightly undulating plains surrounding Otjimbingwe, on Donkerhuk granites, north of the central Khomas Hochland complex. Typical for these granite-derived soils in arid environments is a very high (80% or more) cover by granitic gravel. The altitude ranges between 900 and 1 300 m asl, whilst MAP ranges between 150 and 250 mm.

1.6 *Myrothamno flabellifolii*– *Commiphoroetum dinteri* ass.nov.

Synopsis:

Number of relevés: 42
Type relevé: 1968 (holotype), sampled on 18 February 2004 at 23°01'49"S, 16°07'24"E
Number of species observed: 123
Estimated number of species: 173
Average species density per 1 000 m²: 29

Diagnostic species: *Commiphora dinteri*, *Forsskaolea viridis*, *Sterculia africana*, *Myrothamnus flabellifolius*, *Cheilanthes hirta*, *Talinum cafferum*, *Commiphora glaucescens*, *Elephantorrhiza suffruticosa*, *Calostephane marlothiana*, *Monechma spartioides*, *Blepharis obmitrata*, *Setaria appendiculata*, *Amphiasma divaricatum*, *Triraphis ramosissima*, *Dyerophytum africanum*, *Barleria lancifolia*

Constant species: *Stipagrostis uniplumis* var. *uniplumis*, *Eragrostis nindensis*, *Tribulus zeyheri*, *Tephrosia dregeana* var. *dregeana*

These low open bushlands are characterised by a variety of stem succulents typical of the escarpment zone (Figures 4F and 5F). They occur on the inselberg ranges along the Pre-Namib fringes as well as the lower escarpment zone, at an altitudinal range between 1 050 and 1 500 m asl. The topography consists of steep mountain slopes generally with a gradient of well above 30%, as well as with considerable stone cover (up to 80%), mostly small, medium and large stones. MAP ranges between 100 and 200 mm.

1.7 *Eragrostio nindensis*–*Vachellietum reficientis* ass. nov.

Synopsis:

Number of relevés: 77
Type relevé: 1970 (holotype), sampled on 18 February 2004 at 23°02'24"S, 16°08'18"E
Number of species observed: 97
Estimated number of species: 153
Average species density per 1000 m²: 23

Diagnostic species: none

Constant species: *Eragrostis nindensis*, *Stipagrostis uniplumis* var. *uniplumis*, *Euphorbia glanduligera*, *Tribulus zeyheri*, *Entoplocamia aristulata*, *Catophractes alexandri*, *Monsonia senegalensis*, *Leucosphaera bainesii*

These tall open shrublands are dominated by *Stipagrostis uniplumis* var. *uniplumis*, *Vachellia reficiens*, *Catophractes alexandri*, *Eragrostis nindensis*, *Enneapogon desvauxii*, *Aristida adscensionis* and *Senegalia erubescens* (Figures 4G and 5G). They occur on rolling to moderately steep (10–30%) plains and footslopes of the escarpment, often occurring far inland in valleys of the escarpment. Stone cover is not as high, roughly 40%, again mostly small, medium and large stones. The altitude ranges between 950 and 1 400 m asl, whilst MAP ranges between 100 and 250 mm.

Khomas Hochland proper

The vegetation of the Khomas Hochland is dominated by the plant families Poaceae, Asteraceae, Fabaceae and Scrophulariaceae. The classification resulted in eight associations, which are formally described according to the International Code of Phytosociological Nomenclature (Weber et al. 2000) below (with one exception). The synoptic table for these is presented in online Appendix 1, and the phytosociological table in online Appendix 2.

2.1 *Digitario erianthae*–*Euryopietum walterorum* ass. nov.

Synopsis:

Number of relevés: 6
Type relevé: 1838 (holotype), sampled on 9 February 2004 at 23°20'19"S, 16°13'50"E
Number of species observed: 44
Estimated number of species: 70
Average species density per 1 000 m²: 15

Diagnostic species: *Panicum lanipes*, *Euryops walterorum*, *Eriospermum bakerianum* subsp. *bakerianum*, *Hypertelis salsoloides*, *Boophone disticha*

Constant species: ***Eragrostis nindensis***, ***Digitaria eriantha***

This moderately closed, short shrubland is dominated by the name-giving *Euryops walterorum*, *Eriocephalus dinteri* and *Digitaria eriantha* (Figures 6A and 7A). The occurrence of *Euryops walterorum* is restricted to the Gamsberg Plateau (i.e. a limited-range endemic) (Nordenstam 1966; Loots 2005), which is 210 ha in size. The plateau consists of a fine-grained quartzite layer \pm 30 m thick, at an altitude 2 347 m asl (Wittig 1976; Schalk 1983). The topography is near flat but displays a conspicuous cover by large stones of roughly 40%. The plateau receives an estimated 150 mm MAP, based on general rainfall maps (Mendelsohn et al. 2002). This, however, does not take any possible orographic effects into account.

2.2 *Pennisetum foermerianum*– *Ficus ilicina* association

Synopsis:

Number of relevés: 6
Number of species observed: 97
Estimated number of species: 161
Average species density per 1 000 m²: 23

Diagnostic species: ***Ficus ilicina***, ***Pennisetum foermerianum***, ***Steganotaenia araliacea* var. *araliacea***, *Bulbostylis hispidula*, *Hermannia tigrensis*, *Datura innoxia*, *Cyphostemma hereroense*, *Calostephane divaricata*, *Eragrostis porosa*, *Sporobolus fimbriatus*, *Boscia albitrunca*, *Cheilanthes marlothii*, *Ozoroa crassinervia*, *Pupalia lappacea*

Constant species: ***Tarchonanthus camphoratus***, ***Searsia marlothii***, ***Combretum apiculatum* subsp. *apiculatum***, *Triraphis ramosissima*, *Melinis repens* subsp. *grandiflora*, *Enneapogon cenchroides*, *Senegalia hereroensis*

This association is difficult to assign to a structural type, as the vertical dimension is dominated by the habitat, being near-vertical rock faces (Figures 6B and 7B). Most woody species have a shrub-like habit, making it essentially a short, semi-open shrubland. However, e.g. *Ozoroa crassinervia* grows to a distinct tree. This association occurs on steep rock faces throughout the central Khomas Hochland. Kellner (1986) includes this in his *Pennisetum foermerianum*–*Dombeya rotundifolia* association, even though it is, based on its habitat and species composition, distinctly different. Due to the low sampling density and inherent variability it is not described formally.

2.3 *Eriocephalo dinteri*–*Danthoniopietyum ramosae* ass. nov.

Synopsis:

Number of relevés: 8

Type relevé: 9595 (holotype)
Number of species observed: 69
Estimated number of species: 93
Average species density per 1 000 m²: 27

Diagnostic species: ***Jamesbrittenia pallida***, ***Selago alopecuroides***, ***Eriocephalus dinteri***, ***Frankenia pomonensis***, ***Senecio inaequidens***, ***Cheilanthes hirta***, *Leucas glabrata*, *Hypoestes forskoolii*, *Namacodon schinzianum*, *Danthoniopsis ramosa*, *Lepidium africanum*, *Kalanchoe* species

Constant species: ***Digitaria eriantha***, *Oxalis purpurascens*, *Tarchonanthus camphoratus*, *Eragrostis scopelophila*, *Eragrostis nindensis*

These short, closed grasslands have a dense cover of perennial grasses like *Digitaria eriantha*, *Eragrostis scopelophila*, *Danthoniopsis ramosa* and *Andropogon chinensis* (Figure 6C). Scattered *Tarchonanthus camphoratus* and *Senegalia hereroensis* shrubs also occur. This association occurs on the very steep (> 60%) southern slopes of the Auas Mountain range, at altitudes from 2 150 m asl upwards (Burke & Wittneben 2007; Strohbach 2017). MAP is about 350 mm (Mendelsohn et al. 2002), again not taking any orographic effects into account.

2.4 *Danthoniopio ramosae*– *Oleoetum africanae* ass. nov.

Synopsis:

Number of relevés: 8
Type relevé: 9592 (holotype), sampled on 13 March 2004 at 22°37'05"S, 17°13'14"E
Number of species observed: 122
Estimated number of species: 151
Average species density per 1 000 m²: 63

Diagnostic species: ***Selago angustibractea***, ***Lopholaena cneorifolia***, ***Cheilanthes multifida***, ***Calostephane marlothiana***, ***Adromischus* species**, ***Monsonia burkeana***, ***Anthospermum rigidum***, ***Hypoxis iridifolia***, ***Eriocephalus scariosus***, ***Babiana hypogaea***, ***Brachiaria serrata***, ***Diospyros ramulosa***, ***Thesium lacinulatum***, ***Wahlenbergia denticulata***, ***Ebracteola montis-moltkei***, ***Tristachya superba***, ***Silene burchellii* var. *burchellii***, ***Helichrysum obtusum***, ***Felicia muricata***, ***Olea europaea* subsp. *africana***, ***Polygala uncinata***, ***Cineraria canescens***, ***Cymbopogon caesius***, ***Kalanchoe brachyloba***, ***Stoebe plumosa***, ***Osteospermum montanum***, *Leonotis ocymifolia*, *Anthospermum* species, *Osyris lanceolata*, *Searsia tenuinervis*, *Pegolettia retrofracta*, *Sida ovata*, *Dicoma anomala*, *Danthoniopsis ramosa*, *Ipomoea obscura* var. *obscura*, *Sphedamnocarpus pruriens* subsp. *pruriens*, *Fockea angustifolia*, *Hypoestes forskoolii*, *Themeda triandra*, *Ornithoglossum*

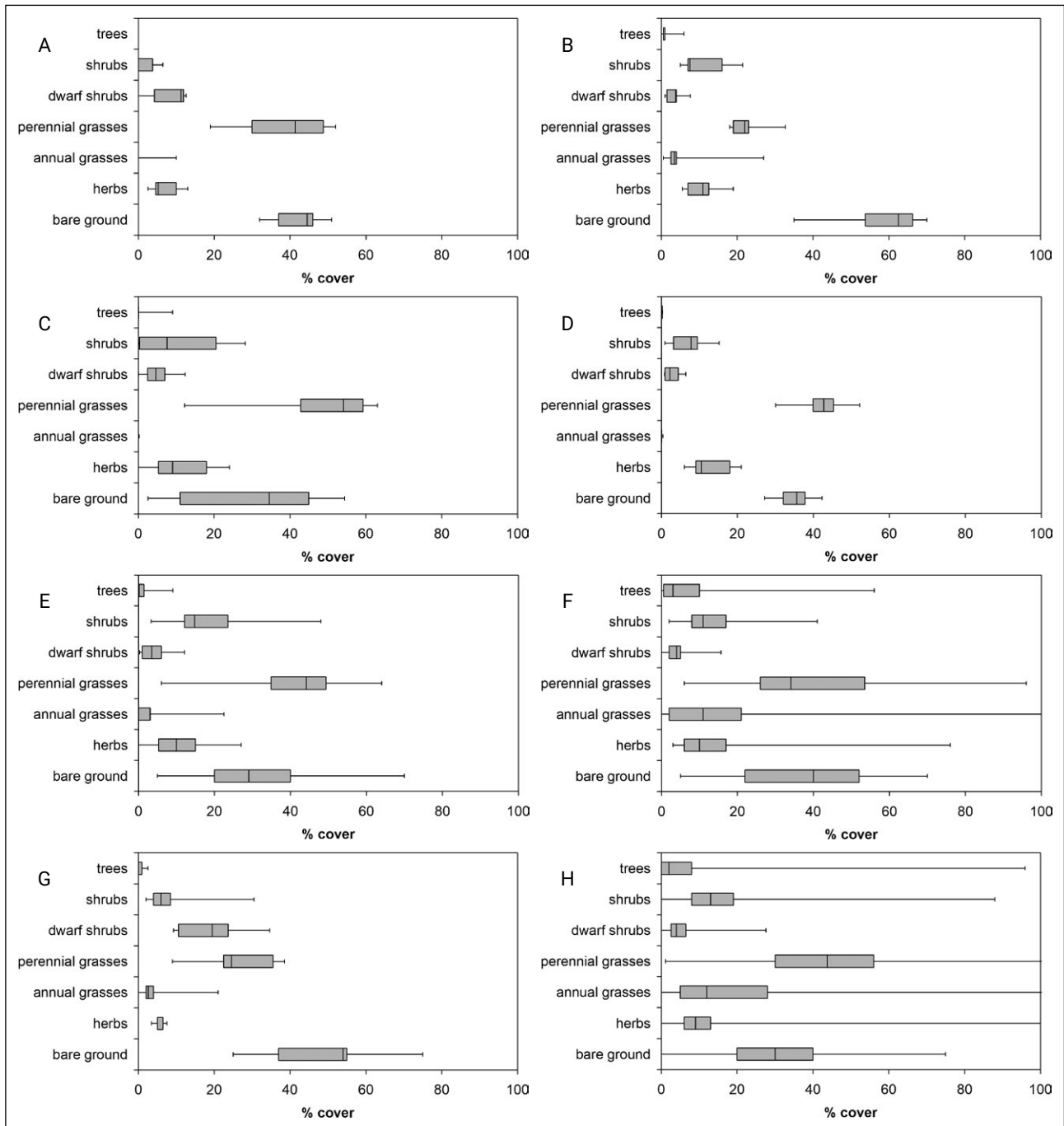


Figure 6. Box-and-Whisker plots of the typical structure of the associations of the Khomas Hochland Proper, based on the relevé data. A, *Digitaria erianthae*–*Euryopietum walterorum*; B, *Pennisetum foermerianum*–*Ficus ilicina* association; C, *Eriocephalo dinteri*–*Danthoniopietum ramosae*; D, *Danthoniopia ramosae*–*Oleoetum africanae*; E, *Senegalia hereroensis*–*Tarchonanthoetum camphorati*; F, *Triraphio ramosissimae*–*Manuleopsietum dinteri*; G, *Ornithoglosso calcicolae*–*Fingerhuthioetum africanae*; H, *Brachiario nigropedatae*–*Senegaliatum hereroensis*.

