Taxonomy, evolutionary history, and ecological dominance of *Themeda* and *Heteropogon*

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DECLARATION

I CAN CONFIRM THAT IS MY OWN WORK AND THE USE OF ALL MATERIAL FROM OTHER SOURCES HAS BEEN PROPERLY AND FULLY ACKNOWLEDGED.

WATCHARA ARTHAN
ROYAL BOTANIC GARDEN, KEW, SEPTEMBER 2022

To my wonderful family, past and present supervisors, colleagues, friends,
and everyone who joined my PhD journey

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ABSTRACT

Heteropogon and *Themeda* grasses are common and significant components of the C_4 savannas which have recently gained more attention for conservation and biodiversity research. The two genera have been the subject of ecological research due to their widespread and dominant species *H. contortus* and *T. themeda.* Like many tropical plant lineages, however, in-depth knowledge necessary for the management of these ecosystems is still lacking. This thesis focuses on the diversity of *Heteropogon* and *Themeda* in respect to evolution, ecology, and systematics.

In this thesis, phylogenetic analyses indicated that the evolutionary history of *Heteropogon* and *Themeda* is being driven by complex evolutionary processes and their origin is dated back to the Miocene grassland expansion. I interpreted those discordant phylogenetic placements between plastid and nuclear trees as underlying polyploidization or hybridization within the groups. Dating analyses indicated that most species originated in the Miocene grassland expansion. Widespread species, *H. contortus* and *T. triandra* did not originate until the Late Miocene and quickly spread throughout the Tropics in the Pleistocene.

Climatic niche characteristics and geographic distributions of *Heteropogon* and *Themeda* shed light on macroecological patterns, adaptation by functional traits, and the evolution of climatic niche and functional traits. I found that *Heteropogon* and *Themeda* species are separated into savanna and wetland groups. This is supported by differences in precipitation regimes of the two habitats and functional traits (e.g., plant height, leaf area, and awns). In an evolutionary context, biomes were shifted from savannas to wetlands, and niche divergence occurred. Functional traits changed by habitat preferences and show lability in the lineage.

Integration of morphology and new ecological and phylogenetic evidence derived from this thesis were used in new generic and species reclassifications of *Heteropogon* and *Themeda*. I conclude that the generic description of *Heteropogon* should be narrowed, and I accept three species, while that of *Themeda* expanded to accept 26 *Themeda* species and 2 varieties. Phylogenetic relationships determine diagnostic morphological characters in generic and species delimitations. This new systematics of *Heteropogon* and *Themeda* demonstrates how to apply various biological data in taxonomic revision, and to summarize biodiversity information of *Heteropogon* and *Themeda*.

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LIST OF ABBREVIATIONS

adh–Alcohol Dehydrogenase gene
AIC–Akaike Information Criterion
AICc–Corrected Akaike information Criterion
ANOVA–Analysis of Variance
AOO–Area of Occupancy
ARD–All Rate Different model
ATP–Adenosine Triphosphate
atpB–ATPase beta-subunit gene
BCD–*Bothriochloa-Capillipedium-Dichanthium* clade
BEP–*Bambusoideae-Ehrhartoideae-Pooideae* clade
BI–Bayesian Inference
BIC–Bayesian Information Criterion
BM–Brownian Motion model
BS–Bootstrap
C–Caryopses
CI–Confident Interval
CIPRES–Cyberinfrastructure for Phylogenetic Research
cpDNA–Chloroplast DNA
DHAR–Dehydrogenase Reductase gene
DNA–Deoxyribonucleic Acid
dNTP–Deoxynucleotide
EB–Early Burst model
EOO–Extent of Occurrence
ER–Equal Rate model
ESS–Effective Sample Size
EST–Expressed Sequence Tags
FAMD–Factor Analysis of Mixed Data
FP–Fertile Spikelet
Gb–Gigabase
GBIF–Global Biodiversity Information Facility
GBSS–Granule-bound Starch Synthase gene

GPAT–Glycerol-3-phosphate Acyltransferase gene

GPWG–Grass Phylogeny Working Group

GTR–General Time-reversible

G3PDH–Glyceraldehyde-3-phosphate Dehydrogenase gene

H–Homogamous spikelet

HP–Homogamous Pair

HPD–Height Posterior Density

HSD–Tukey’s Honestly Significant Difference

IDH–Intermediate Disturbance Hypothesis

InL–Log-likelihood