vulgare, *Gladiolus saccatus*, *Rhynchosia totta*, *Cymbopogon pospischilii*, *Andropogon chinensis*, *Jamesbrittenia lyperioides*, *Crassula capitella*, *Cotyledon orbiculata*, *Gymnosporia buxifolia*, *Ocimum americanum* var. *americanum*, *Moraea polystachya*, *Hebenstretia integrifolia*, *Cyperus margaritaceus*, *Boophone disticha*, *Gladiolus permeabilis* subsp. *edulis*, *Euphorbia spartaria*, *Aptosimum lineare*, *Hibiscus trionum*, *Heliophila carnosa*, *Solanum delagoense*, *Jamesbrittenia huillana*

Constant species: ***Digitaria eriantha***, ***Senegalia hereroensis***, ***Tarchonanthus camphoratus***, ***Oxalis purpurascens***, ***Eragrostis nindensis***, *Pellaea calomelanos*, *Eragrostis scopelophila*, *Chascanum pinnatifidum*, *Searsia marlothii*, *Melinis repens* subsp. *repens*, *Heteromorpha arborescens*, *Commelina africana*

This association is best described as a short, closed grassland dominated by *Danthoniopsis ramosa* and *Heteropogon contortus*, with some sparse shrub cover.

Shrubs also occur only on the lower reaches, whilst the mountain tops are distinctly grass covered (Figures 6D and 7C). It occurs on the northern face of the Auas Mountain range at an altitudinal range of 2 200 m asl and above (Burke & Wittneben 2007; Strohbach 2017). The soil surface is rock-strewn, with quartzite boulders and solid rock of the Auas formation (Geological Survey 1980; South African Committee for Stratigraphy 1980). MAP is between 350 and 400 mm, without taking any orographic effects into account.

2.5 *Senegalia hereroensis*– *Tarchonanthoetum* *camphorati* ass. nov.

Synopsis:

Number of relevés: 22
Type relevé: 1123 (holotype), sampled on 25 April 2002 at 22°48'34"S, 17°02'00"E
Number of species observed: 171
Estimated number of species: 237
Average species density per 1 000 m²: 43

Diagnostic species: *Sida chrysantha*, *Phyllanthus species*, *Brachiaria nigropedata*, *Dyschoriste pseuderecta*

Constant species: *Senegalia hereroensis*, *Tarchonanthus camphoratus*, *Pellaea calomelanos*, *Melinis repens* subsp. *repens*, *Heteropogon contortus*, *Eragrostis scopelophila*, *Eragrostis nindensis*, *Digitaria eriantha*, *Searsia marlothii*, *Hypoestes forskalii*

This tall, semi-open shrubland is dominated by *Tarchonanthus camphoratus*, *Searsia marlothii* and *Senegalia hereroensis*, with the grasses *Brachiaria nigropedata*, *Eragrostis scopelophila* and *Digitaria eriantha* dominating the grass layer (Figures 6E and 7D). This association occurs on the Auas Mountain and Lichtenstein ranges at mid-altitude, between 2 000 and 2 300 m asl. No evidence could be found for a differentiation between north- and south-facing sides of the mountains, unlike reported by Burke and Wittneben (2007) or Strohbach (2017). These slopes are steep (30–60%) with considerable quartzite stone cover, especially medium to large stones, even rocks (\pm 80% stone and rock cover), of the Auas formation.

2.6 *Triraphio ramosissimae*– *Manuleopsietum dinteri* ass. nov.

Synopsis:

Number of relevés: 53
Type relevé: 1011 (holotype), sampled on 16 March 2000 at 22°46'43"S, 16°46'41"E
Number of species observed: 170
Estimated number of species: 258
Average species density per 1 000 m²: 32

Diagnostic species: *Pennisetum foermerianum*, *Triraphis ramosissima*

Constant species: *Cheilanthes marlothii*, *Searsia marlothii*, *Cenchrus ciliaris*, *Melinis repens* subsp. *grandiflora*, *Eragrostis nindensis*, *Enneapogon cenchroides*, *Antheophora pubescens*, *Stipagrostis uniplumis* var. *uniplumis*

Typical for this short, semi-open shrubland are trees and shrubs of *Combretum apiculatum* subsp. *apiculatum*, *Ozoroa crassinervia*, *Dombeya rotundifolia* and occasionally *Euphorbia avasmontana*, together with other highland savanna species. The grass layer is also dominated by rock-specialists like *Pennisetum foermerianum*, *Triraphis ramosissima*, *Eragrostis scopelophila* and *Danthoniopsis ramosa* (Figures 6F and 7E). This association occurs on smaller mica-schist rock outcrops common within the central Khomas Hochland, as part of the Kuiseb formation. These are normally between 10 × 10 to over 50 × 50 m in surface area, but always broken, never solid rock faces. Due to the nature of the rock beds of the Khomas Hochland, many of these rock outcrops face south (but not exclusively). Altitude ranges between 1 600 and 1 800 m asl, whilst MAP ranges between 250 and 400 mm.

Kellner (1986) distinguishes two forms of this association, being a *Pennisetum foermerianum*–*Dombeya rotundifolia* community on broken rock outcrops, as well as a *Triraphis ramosissima*–*Combretum apiculatum* community on more solid, platy rock outcrops, generally also with more gentle slopes. This subdivision was neither confirmed in this study, nor by Strohbach (2017). Volk and Leippert (1971) also describe a *Combretum apiculatum*–*Eragrostis scopelophila* association, unfortunately without proper synopsis.

2.7 *Ornithoglosso calcicolae*– *Fingerhuthioetum africanae* ass. nov.

Synopsis:

Number of relevés: 9
Type relevé: 1095 (holotype), sampled on 23 April 2002 at 22°58'29"S, 17°07'00"E
Number of species observed: 98
Estimated number of species: 136
Average species density per 1 000 m²: 37

Diagnostic species: *Ornithoglossum calcicola*, *Melania damarana*, *Monechma genistifolium*, *Zygophyllum pubescens*, *Cleome suffruticosa*, *Stipagrostis hirtigluma*, *Enneapogon desvauxii*, *Otoptera burchellii*, *Leucosphaera bainesii*, *Euphorbia lignosa*, *Crotalaria kurtii*, *Blepharis mitrata*, *Enneapogon scoparius*, *Stipagrostis ciliata*, *Polygala pallida*, *Fingerhuthia africana*, *Sericorema sericea*, *Polygala leptophylla*, *Thesium xerophyticum*, *Seidelia*

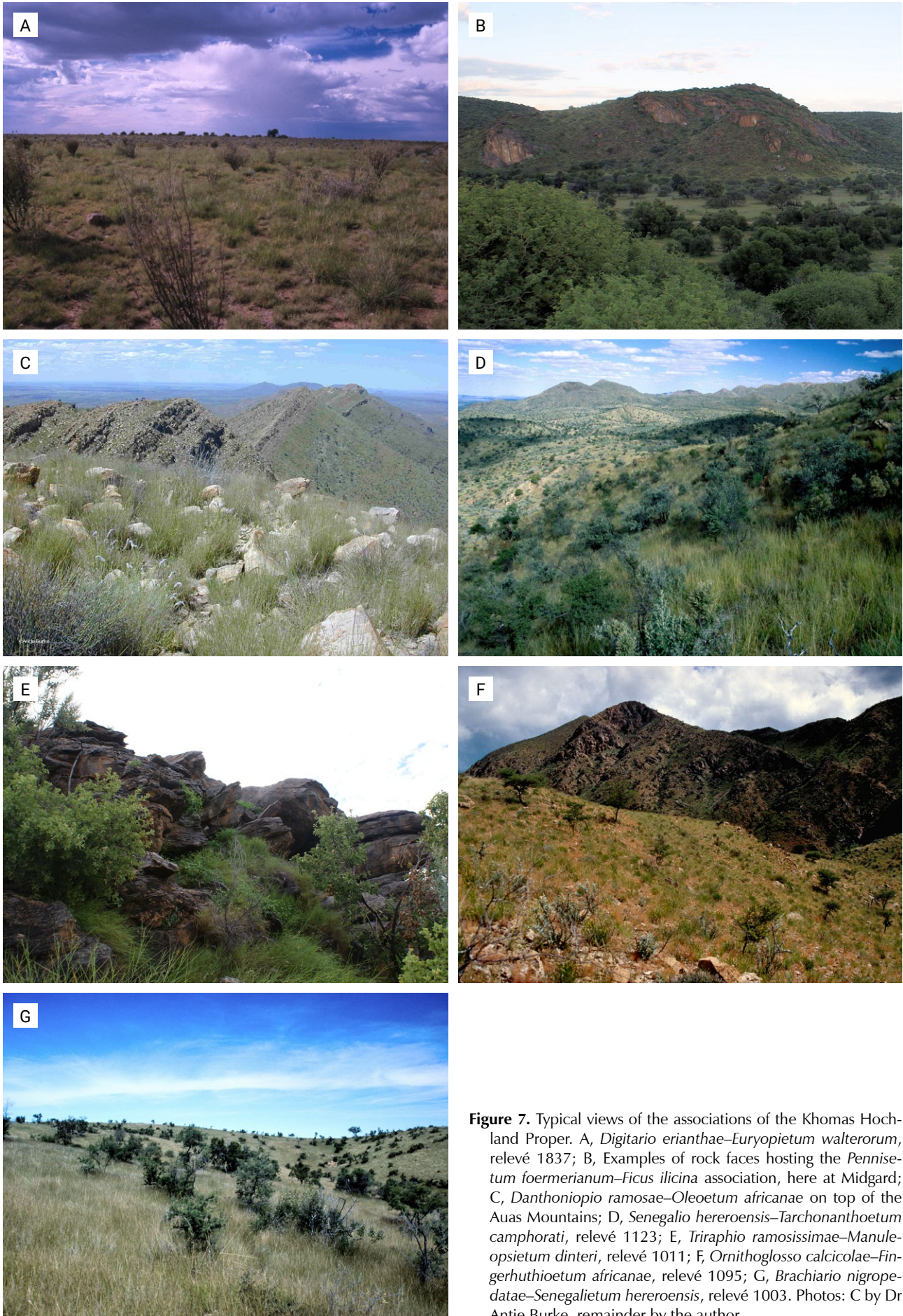


Figure 7. Typical views of the associations of the Khomas Hochland Proper. A, *Digitario erianthae*–*Euryopietum walterorum*, relevé 1837; B, Examples of rock faces hosting the *Pennisetum foermerianum*–*Ficus ilicina* association, here at Midgard; C, *Danthoniopia ramosae*–*Oleoetum africanae* on top of the Auas Mountains; D, *Senegalia hereroensis*–*Tarchonantheum camphorati*, relevé 1123; E, *Triraphio ramosissimae*–*Manuleopsietum dinteri*, relevé 1011; F, *Ornithoglosso calcicolae*–*Fingerhuthioetum africanae*, relevé 1095; G, *Brachiario nigropedatae*–*Senegalietum hereroensis*, relevé 1003. Photos: C by Dr Antje Burke, remainder by the author.

firmula, *Sarcostemma viminale*, *Senegalia mellifera* subsp. *detinens*, *Hermannia abrotanoides*, *Eriocephalus luederitzianus*, *Croton gratissimus*, *Grewia flava*, *Aizoon virgatum*, *Catophractes alexandri*, *Monelytrum luederitzianum*, *Helinus spartioides*, *Pentzia monocephala*, *Justicia guerkeana*, *Barleria lancifolia*, *Aristida effusa*, *Pelargonium otaviense*, *Eragrostis echinochloidea*

Constant species: ***Searsia marlothii***, ***Senegalia hereroensis***, ***Eragrostis nindensis***, *Enneapogon cenchroides*, *Talinum cafferum*

This short, semi-open shrubland is dominated by the dwarf shrub *Monechma genistifolium* and the grass *Fingerhuthia africana* (Figures 6G and 7F). The occasional occurrence of *Senegalia hereroensis* indicates the relationship to the central Khomas Hochland. This association occurs on the slopes of the Oamites Mountain, which is made up of grey quartzite and sericite phyllite of the Billstein formation (Geological Survey 1980; South African Committee for Stratigraphy 1980). The steep to very steep slopes are covered with rocks (up to 40%) and a mixture of small, medium and large stones (combined over 40%), at an altitudinal range of between 1 700 and 1 800 m asl, and a MAP of 350 mm.

2.8 *Brachiario nigropedatae*– *Senegaliatum hereroensis* ass. nov.

Synopsis:

Number of relevés: 238
Type relevé: 1003 (holotype), sampled on 16 March 2000 at 22°49'33"S, 16°50'00"E
Number of species observed: 287
Estimated number of species: 403
Average species density per 1 000 m²: 36

Diagnostic species: *Aristida meridionalis*, *Gnidia polycephala*, *Schmidtia pappophoroides*, *Eragrostis superba*, *Pogonarthria fleckii*

Constant species: ***Senegalia hereroensis***, ***Eragrostis nindensis***, ***Antheophora pubescens***, ***Searsia marlothii***, ***Melinis repens* subsp. *grandiflora***, *Brachiaria nigropedata*, *Stipagrostis uniplumis* var. *uniplumis*, *Monelytrum luederitzianum*, *Enneapogon cenchroides*, *Ziziphus mucronata*, *Cenchrus ciliaris*

These short, semi-open bushlands are dominated by shrubs of *Senegalia hereroensis*, with scattered low trees and shrubs of *Tarchonanthus camphoratus*, *Ziziphus mucronata*, *Combretum apiculatum* subsp. *apiculatum*, *Senegalia mellifera* subsp. *detinens*, *Euclea undulata*, *Vachellia tortilis*, *Albizia anthelmintica* and *Vachellia reficiens*. The grass layer is rather species-rich, with *Eragrostis nindensis*, *Enneapogon cenchroides*, *Monelytrum luederitzianum*, *Aristida adscensionis*, *Cenchrus*

ciliaris, *Brachiaria nigropedata*, *Aristida meridionalis*, *Melinis repens* subsp. *grandiflora*, *Antheophora pubescens*, *Triraphis ramosissima* and *Stipagrostis uniplumis* var. *uniplumis* being the dominating species (Figures 6H and 7G). The veld of the central Khomas Hochland occurs on moderately steep to steep hills and mountains with shallow (< 30 cm deep) soils on mica schists of the Kuiseb Formation (Geological Survey 1980, Schneider 2004). The stone cover is dominated by pebbles and medium-sized quartz stones up to 40%, with only occasional sub-outcropping mica schists. This association is the most extensive association within the central Khomas Hochland and occurs at an altitude of between 1 600 and 2 000 m asl. MAP ranges between 200 and nearly 400 mm.

Riverine vegetation

The vegetation of the riverine habitats is dominated by the plant families Poaceae, Asteraceae, Fabaceae and Amaranthaceae. The classification resulted in seven associations, which are formally described according to the International Code of Phytosociological Nomenclature (Weber et al. 2000) below. The synoptic table for these is presented in online Appendix 1, and the phytosociological table in online Appendix 2.

3.1 *Eragrostio rotiferi*–*Oleoetum africanae* ass. nov.

Synopsis:

Number of relevés: 3
Type relevé: 11525 (holotype), sampled on 16 April 2014 at 22°08'04"S, 17°17'45"E
Number of species observed: 51
Estimated number of species: 66
Average species density per 1 000 m²: 34

Diagnostic species: ***Olea europaea* subsp. *africana***, ***Brachylaena huillensis***, ***Diospyros lycioides***, ***Oxalis purpurascens***, ***Searsia lancea***, ***Alternanthera nodiflora***, ***Digitaria eriantha***, ***Kohautia azurea***, ***Gladius permeabilis* subsp. *edulis***, ***Crassula capitella***, ***Commelina subulata***, ***Cymbopogon pospischilii***

Constant species: ***Ziziphus mucronata***, ***Tagetes minuta***, ***Eragrostis rotifer***, ***Commelina benghalensis***, ***Chloris virgata***, ***Bidens biternata***, *Sporobolus fimbriatus*, *Setaria verticillata*, *Schoenoplectus muricinax*, *Pogonarthria fleckii*, *Panicum maximum*, *Oxygonum alatum*, *Melinis repens* subsp. *grandiflora*, *Eragrostis superba*, *Eragrostis lehmanniana*, *Eragrostis echinochloidea*, *Dactyloctenium aegyptium*, *Asparagus nelsii*, *Achyranthes aspera*, *Vachellia karroo*

These short, moderately closed woodlands occur in narrow, steep-sided ravines in the Khomas Hochland,

forming the headwaters of the rivers. The riverbed is not well-developed, often formed by boulders and eroded rock crevices and is generally overgrown (Figures 8A and 9A). Due to the narrowness of this bed, it was sampled with the banks. Rock cover is up to 40%, with considerable small, medium and large stone cover as well. Due to the relatively small sample, no reliable indication is available on the distribution, altitudinal range or MAP. The sampled relevés range between 1 780 and 1 800 m asl, at a MAP of 350 mm.

3.2 *Cynodo dactylonis*–*Eragrostioetum rotiferi* ass. nov.

Synopsis:

Number of relevés: 17
 Type relevé: 11520 (holotype), sampled on 16 April 2014 at 22°06'36"S, 17°17'40"E
 Number of species observed: 79
 Estimated number of species: 148
 Average species density per 1 000 m²: 18

Diagnostic species: *Hyparrhenia hirta*, *Gomphostigma virgatum*, *Datura innoxia*, *Eragrostis rotifer*

Constant species: *Chloris virgata*, *Eragrostis echinochloidea*, *Cynodon dactylon*, *Cenchrus ciliaris*, *Eragrostis superba*, *Bidens biternata*, *Tagetes minuta*, *Melinis repens* subsp. *grandiflora*

As the rivers widen, a distinct near-flat, coarse sandy bed is formed, on which this sparse short grassland establishes (Figures 8B and 9B). Depending on the flow regime (fast- or slow flowing, or even standing or seepage areas), a variety of species establish, often of ephemeral nature. Generally, *Chloris virgata*, *Sporobolus fimbriatus*, *Eragrostis rotifer*, *Eragrostis omahekensis*, *Eragrostis echinochloidea* and *Cynodon dactylon* dominate this association. This association occurs widespread in the study area as important part of the drainage system.

3.3 *Stipagrostioetum namaquensis* ass. nov.

Synopsis:

Number of relevés: 4
 Type relevé: 973 (holotype), sampled on 20 April 2000 at 22°49'08"S, 16°49'36"E
 Number of species observed: 61
 Estimated number of species: 83
 Average species density per 1 000 m²: 30

Diagnostic species: *Felicia clavipilosa*, *Stipagrostis namaquensis*, *Oxygonum alatum*

Constant species: *Pogonarthria fleckii*, *Acrotome fleckii*, *Tragus racemosus*, *Tagetes minuta*, *Melinis repens* subsp. *grandiflora*, *Melanthus comosus*, *Kyllinga*

alata, *Galenia africana*, *Enneapogon cenchroides*, *Chloris virgata*, *Bulbostylis hispidula*, *Bidens biternata*, *Vachellia karroo*, *Tetragonia calycina*, *Stachys spathulata*, *Schmidtia kalahariensis*, *Schkuhria pinnata*, *Ocimum americanum* var. *americanum*, *Monechma spartioides*, *Limeum sulcatum*, *Indigofera alternans*, *Hermstaedtia odorata*, *Heliotropium nelsonii*, *Geigeria pectidea*, *Eragrostis trichophora*, *Eragrostis porosa*, *Eragrostis omahekensis*, *Cucumis africanus*, *Cenchrus ciliaris*, *Anthephora schinzii*, *Anthephora pubescens*, *Amaranthus thunbergii*, *Achyranthes aspera* var. *sicula*

Larger rivers in relatively low-gradient environments (e.g. the Oanob) form deep sandbanks adjacent to the main flow channels, on which this tall, moderately closed grassland occurs (Figures 8C and 9C). Unlike the *Cynodo dactylonis*–*Eragrostioetum rotiferi*, this association is of more permanent nature, with *Stipagrostis namaquensis* stabilising the sand bank, and allowing sedimentation on this sand bank. This eco-engineer also forms a suitable habitat for phanerophytic species (commonly *Vachellia karroo*, but also *Vachellia erioloba*, *Faidherbia albida* and *Euclea pseudebenus*) to establish. The sandbanks found in the Oanob River form the western-most occurrence of this association, with extensive sandbanks found further east in the Seis and Nossob river systems. These sand banks occur within the study area at an altitude of between 1 850 and 1 950 m asl, and a MAP of between 300 and 350 mm.

3.4 *Themedio triandrae*–*Chloroetum virgatae* ass. nov.

Synopsis:

Number of relevés: 8
 Type relevé: 939 (holotype), sampled on 10 April 2000 at 22°45'24" S, 16°52'28" E
 Number of species observed: 130
 Estimated number of species: 185
 Average species density per 1 000 m²: 42

Diagnostic species: *Tragus berteronianus*, *Schmidtia pappophoroides*, *Themeda triandra*, *Talinum caffrum*, *Platycarphella carlinoides*, *Monsonia angustifolia*, *Microchloa caffra*, *Eragrostis superba*, *Geigeria pectidea*

Constant species: *Chloris virgata*, *Eragrostis porosa*, *Eragrostis echinochloidea*, *Anthephora pubescens*, *Vachellia karroo*, *Ursinia nana*, *Tribulus zeyheri*, *Kyllinga alata*, *Heliotropium nelsonii*, *Eragrostis nindensis*, *Aristida congesta* subsp. *congesta*, *Vachellia erioloba*, *Urochloa brachyura*, *Tragus racemosus*, *Tetragonia calycina*, *Schkuhria pinnata*, *Pogonarthria fleckii*, *Lycium bosciifolium*, *Limeum sulcatum*, *Eragrostis trichophora*, *Eragrostis rotifer*, *Enneapogon cenchroides*, *Cymbopogon pospischilii*, *Cenchrus ciliaris*, *Acrotome fleckii*

In the low-gradient landscape of the Oanob Plateau, but also other low-gradient areas like the Regenstein Valley and at Neudamm, valleys have been filled with sediments, forming a low-gradient, overgrown ephemeral wetland locally referred to as an *omuramba* (plural – *omirimbi*) (King 1963, Strohbach 2008). This forms the habitat for the *Themedio triandrae–Chloroetum virgatae*, a short, moderately-closed grassland (Figures 8D and 9D), dominated by ephemeral species like *Geigeria pectidea*, *Tribulus terrestris*, *Chloris virgata*, *Aristida hordeacea* and *Aristida adscensionis*. Only *Aristida congesta* subsp. *congesta* is a prominent perennial species, whilst the name-giving *Themedia triandra* is a rare species, often only occurring as remnant of the original lush grassland described by Volk and Leippert (1971). These authors already noted the generally poor state of this vegetation, which is prone to degradation and erosion. Once erosion sets in, the sediments are soon washed away to form a low-productive riverbed similar to the *Cynodo dactylonis–Eragrostioetum rotiferi*, with shrubs and trees establishing on the sides to form the start of the *Chloro virgatae–Vachellietum karroo*. The *Themedio triandrae–Chloroetum virgatae* occurs at an altitudinal range of between 1 740 and 2 200 m asl, and at a MAP of between 300 and 400 mm.

3.5 *Chloro virgatae–Vachellietum karroo* ass. nov.

Synopsis:

Number of relevés: 37
 Type relevé: 11519 (holotype), sampled on 16 April 2014 at 22°06'35" S, 17°17'40" E
 Number of species observed: 218
 Estimated number of species: 312
 Average species density per 1 000 m²: 26

Diagnostic species: ***Senegalia mellifera* subsp. *detinens***, *Phaeoptilum spinosum*, *Grewia flava*, *Aristida adscensionis*, *Eragrostis rigidior*, *Monechma divaricatum*

Constant species: ***Vachellia karroo***, *Eragrostis porosa*, *Enneapogon cenchroides*, *Eragrostis echinochloidea*, *Ziziphus mucronata*, *Cenchrus ciliaris*, *Vachellia erioloba*, *Chloris virgata*, *Stipagrostis uniplumis* var. *uniplumis*, *Pogonarthria fleckii*, *Melinis repens* subsp. *grandiflora*, *Aristida congesta* subsp. *congesta*, *Bidens biternata*

These tall, closed thickets are dominated by the tree and shrub species *Vachellia karroo*, *Vachellia tortilis*, *Senegalia mellifera* subsp. *detinens* and *Ziziphus mucronata* (Figures 8E and 9E). The herb layer consists of a mixture of various species, often shade tolerant species. The *Chloro virgatae–Vachellietum karroo* form the riparian forests lining most major inland rivers in the Komas Hochland and have strong affinities to the *Ziziphus mucronata–Acacia tortilis* association described for the Thornbush savanna (Strohbach 2019). Both Kellner

(1986) and Strohbach (2017) refer to the *Chloro virgatae–Vachellietum karroo* as *Cynodon dactylon–Acacia karroo* association, a name which was rejected as the name-giving *Cynodon dactylon* was neither a diagnostic nor constant species in this association.

The *Chloro virgatae–Vachellietum karroo* generally have a steep bank towards the riverbed but are fairly flat beyond the bank. Stone cover is low, rather occasional, mostly deposited by extreme flood events. This association occurs at altitudes of between 1 540 and 1 950 m asl, and MAP of between 250 and 400 mm.

3.6 *Salvadora persicae–Eucleetum pseudebeno* ass. nov.

Synopsis:

Number of relevés: 5
 Type relevé: 1929 (holotype), sampled on 16 February 2004 at 23°10'21" S, 16°02'28" E
 Number of species observed: 48
 Estimated number of species: 66
 Average species density per 1 000 m²: 21

Diagnostic species: ***Stipagrostis hochstetteriana***, ***Euclea pseudebenus***, ***Salvadora persica***, ***Tribulus zeyheri***, ***Portulaca oleracea***

Constant species: ***Cenchrus ciliaris***, *Vachellia erioloba*, *Ziziphus mucronata*, *Pergularia daemia*, *Heliotropium nelsonii*, *Gisekia africana*, *Faidherbia albida*, *Amaranthus thunbergii*

The *Salvadora persicae–Eucleetum pseudebeno* forms a tall, semi-open woodland dominated by *Faidherbia albida* and *Salvadora persica* (Figures 8F and 9F). This association forms the riparian forests along the bigger rivers in the western (Pre-Namib) part of the study area, i.e. the middle reaches of the Swakop, Kuiseb and Gaub rivers. The relationship to the lower Kuiseb vegetation (Theron et al. 1980) needs to be investigated further.

The *Salvadora persicae–Eucleetum pseudebeno* occurs in the lower rainfall areas, with a MAP of less than 200 mm, and at altitudes less than 1 100 m asl. Similar to its inland equivalents (the *Chloro virgatae–Vachellietum karroo* and the *Setario finitae–Vachellietum eriolobae*), this association displays low slope gradients (flat to gently undulating) with little stone cover.

3.7 *Setario finitae–Vachellietum eriolobae* ass. nov.

Synopsis:

Number of relevés: 18
 Type relevé: 11488 (holotype), sampled on 30 March 2014 at 22°02'29" S, 17°22'08" E
 Number of species observed: 69

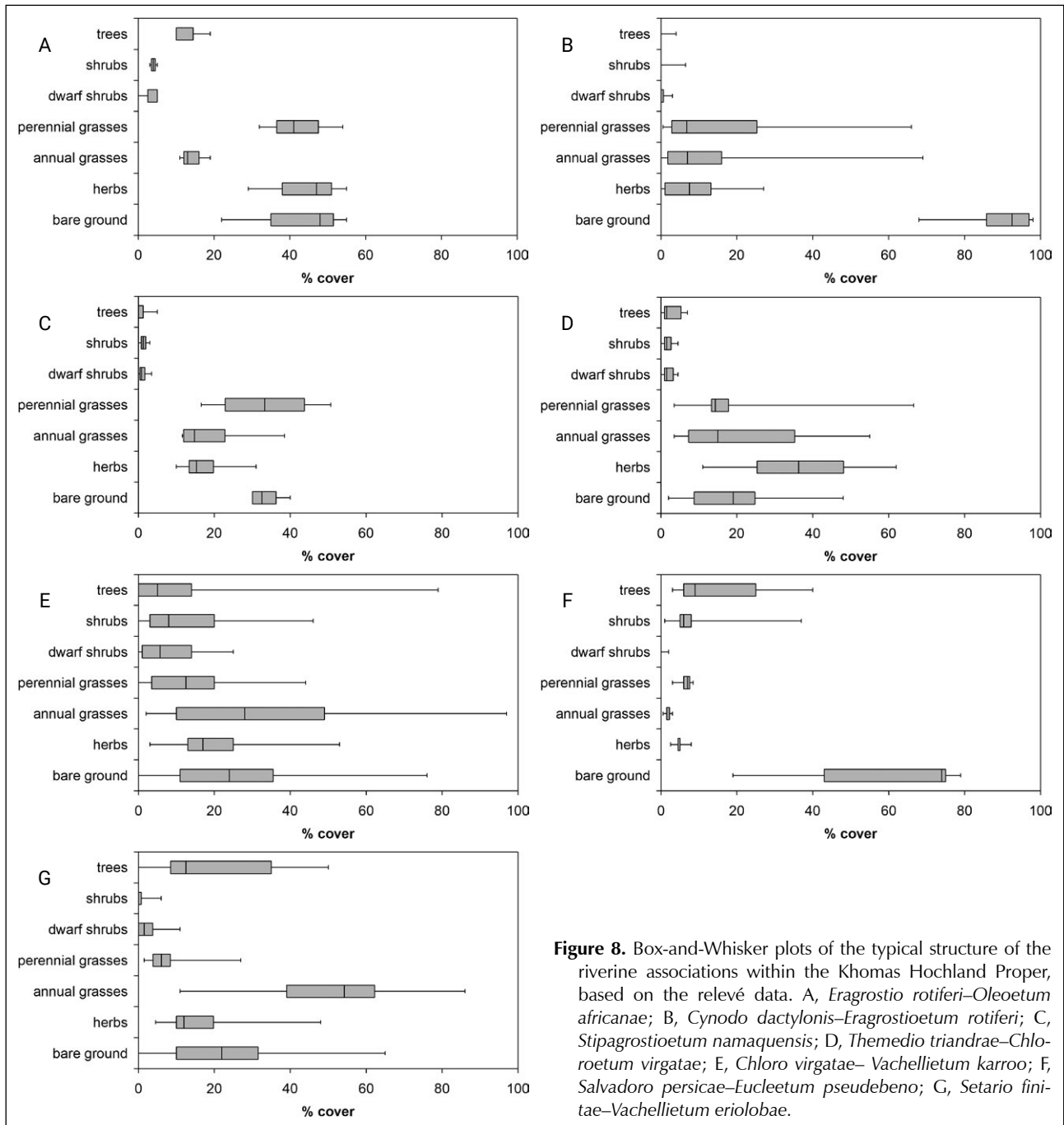


Figure 8. Box-and-Whisker plots of the typical structure of the riverine associations within the Khomas Hochland Proper, based on the relevé data. A, *Eragrostio rotiferi*–*Oleoetum africanae*; B, *Cynodo dactylonis*–*Eragrostioetum rotiferi*; C, *Stipagrostioetum namaquensis*; D, *Themedia triandrae*–*Chloroetum virgatae*; E, *Chloro virgatae*–*Vachellietum karroo*; F, *Salvadoro persicae*–*Eucleetum pseudebeno*; G, *Setario finitae*–*Vachellietum eriolobae*.

Estimated number of species: 101

Average species density per 1 000 m²: 25

Diagnostic species: *Setaria finita*, *Eragrostis cilianensis*, *Digitaria velutina*, *Zehneria marlothii*, *Cenopodium petiolariforme*, *Cyperus squarrosus*, *Sporobolus fimbriatus*, *Urochloa brachyura*, *Solanum delagoense*, *Cucumis meeusei*, *Schmidtia kalahariensis*, *Pechuel-Loeschea leubnitziae*

Constant species: *Bidens biternata*, *Pogonarthria fleckii*, *Chloris virgata*, *Vachellia erioloba*, *Ziziphus mucronata*, *Schkuhria pinnata*, *Cenchrus ciliaris*, *Bulbostylis hispidula*, *Vachellia karroo*, *Setaria verticillata*,

Eragrostis echinochloidea, *Tagetes minuta*, *Eragrostis trichophora*, *Dactyloctenium aegyptium*, *Antheaphora schinzii*, *Amaranthus thunbergii*

This tall, moderately closed woodland is found along the banks of the big inland rivers of the Khomas Hochland, notably the upper reaches of the Swakop River, but also its tributaries like the Gammams and Otjiseva rivers (Figures 8G and 9G). It is dominated by *Ziziphus mucronata*, *Vachellia karroo* and *Vachellia erioloba* trees, with *Faidherbia albida* also occurring occasionally.

The *Setario finitae*–*Vachellietum eriolobae* often forms islands within broad riverbeds, indicating a relationship,

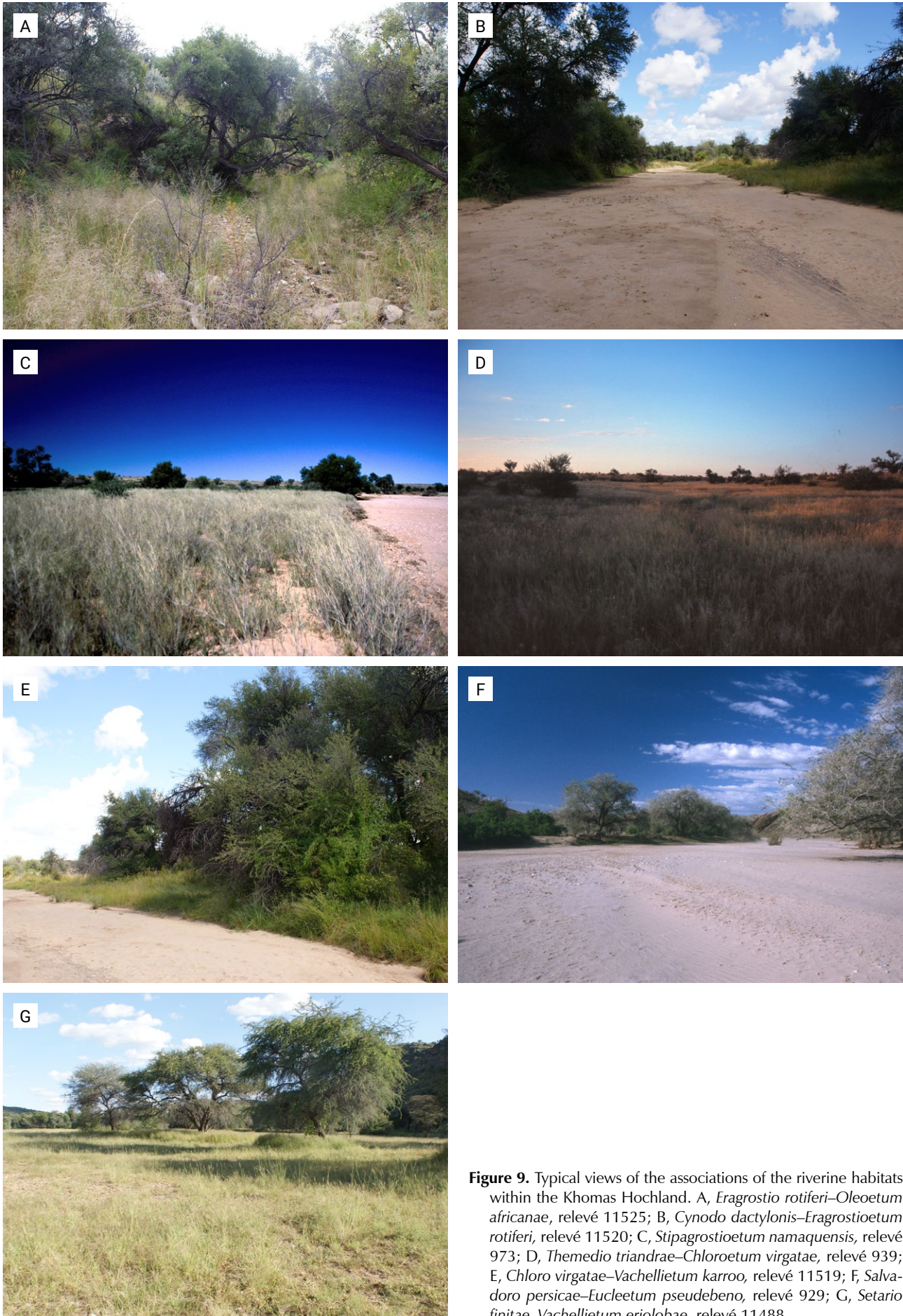


Figure 9. Typical views of the associations of the riverine habitats within the Khomas Hochland. A, *Eragrostio rotiferi*–*Oleoetum africanae*, relevé 11525; B, *Cynodo dactylonis*–*Eragrostioetum rotiferi*, relevé 11520; C, *Stipagrostioetum namaquensis*, relevé 973; D, *Themedio triandrae*–*Chloroetum virgatae*, relevé 939; E, *Chloro virgatae*–*Vachellietum karroo*, relevé 11519; F, *Salvadora persicae*–*Eucleetum pseudebeno*, relevé 929; G, *Setario finitae*–*Vachellietum eriobae*, relevé 11488.

possibly even a successional advanced stage, of the *Stipagrostietum namaquensis*. It has been found at altitudes of between 1 550 and 1 600 m asl, and MAP range of between 300 and 400 mm.

Lowlands surrounding the Khomas Hochland

The vegetation of the surrounding lowlands is dominated by the plant families Poaceae, Fabaceae, Asteraceae and Amaranthaceae. Eight associations, one with four sub-associations, were identified and are formally described following guidelines of the ICPN below (with one exception). Their composition is presented in Appendices 1 and 2 as synoptic and phytosociological tables.

4.1 *Pseudogaltonia clavatae*–*Eriocephaloetum luederitziana* ass. nov.

Synopsis:

Number of relevés: 35
 Type relevé: 10624 (holotype), sampled on 18 April 2011 at 23°07'18" S, 16°54'00" E
 Number of species observed: 131
 Estimated number of species: 217
 Average species density per 1 000 m²: 37

Diagnostic species: *Stipagrostis obtusa*, *Senecio windhoekensis*, *Rosenia humilis*, *Sporobolus nervosus*, *Enneapogon desvauxii*, *Sida ovata*, *Polygala pallida*, *Aizoon schellenbergii*, *Pentzia calva*, *Sericorema sericea*, *Eragrostis echinocloidea*, *Melhanina virescens*, *Pseudogaltonia clavata*, *Aptosimum lineare*, *Leobordea platycarpa*, *Pteronia mucronata*

Constant species: *Leucosphaera bainesii*, *Stipagrostis uniplumis* var. *uniplumis*, *Hirpicium gazanioides*, *Eragrostis nindensis*, *Eriocephalus luederitzianus*, *Fingerhuthia africana*, *Cenchrus ciliaris*, *Stipagrostis ciliata*, *Eragrostis porosa*, *Melinis repens* subsp. *grandiflora*, *Hermannia modesta*, *Barleria rigida*, *Vachellia erioloba*, *Tribulus zeyheri*, *Pogonarthria fleckii*, *Enneapogon cenchroides*

This low, moderately closed shrubland has a distinct karoid character, being dominated by the dwarf shrub species *Eriocephalus luederitzianus*, *Monechma genistifolium*, *Leucosphaera bainesii* and *Aizoon schellenbergii* (Figures 10A and 11A). This association is limited to the Narais plains towards Rehoboth, occurring on shallow loamy soils on calcretes, which have formed over the quartzites of the Duruchaus formation. Stone cover is about 20%, mostly calcrete gravel and small stones. Occasional deep pockets in the subsurfacing calcretes allow *Vachellia erioloba* trees to establish, adding a very sparse tree layer to this association's structure (Jürgens

et al. 2010). This association receives between 250 and 300 mm MAP and is at an altitudinal range of between 1 580 and 1 640 m asl. The topography is generally flat.

4.2 *Panico lanipedis*–*Pentzietum incanae* ass. nov.

Synopsis:

Number of relevés: 59
 Type relevé: 1020 (holotype), sampled on 17 March 2000 at 22°48'42" S, 16°51'40" E
 Number of species observed: 180
 Estimated number of species: 232
 Average species density per 1 000 m²: 52

Diagnostic species: *Panicum lanipes*, *Blepharis integrifolia*, *Eriospermum flagelliforme*, *Plinthus sericeus*, *Pteronia eenii*, *Pentzia incana*, *Ipomoea bolusiana*, *Talinum cafferum*, *Monelytrum luederitzianum*, *Commelina africana*, *Oxygenum sinuatum*, *Ursinia nana*

Constant species: *Eriocephalus luederitzianus*, *Eragrostis nindensis*, *Senegalia mellifera* subsp. *detinens*, *Microchloa caffra*, *Kyphocarpa angustifolia*, *Aristida adscensionis*, *Phaeoptilum spinosum*, *Hermannia modesta*, *Leucosphaera bainesii*, *Chascanum pinnatifidum*, *Schmidtia pappophoroides*, *Barleria rigida*, *Aptosimum spinescens*, *Melinis repens* subsp. *grandiflora*, *Hirpicium gazanioides*, *Pogonarthria fleckii*, *Hibiscus discophorus*, *Tragus berteronianus*, *Lycium eenii*, *Catophractes alexandri*, *Stipagrostis uniplumis* var. *uniplumis*, *Ocimum americanum* var. *americanum*, *Fingerhuthia africana*, *Eragrostis porosa*, *Aristida congesta* subsp. *congesta*, *Vachellia hebeclada* subsp. *hebeclada*, *Tarhonanthus camphoratus*, *Platycarphella carlinoides*, *Enneapogon cenchroides*, *Geigeria ornativa*, *Antheophora pubescens*, *Senegalia hereroensis*, *Searsia marlothii*, *Raphionacme velutina*, *Eragrostis trichophora*, *Cyperus palmatus*

The *Panico lanipedis*–*Pentzietum incanae* varies from a low, open to semi-open shrubland to a tall, moderately-closed shrubland, depending on its state of encroachment by savanna species. In its natural state it has a distinct karoid character, being dominated by *Leucosphaera bainesii* and *Eriocephalus luederitzianus* (Figures 10B and 11B). This association is however prone to encroachment by specifically *Senegalia mellifera* subsp. *detinens*, *Catophractes alexandri* and/or *Vachellia reficiens*, which causes the structure to change to a tall, denser shrubland. It occurs specifically on the rolling to moderately steep Oanob plateau, whilst similar vegetation has been also observed on the Hoffnung plateau east of Windhoek as well as at Neu Heusis west of Windhoek. As with the surrounding *Brachiario nigropedatae*–*Senegaliatum hereroensis*, the subsurface geology are mica schists of the Kuiseb formation. However, the landscape is a gentler, undulating to rolling

plateau at an altitudinal range of between 1 800 and 1 900 m asl. Stone cover is about 40%, mainly by small and medium-sized stones. MAP is between 300 and 350 mm.

4.3 *Aptosimo spinescentis*– *Galenietum africanae* ass. nov.

Synopsis:

Number of relevés: 8
Type relevé: 2155 (holotype), sampled on 11 February 2005 at 23°16'25" S, 16°31'06" E
Number of species observed: 83
Estimated number of species: 136
Average species density per 1 000 m²: 32

Diagnostic species: ***Eriocephalus ericoides***, ***Galenia africana***, ***Geigeria pectidea***, *Hermannia comosa*, *Aptosimum spinescens*

Constant species: *Stipagrostis uniplumis* var. *uniplumis*, *Eragrostis porosa*, *Eragrostis nindensis*, *Aristida adscensionis*, *Tribulus terrestris*, *Platycarphella carlinoides*, *Phaeoptilum spinosum*, *Eragrostis echinocloidea*, *Stipagrostis ciliata*, *Pentzia calva*, *Ocimum americanum* var. *americanum*, *Kohautia cynanchica*, *Eriocephalus luederitzianus*, *Eragrostis lehmanniana*, *Enneapogon desvauxii*, *Enneapogon cenchroides*, *Chascanum pinnatifidum*, *Aristida congesta* subsp. *congesta*, *Aptosimum albomarginatum*, *Vachellia erioloba*

These short, semi-open shrublands are limited to the alluvial plains around the farm Göllschau (H.E.S.S. project) in the southwestern Khomas Hochland (Figures 10C and 11C). The plains are dominated by the grasses *Stipagrostis uniplumis* var. *uniplumis*, *Aristida adscensionis* and *Sporobolus nervosus*, whilst the dwarf shrubs *Eriocephalus ericoides* and *Galenia africana* give it a karoid character. Occasional trees of *Vachellia erioloba* also occur here. The alluvial soils are derived from granites of the Gamsberg suite, which is sub-outcropping here (less than 5% cover). Slopes are generally flat to gently undulating, at an altitudinal range of 1 750 to 1 800 m asl. MAP is about 250 mm.

4.4 *Panicum arbusculi*–*Senegalietum detinentis* ass. nov.

Synopsis:

Number of relevés: 28
Type relevé: 2130 (holotype), sampled on 9 February 2005 at 23°05'29" S, 16°39'29" E
Number of species observed: 156
Estimated number of species: 209
Average species density per 1 000 m²: 51

Diagnostic species: ***Panicum arbusculum***, *Hibiscus discophorus*, *Ipomoea obscura* var. *obscura*, *Aristida meridionalis*, *Talinum arnotii*, *Blepharis mitrata*, *Brachiaria nigropedata*, *Catophractes alexandri*

Constant species: ***Senegalia mellifera* subsp. *detinens***, ***Leucosphaera bainesii***, ***Kyphocarpa angustifolia***, ***Eragrostis nindensis***, *Phaeoptilum spinosum*, *Microchloa caffra*, *Chascanum pinnatifidum*, *Stipagrostis uniplumis* var. *uniplumis*, *Fingerhuthia africana*, *Grewia flava*, *Ptychobolium biflorum*, *Melinis repens* subsp. *grandiflora*, *Eriocephalus luederitzianus*, *Schmidtia pappophoroides*, *Melhania virescens*, *Limeum myosotis*, *Aristida adscensionis*, *Aptosimum albomarginatum*, *Aizoon schellenbergii*, *Otoptera burchellii*, *Ocimum americanum* var. *americanum*, *Monechma luederitzianum*, *Hermannia modesta*, *Enneapogon cenchroides*, *Cenchrus ciliaris*, *Aptosimum spinescens*, *Lycium eenii*, *Lycium bosciifolium*, *Hirpicium gazanioides*, *Barleria rigida*, *Asparagus exuvialis*, *Searsia marlothii*, *Raphionacme velutina*, *Phyllanthus maderaspatensis*, *Antizoma angustifolia*, *Kyllinga alba*, *Dicoma capensis*, *Anthepphora pubescens*

These tall, moderately closed shrublands are dominated by *Senegalia mellifera* subsp. *detinens*, *Catophractes alexandri*, *Rhigozum trichotomum* and *Monechma genistifolium*. The grass layer contains *Panicum arbusculum*, *Stipagrostis uniplumis* var. *uniplumis*, *Melinis repens* subsp. *grandiflora*, *Eragrostis nindensis* and *Aristida congesta* subsp. *congesta* (Figures 10D and 11D). The presence of *Rhigozum trichotomum* and *Panicum arbusculum* within this southern Khomas Hochland is indicative of the transitional nature of these shrublands to the Dwarf Shrub Savanna *sensu* Giess (1998) or Nama Karoo. This association occurs on the rolling to moderately steep hilly landscape of the southern Khomas Hochland, and is especially well-represented along the C26. The underlying geology is formed by the mixtites of the Chuos Formation. Stone cover is about 40%, mainly small and medium-sized stones. The altitude ranges between 1 650 and 1 850 m asl, whilst the MAP ranges between 200 and 300 mm.

4.5 *Elephantorrhizo suffruticosae*– *Euphorbietum guerichianae* ass. nov.

Synopsis:

Number of relevés: 24
Type relevé: 2019 (holotype), sampled on 20 February 2004 at 23°15'04" S, 16°19'02" E
Number of species observed: 114
Estimated number of species: 172
Average species density per 1 000 m²: 35

Diagnostic species: ***Euphorbia guerichiana***, ***Heliotropium nelsonii***, ***Elephantorrhiza suffruticosa***, ***Cheilanthes marlothii***, *Commiphora glandulosa*, *Setaria*

appendiculata, *Helichrysum tomentosulum*, *Triraphis ramosissima*, *Blepharis obmitrata*, *Tephrosia dregeana* var. *dregeana*, *Emilia marlothiana*, *Antheophora pubescens*, *Cyphostemma currorii*, *Ozoroa crassinervia*, *Manuleopsis dinteri*, *Montinia caryophyllacea*, *Tribulus zeyheri*, *Boscia albitrunca*

Constant species: *Stipagrostis uniplumis* var. *uniplumis*, *Ooptera burchellii*, *Eragrostis nindensis*, *Talinum caffrum*, *Searsia marlothii*, *Fingerhuthia africana*, *Phaeoptilum spinosum*, *Hermannia modesta*, *Monechma spartioides*, *Cenchrus ciliaris*, *Vachellia reficiens*, *Melinis repens* subsp. *grandiflora*, *Combretum apiculatum* subsp. *apiculatum*, *Chascanum pinnatifidum*, *Aristida adscensionis*

These short, moderately closed bushlands occur in the upper reaches of the escarpment zone, between 1 450 and 1 780 m asl. The slopes are generally very steep (Figures 10E and 11E). This association is dominated by *Vachellia reficiens*, *Elephantorrhiza suffruticosa*, *Senegalia*

erubescens, as well as the grasses *Stipagrostis uniplumis* var. *uniplumis*, *Eragrostis nindensis* and *Setaria appendiculata*. The latter again is an indication of a transition to mountainous habitats in the Nama Karoo biome. Geology is varied, however mostly mica schists of the Kuiseb Formation and quartzites of the Auas formation (Geological Survey 1980; South African Committee for Stratigraphy 1980). Especially rock cover is high, with up to 80% of the surface covered by large stones and/or rocks. MAP ranges between 200 and 300 mm, not taking any orographic effects into account.

4.6 *Dichrostachyo cinereae*–*Senegaliatum erubescens* ass. nov.

Synopsis:

Number of relevés: 91

Type relevé: 9494 (holotype), sampled on 16 March 2009 at 22°18'10" S, 16°27'40" E

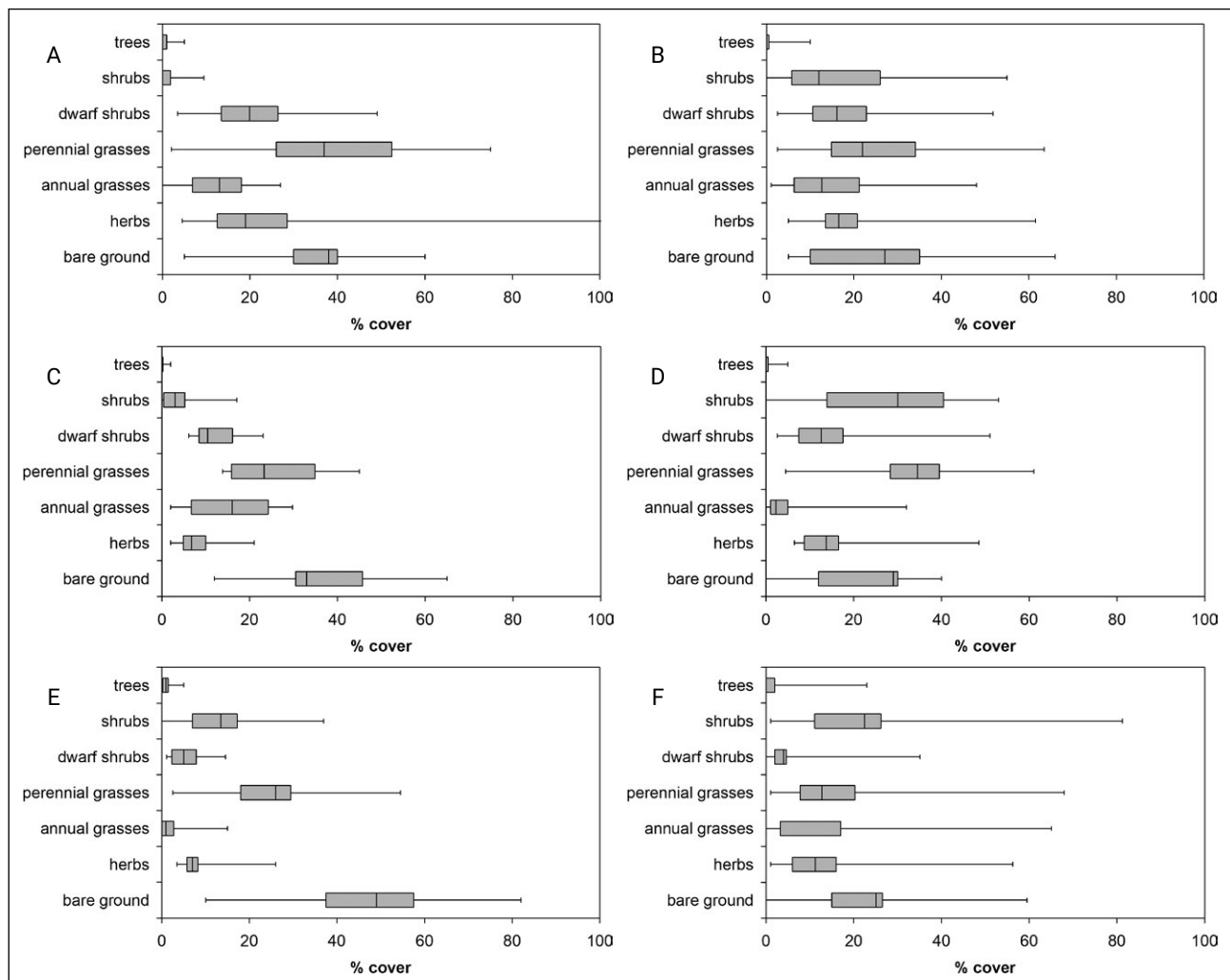


Figure 10. Box-and-Whisker plots of the typical structure of the associations of the Khomas Hochland Proper, based on the relevé data. A, *Pseudogaltonia clavatae*–*Eriocephaloetum luederitziana*; B, *Panicum lanipedis*–*Pentzietum incanae*; C, *Aptosimo spinescens*–*Galenietum africanae*; D, *Panicum arbusculi*–*Senegaliatum detinentis*; E, *Elephantorrhiza suffruticosa*–*Euphorbietum guerichiana*; F, *Dichrostachyo cinereae*–*Senegaliatum erubescens*.

Number of species observed: 270
 Estimated number of species: 383
 Average species density per 1 000 m²: 39

Diagnostic species: *Senegalia erubescens*, *Dichrostachys cinerea*, *Grewia flavescens*, *Combretum apiculatum* subsp. *apiculatum*, *Hibiscus elliotiae*

Constant species: *Stipagrostis uniplumis* var. *uniplumis*, *Enneapogon cenchroides*, *Senegalia mellifera* subsp. *detinens*, *Melinis repens* subsp. *grandiflora*, *Eragrostis nindensis*, *Cenchrus ciliaris*, *Catophractes alexandri*, *Vachellia reficiens*, *Pogonarthria fleckii*, *Kyphocarpa angustifolia*, *Triraphis ramosissima*, *Aristida effusa*, *Antheophora pubescens*, *Pupalia lappacea*, *Grewia flava*, *Boscia albitrunca*, *Ptycholibium biflorum*

These high, moderately closed shrublands are dominated by the shrub species *Senegalia erubescens*, *Vachellia reficiens*, *Senegalia mellifera* subsp. *detinens*, *Melinis repens* subsp. *grandiflora* and *Dichrostachys cinerea*. The

grass layer is dominated by *Enneapogon cenchroides*, *Eragrostis nindensis*, *Stipagrostis uniplumis* var. *uniplumis* and *Schmidtia kalahariensis* (Figures 10F and 11F). This association occurs in the rolling to moderately steep lowlands in the Windhoek valley, as well as Swakop valley around Okahandja. Some patches of this have also been observed in the upper Kuiseb valley. The altitude ranges between 1 300 and 1 800 m asl. Geology is varied, mainly mica schists from the Kuiseb formation, but also various intrusive granitic formations in the Swakop valley around Okahandja. Surface stone cover reaches between 40 and 80%, mainly small and medium stones. MAP ranges between 200 and 350 mm.

4.7 *Schmidtia kalahariensis*– *Vachellietum eriolobae* ass. nov.

Synopsis:

Number of relevés: 26

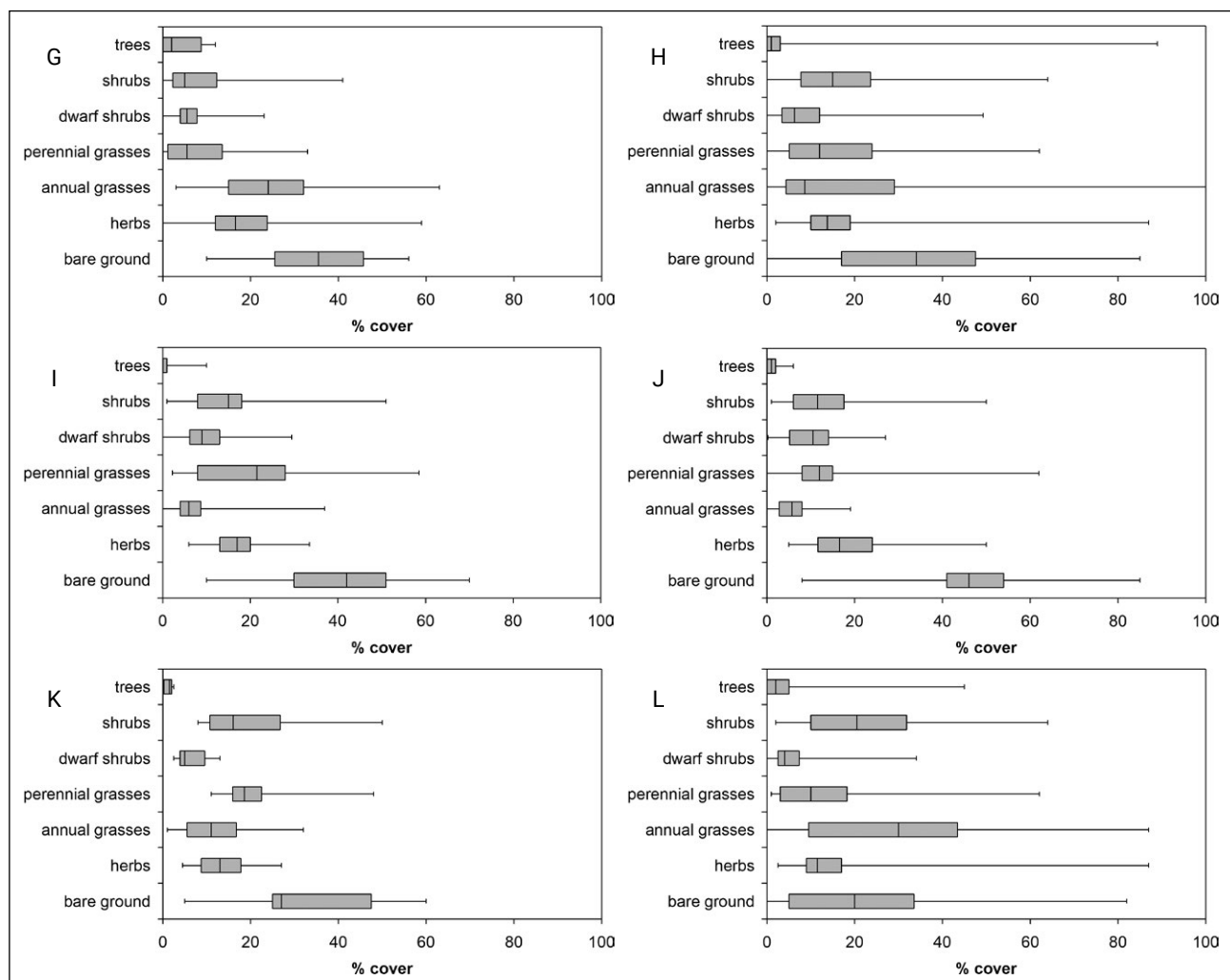


Figure 10 (continued). Box-and-Whisker plots of the typical structure of the associations of the Khomas Hochland Proper, based on the relevé data. G, *Schmidtia kalahariensis*–*Vachellietum eriolobae*; H, *Stipagrostis uniplumis*–*Senegalia detinens* association; I, *Stipagrostis uniplumis*–*Senegalia detinens* typical sub-association; J, *Stipagrostis uniplumis*–*Senegalia detinens* *tarchonanthus camphoratus* sub-association; K, *Stipagrostis uniplumis*–*Senegalia detinens* *vachellia tortilis* sub-association; L, *Stipagrostis uniplumis*–*Senegalia detinens* *vachellia reficiens* sub-association.

Type relevé: 1082 (holotype), sampled on 22 April 2002 at 22°52'49" S, 17°06'13" E
 Number of species observed: 103
 Estimated number of species: 161
 Average species density per 1 000 m²: 27

Diagnostic species: ***Schmidtia kalahariensis***, *Hermbstaedtia fleckii*, *Eragrostis cylindriflora*

Constant species: *Phaeoptilum spinosum*, *Vachellia erioloba*, *Stipagrostis uniplumis* var. *uniplumis*, *Enneapogon cenchroides*, *Acrotome fleckii*, *Senegalia mellifera* subsp. *detinens*, *Pollichia campestris*, *Eragrostis porosa*, *Gisekia africana*, *Geigeria pectidea*

These tall, semi-open bushlands are dominated by *Vachellia erioloba* trees, interspersed by shrubs of *Senegalia mellifera* subsp. *detinens* and *Lycium bosciifolium*. The grass layer is dominated by *Schmidtia kalahariensis* and *Stipagrostis uniplumis* var. *uniplumis*. Conspicuous are the suffrutex *Elephantorrhiza elephantina* and the forb *Geigeria pectidea* (Figures 10G and 11G). This association occurs on the alluvial plains around Aris and at Omeya south of Windhoek but has also been observed in the Brakwater/Döbra area in the valley north of Windhoek. The slopes are flat to gently undulating, with hardly any stone cover (mostly gravel and small stones, less than 2%). The altitude ranges between 1 600 and 1 770 m asl, with MAP of between 300 and 350 mm.

4.8 *Stipagrostis uniplumis*–*Senegalia detinens* association

Synopsis:

Number of relevés: 162
 Number of species observed: 317
 Estimated number of species: 473
 Average species density per 1 000 m²: 41

Diagnostic species: none

Constant species: ***Senegalia mellifera* subsp. *detinens***, ***Stipagrostis uniplumis* var. *uniplumis***, *Enneapogon cenchroides*, *Kyphocarpa angustifolia*, *Cenchrus ciliaris*, *Ocimum americanum* var. *americanum*, *Melinis repens* subsp. *grandiflora*, *Eragrostis nindensis*, *Catophractes alexandri*, *Eragrostis porosa*, *Grewia flava*, *Boscia albitrunca*, *Aristida adscensionis*, *Ziziphus mucronata*, *Lycium bosciifolium*, *Ooptera burchellii*, *Phaeoptilum spinosum*, *Pogonarthria fleckii*, *Ptycholobium biflorum*

These tall, semi-open shrublands are dominated by *Senegalia mellifera* subsp. *detinens*, *Catophractes alexandri*, *Vachellia reficiens* and *Phaeoptilum spinosum* (Figure 10H). This association is often associated with degradation within various units in the Khomas Hochland, but also the regular Thornbush savanna elements to the

east and north of the Khomas Hochland. Although four distinct forms have been recognised (and described as sub-associations below), there is still sufficient uncertainty regarding the classification not to allow a formal description of these communities yet.

4.8.1 *Stipagrostis uniplumis*–*Senegalia detinens* typical sub-association

Synopsis:

Number of relevés: 46
 Number of species observed: 193
 Estimated number of species: 286
 Average species density per 1 000 m²: 42

Diagnostic species: none

Constant species: ***Stipagrostis uniplumis* var. *uniplumis***, *Phaeoptilum spinosum*, *Senegalia mellifera* subsp. *detinens*, *Ocimum americanum* var. *americanum*, *Eragrostis nindensis*, *Kyphocarpa angustifolia*, *Grewia flava*, *Enneapogon cenchroides*, *Schmidtia pappophoroides*, *Talinum caffrum*, *Hirpicium gazanioides*, *Ooptera burchellii*, *Catophractes alexandri*, *Aristida congesta* subsp. *congesta*, *Ziziphus mucronata*, *Hermannia modesta*, *Vachellia hebeclada* subsp. *hebeclada*, *Kyllinga alba*, *Gisekia africana*, *Aristida adscensionis*, *Indigofera vicioides*, *Eragrostis porosa*, *Dicoma capensis*, *Cenchrus ciliaris*, *Boscia albitrunca*, *Lycium eenii*, *Chascanum pinnatifidum*

These tall, semi-open shrublands are the typical form of the *Stipagrostis uniplumis*–*Senegalia detinens* association (Figures 10I and 11H). Strohbach (2017) referred to this as the '*Pupalia lappacea*–*Acacia mellifera* bush encroached lowlands', indicating that this association is often a degradation state of other associations. As *Pupalia lappacea* however was not found to be a diagnostic nor constant species, the proposed name was rejected. This sub-association is found as patches in various components and associations within the Khomas Hochland. Especially the *Brachiario nigropedatae*–*Senegaliatum hereroensis*, the *Panico arbusculi*–*Senegaliatum detinentis* and the *Panico lanipedis*–*Pentzietum incanae* seem prone to degradation to this state.

The *Stipagrostis uniplumis*–*Senegalia detinens* typical sub-association occurs on undulating to rolling slopes, often with up to 40% gravel and small stone cover, at altitudinal ranges between 1 650 and 1 800 m asl.

4.8.2 *Stipagrostis uniplumis*–*Senegalia detinens tarchonanthus camphoratus* sub-association

Synopsis:

Number of relevés: 35
 Number of species observed: 194

Estimated number of species: 300
Average species density per 1 000 m²: 42

Diagnostic species: *Tarchonanthus camphoratus*

Constant species: ***Senegalia mellifera* subsp. *detinens***, ***Stipagrostis uniplumis* var. *uniplumis***, *Enneapogon cenchroides*, *Ocimum americanum* var. *americanum*, *Cenchrus ciliaris*, *Boscia albitrunca*, *Phaeoptilum spinosum*, *Lycium eonii*, *Ziziphus mucronata*, *Schmidtia pappophoroides*, *Ooptera burchellii*, *Grewia flava*, *Eragrostis porosa*, *Eragrostis nindensis*, *Achyranthes aspera* var. *sicula*, *Searsia marlothii*, *Pavonia burchellii*, *Catophractes alexandri*, *Kyphocarpa angustifolia*, *Vachellia erioloba*, *Pogonarthria fleckii*, *Monechma spartioides*, *Melinis repens* subsp. *grandiflora*, *Hermannia modesta*, *Talinum caffrum*, *Leucosphaera bainesii*, *Leucas pechuelii*, *Gisekia africana*, *Eragrostis echinochloidea*, *Ehretia rigida*

These high, semi-open shrublands are also dominated by *Senegalia mellifera* subsp. *detinens* and *Catophractes alexandri* (Figures 10J and 11I). The occurrence of *Tarchonanthus camphoratus* indicates slightly moister conditions, reflected in deeper, sandier soils, but also higher rainfall regimes (between 350 and 400 mm MAP). This sub-association is found in the eastern parts of the study area, linking into the thornbush savanna types to the east of Windhoek. The altitude ranges between 1 550 and 1 830 m asl, with rolling to moderately steep slopes. The subsurface geology are granites and gneiss from the Hohewarte complex and Gamsberg Suite. Stone cover is low (< 15%), mostly gravel and small stones.

4.8.3 *Stipagrostis uniplumis*– *Senegalia detinens vachellia* *tortilis* sub-association

Synopsis:

Number of relevés: 12
Number of species observed: 156
Estimated number of species: 267
Average species density per 1 000 m²: 39

Diagnostic species: none

Constant species: ***Melinis repens* subsp. *grandiflora***, ***Enneapogon cenchroides***, ***Cenchrus ciliaris***, *Pogonarthria fleckii*, *Eragrostis porosa*, *Ziziphus mucronata*, *Stipagrostis uniplumis* var. *uniplumis*, *Eragrostis nindensis*, *Senegalia mellifera* subsp. *detinens*, *Searsia marlothii*, *Phaeoptilum spinosum*, *Aristida adscensionis*, *Anthephora pubescens*, *Triraphis ramosissima*, *Schmidtia pappophoroides*, *Eragrostis rigidior*, *Aristida congesta* subsp. *congesta*, *Ocimum americanum* var. *americanum*, *Nidorella resedifolia*, *Monechma divaricatum*, *Lycium bosciifolium*, *Eragrostis echinochloidea*

These short, semi-open bushlands are dominated by *Vachellia reficiens*, *Senegalia mellifera* subsp. *detinens* and *Vachellia tortilis* (Figure 10K). It has a limited occurrence in patches in the Khomas Hochland and has mainly been observed west of Windhoek in the Daan Viljoen Game Reserve. This sub-association occurs on moderately steep to steep slopes at altitudinal ranges between 1 500 and 1 800 m asl. Stone cover is fairly high, above 40%, mostly small and medium stones. Larger stones, and occasional rock outcrops, are also present. The subsurface geology is also mica-schists of the Kuiseb Formation.

4.8.4 *Stipagrostis uniplumis*– *Senegalia detinens vachellia* *reficiens* sub-association

Synopsis:

Number of relevés: 69
Type relevé: 9504 (holotype), sampled on 16 March 2009 at 21°55'51" S, 16°34'36" E
Number of species observed: 219
Estimated number of species: 341
Average species density per 1 000 m²: 39

Diagnostic species: none

Constant species: ***Senegalia mellifera* subsp. *detinens***, ***Stipagrostis uniplumis* var. *uniplumis***, ***Vachellia reficiens***, *Enneapogon cenchroides*, *Lycium bosciifolium*, *Melinis repens* subsp. *grandiflora*, *Albizia anthelmintica*, *Kyphocarpa angustifolia*, *Catophractes alexandri*, *Aristida adscensionis*, *Cenchrus ciliaris*, *Ptychobolium biflorum*, *Eragrostis porosa*, *Boscia albitrunca*, *Aristida effusa*, *Pupalia lappacea*, *Schmidtia kalahariensis*, *Leucosphaera bainesii*, *Pogonarthria fleckii*, *Commelina benghalensis*, *Ocimum americanum* var. *americanum*, *Achyranthes aspera* var. *sicula*

These short, moderately closed bushlands are dominated by *Senegalia mellifera* subsp. *detinens*, *Vachellia reficiens* and *Catophractes alexandri* (Figures 10L and 11J). The grass layer is dominated by *Schmidtia kalahariensis*, *Enneapogon cenchroides*, *Stipagrostis uniplumis* var. *uniplumis* and *Aristida adscensionis*. This sub-association occurs in mosaic with the *Dichrostachyo cinereae*–*Senegaliatum erubescens* in the Windhoek valley and the Swakop Valley to the west of Okahandja. The relationship between these two syntaxa is not clear.

The *Stipagrostis uniplumis*–*Senegalia detinens vachellia reficiens* sub-association occurs at an altitudinal range of between 1 500 and 1 800 m asl, on rolling to moderately steep slopes. Geology is varied, mostly mica schists and granites. Stone cover is mostly by gravel, small and medium sized stones, less than 40%. MAP ranges between 200 and 400 mm.

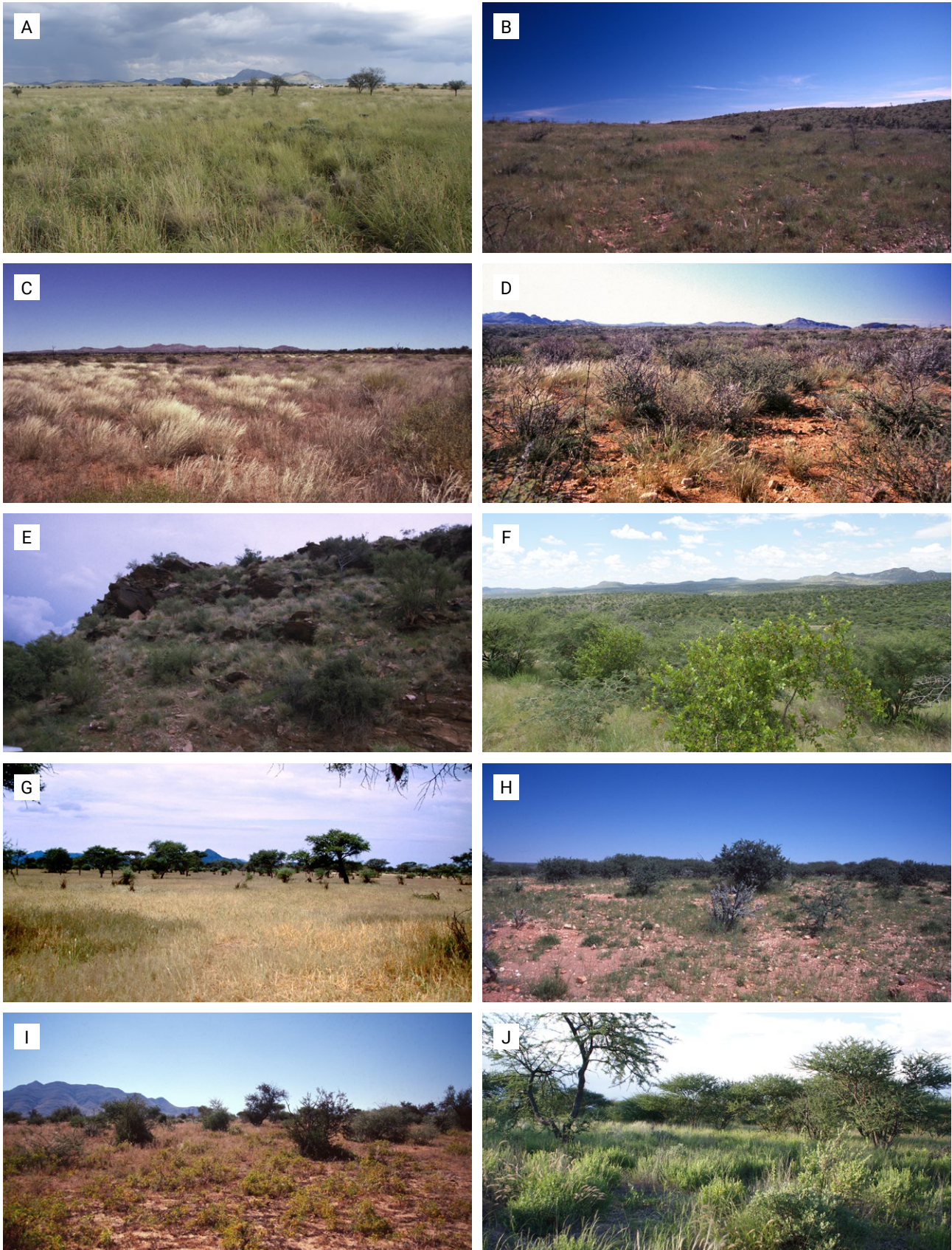


Figure 11. Typical views of the associations of the Khomas Hochland Proper. A, *Pseudogaltonia clavatae*–*Eriocphaloetum luederitziana*; B, *Panicum lanipedis*–*Pentzietum incanae*, relevé 1020; C, *Aptosimo spinescentis*–*Galenietum africanae*, relevé 2155; D, *Panicum arbusculi*–*Senegaliatum detinentis*, relevé 2153; E, *Elephantorrhiza suffruticosa*–*Euphorbietum guerichiana*, relevé 2017; F, *Dichrostachyo cinerea*–*Senegaliatum erubescens*, relevé 9494; G, *Schmidtia kalahariensis*–*Vachellietum erioloba*, relevé 1082; H, *Stipagrostis uniplumis*–*Senegalia detinens* typical sub-association, relevé 982; I, *Stipagrostis uniplumis*–*Senegalia detinens tarchonanthus camphoratus* sub-association, relevé 1146; J, *Stipagrostis uniplumis*–*Senegalia detinens vachellia reficiens* sub-association, relevé 9504.

Higher syntaxonomy

The classification of the synoptic relevés of 30 associations yielded a classification with crispness peaks at 4, 8, and 14/15 divisions. Accordingly, a classification with 15 clusters was accepted and interpreted. The 15 clusters were interpreted as alliances, whilst these alliances were grouped into orders between level 4 and level 8 divisions (Figure 12). An overview of associations, associated with their relevant alliances, orders and broad habitats are given in Table 3.

The *Senegalia hereroensis*–*Tarchonanthoetalia camphorati* is typified by the *Senegalia hereroensis*–*Tarchonanthion camphorati*. This order represents the high mountains of central Namibia. Based on the present data, it can be subdivided into two alliances, being the *Senegalia hereroensis*–*Tarchonanthion camphorati*, representing the Auas Mountains, as well as the *Digitario erianthae*–*Euryion walterorum*, representing the Gamsberg Mountain. The *Senegalia hereroensis*–*Tarchonanthion camphorati* is typified by the *Senegalia hereroensis*–*Tarchonanthoetum camphorati* and contains also the two other associations occurring on the Auas Mountains. The *Digitario erianthae*–*Euryion walterorum* is typified by the *Digitario erianthae*–*Euryopietum walterorum* and contains only this association.

The *Cynodo dactylonis*–*Eragrostioetalia rotiferi* is recognised as a provisional order representing the riverine habitats. According to the present classification, it breaks up into five alliances, each representing a single association. Due to this, and as other, similar habitats exist in central and southern Namibia, this provisional order is not yet formally described pending a thorough revision.

The *Brachiario nigropedatae*–*Senegalietaalia hereroensis* is typified by the *Brachiario nigropedatae*–*Senegalion hereroensis*, which is also the only alliance to this order. This

order represents the vegetation of the central Khomas Hochland. The *Brachiario nigropedatae*–*Senegalion hereroensis* in turn is typified by the *Brachiario nigropedatae*–*Senegalietaum hereroensis*. In addition to the typical association, three other associations have been grouped into this alliance. Two of these represent rocky habitats typical for the central Khomas Hochland, the third represents smaller rivers within the Khomas Hochland.

The sandy and/or specialised habitats in desert environment form a cluster of associations, each being represented by an own alliance, and possibly (depending on interpretation), even own orders. One of these associations, the *Salvadoro persicae*–*Euclietum pseudebeno*, could possibly also be grouped with the *Cynodo dactylonis*–*Eragrostioetalia rotiferi* due to its habitat. This is speculative, and subject to review in future. Because of this, no formal higher syntaxonomic groupings are described here.

The *Eragrostio nindensis*–*Vachellietalia reficientis* is typified by the *Eragrostio nindensis*–*Vachellion reficientis*. This order represents the Pre-Namib as well as the escarpment zone. The classification does not present any evidence of this order to be split into two alliances, yet, based on the habitat and vegetation of the associations in this order, a split was made between the name-giving alliance and the *Enneapogono desvauxii*–*Eragrostion nindensis*. The *Eragrostio nindensis*–*Vachellion reficientis* is typified by the *Eragrostio nindensis*–*Vachellietum reficientis* and includes two other association within the escarpment zone. The *Enneapogono desvauxii*–*Eragrostion nindensis* is typified by the *Enneapogono desvauxii*–*Eragrostietum nindensis* and includes the closely related *Enneapogono desvauxii*–*Adenoloboetum pechuelii*, as part of the Pro-Namib landscape.

The *Panico arbusculi*–*Senegalietaalia detinentis* is typified by the *Panico arbusculi*–*Senegalion detinentis*. It includes

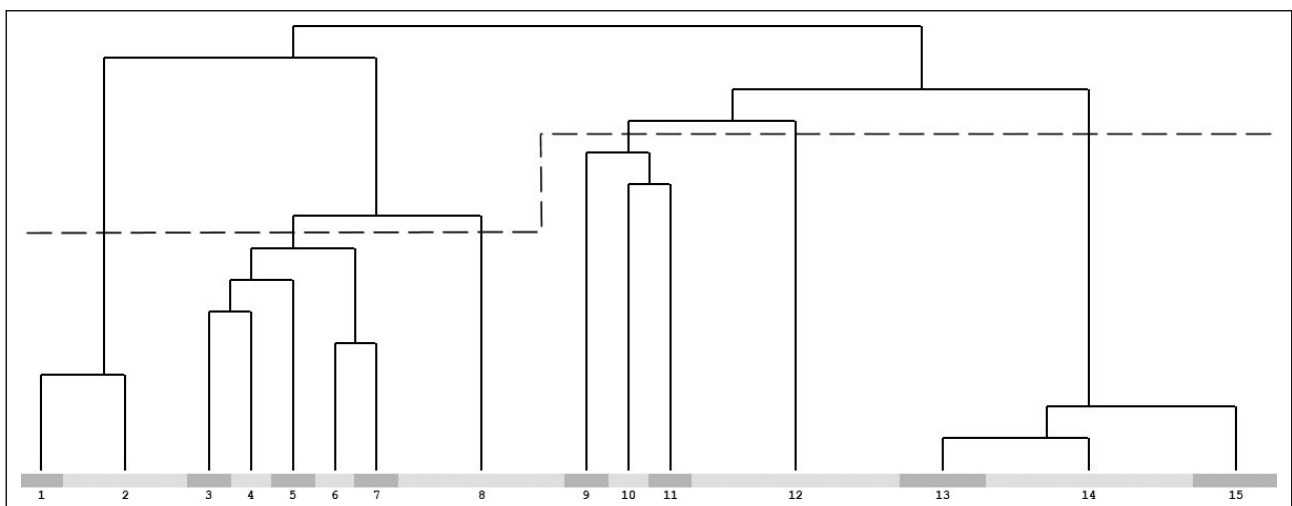


Figure 12. Dendrogram of the classification of synoptic relevés representing various associations. Groupings above the stippled line were interpreted as orders, whilst the final groupings were interpreted as alliances.

Table 3. Overview of the higher syntaxonomy of associations described in this study

Association	Alliance	Order
2.1 <i>Digitario erianthae</i> – <i>Euryopietum walterorum</i>	<i>Digitario erianthae</i> – <i>Euryion walterorum</i>	<i>Senegalia hereroensis</i> – <i>Tarchonanthoetalia camphorati</i>
2.3 <i>Eriocephalo dinteri</i> – <i>Danthoniopietum ramosae</i>	<i>Senegalia hereroensis</i> – <i>Tarchonanthion camphorati</i>	High Mountains
2.5 <i>Senegalia hereroensis</i> – <i>Tarchonanthoetum camphorati</i>	Auas Mountains	
2.4 <i>Danthoniopio ramosae</i> – <i>Oleoetum africanae</i>		
3.1 <i>Eragrostio rotiferi</i> – <i>Oleoetum africanae</i>		<i>Cynodo dactylonis</i> – <i>Eragrostioetalia rotiferi</i>
3.7 <i>Setario finitae</i> – <i>Vachellietum eriolobae</i>		Rivers
3.3 <i>Stipagrostioetum namaquensis</i>		
3.2 <i>Cynodo dactylonis</i> – <i>Eragrostioetum rotiferi</i>		
3.4 <i>Themedio triandrae</i> – <i>Chloroetum virgatae</i>		
2.2 <i>Pennisetum foermerianum</i> – <i>Ficus ilicina</i> association	<i>Brachiario nigropedatae</i> – <i>Senegalion hereroensis</i>	<i>Brachiario nigropedatae</i> – <i>Senegaliotalia hereroensis</i>
2.6 <i>Triraphio ramosissima</i> – <i>Manuleopsietum dinteri</i>	Khomas Hochland proper	Khomas Hochland proper
3.5 <i>Chloro virgatae</i> – <i>Vachellietum karroo</i>		
2.8 <i>Brachiario nigropedatae</i> – <i>Senegaliatum hereroensis</i>		
1.4 <i>Tribulocarpus dimorphantho</i> – <i>Vachellietum eriolobae</i>		
1.3 <i>Crotalaria podocarpae</i> – <i>Stipagrostioetum obtusae</i>		Sandy and/or specialised habitats in desert environment
3.6 <i>Salvadoro persicae</i> – <i>Eucleetum pseudebeno</i>		
1.1 <i>Enneapogono desvauxii</i> – <i>Adenoloboetum pechuellii</i>	<i>Enneapogono desvauxii</i> – <i>Eragrostion nindensis</i>	<i>Eragrostio nindensis</i> – <i>Vachellietalia reficientis</i>
1.2 <i>Enneapogono desvauxii</i> – <i>Eragrostietum nindensis</i>	Pre-Namib	Desert & escarpment
1.6 <i>Myrothamno flabellifolii</i> – <i>Commiphoroetum dinteri</i>	<i>Eragrostio nindensis</i> – <i>Vachellion reficientis</i>	
1.5 <i>Geigerio acaulis</i> – <i>Commiphoroetum glaucescentis</i>	Escarpment	
1.7 <i>Eragrostio nindensis</i> – <i>Vachellietum reficientis</i>		
2.7 <i>Ornithoglosso calcicolae</i> – <i>Fingerhuthioetum africanae</i>	<i>Elephantorrhizo suffruticosa</i> – <i>Euphorbion guerichianae</i>	<i>Panico arbusculi</i> – <i>Senegaliotalia detinentis</i>
4.5 <i>Elephantorrhizo suffruticosa</i> – <i>Euphorbietum guerichianae</i>	Mountainous fringes of the Khomas Hochland	Lowlands along the Khomas Hochland fringes
4.7 <i>Schmidtio kalahariensis</i> – <i>Vachellietum eriolobae</i>	<i>Panico arbusculi</i> – <i>Senegalion detinentis</i>	

Table 3. Overview of the higher syntaxonomy of associations described in this study (continued)

Association	Alliance	Order
4.1 <i>Pseudogaltonia clavatae</i> – <i>Eriocephaloetum luederitziana</i>		
4.3 <i>Aptosimo spinescentis</i> – <i>Galenietum africanae</i>	Southern fringe communities – ecotone to Nama Karoo	
4.4 <i>Panico arbusculi</i> – <i>Senegaliatum detinentis</i>		
4.2 <i>Panico lanipedis</i> – <i>Pentzietum incanae</i>		
4.6 <i>Dichrostachyo cinerea</i> – <i>Senegaliatum erubescens</i>	<i>Dichrostachyo cinerea</i> – <i>Senegalion erubescens</i>	
4.8 <i>Stipagrostis uniplumis</i> – <i>Senegalia detinens</i> association	Northern and eastern fringe lowlands	

two other alliances, being the *Elephantorrhizo suffruticosae*–*Euphorbion guerichiana* and the *Dichrostachyo cinerea*–*Senegalion erubescens*. This order represents the fringes to the Khomas Hochland to the south, east, north and, in the form of the upper escarpment, west. The *Panico arbusculi*–*Senegalion detinentis* in turn is typified by the *Panico arbusculi*–*Senegaliatum detinentis*, and, together with four other associations, forms the transition to the Nama Karoo biome to the south. The *Schmidtio kalahariensis*–*Vachellietum eriobae* is closely related to the vegetation of the southern Kalahari (Strohbach et al. 2019).

The *Elephantorrhizo suffruticosae*–*Euphorbion guerichiana* is typified *Elephantorrhizo suffruticosae*–*Euphorbietum guerichiana* and represents the mountainous habitats along the southern and western fringes of the Khomas Hochland. It contains one other association, the *Ornithoglossa calcicola*–*Fingerhuthioetum africanae* of the Oamites mountain.

The *Dichrostachyo cinerea*–*Senegalion erubescens* is typified by the *Dichrostachyo cinerea*–*Senegaliatum erubescens* and includes the as yet not formally described *Stipagrostis uniplumis*–*Senegalia detinens* association. This alliance represents the northern and eastern lowlands associated with the Khomas Hochland.

Discussion and conclusion

The higher syntaxonomy confirmed several preliminary observations. The initial classification into Pre-Namib and Escarpment, Khomas Hochland proper, Riverine habitats as well as surrounding lowlands are largely reflected in the orders *Cynodo dactylonis*–*Eragrostioetalia rotiferi*, the *Brachiario nigropedatae*–*Senegaliatalia hereroensis*, the *Eragrostio nindensis*–*Vachellietalia reficientis*

and the *Panico arbusculi*–*Senegaliatalia detinentis*. This is also in line with the groupings proposed by Giess (1998), i.e. the Central Namib, the Desert transition and escarpment Zone as well as the Highland savanna.

A notable exception is the *Senegalia hereroensis*–*Tarchonanthoetalia camphorati* (high mountains), which is highlighted as a grouping on its own. This also confirms the findings of Strohbach (2017), who has highlighted the high Auas Mountain vegetation as a separate grouping. The *Senegalia hereroensis*–*Tarchonanthoetalia camphorati* has close affinities to the grassland biome of South Africa, with its dominant cover of grasses, in particular *Digitaria eriantha* (Mucina & Rutherford 2006). Prominent representatives of the Asteraceae in this order, amongst others *Eriocephalus* spp., *Stoebe plumosa* and *Euryops walterorum*, also have close relatives in the grasslands and adjacent Karoo vegetation in South Africa (cf. Nordenstam 1966; Müller et al. 2001; Njenga 2005), indicating a biogeographic relationship to these biomes, rather than the surrounding savanna biome.

The other notable exception is the formation of a cluster of specialised habitats within the desert biome environment. Although the *Salvadoro persicae*–*Euclietum pseudebeno* has distinct affinities to the inland rivers, it still groups into the desert environment rather than the inland savanna environment. Of the other two associations in this cluster, the *Crotalaria podocarpae*–*Stipagrostioetum obtusae* has affinities to the arid grasslands of the Nama Karoo biome (Mucina & Rutherford 2006), whilst the *Tribulocarpus dimorphantho*–*Vachellietum eriobae* has affinities to the Kalahari duneveld *sensu* Mucina and Rutherford (2006) or southern Kalahari *sensu* Giess (1998).

The vegetation classification and description presented in this paper represents a broad overview, as dictated by the ‘reconnaissance level’ scale. Intensified sampling in several specialist habitats, e.g. the riverine habitats,

the high mountains (in particular the Hakos mountains, as well as ranges like the Bismark Mountains east of the Auas and various ranges of the Kamtsas and Sinclair formations south of Windhoek) and the Matchless Member dissecting the central Khomas Hochland, will likely yield further associations. The higher syntaxonomy will likely also be clarified and strengthened once more such studies are available and included in the analysis.

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Appendix 1

Synoptic table for the Pre-Namib and Escarpment Zone communities, with fidelity (phi coeff.) and frequency of occurrence (%)

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Appendix 2

Phytosociological Table

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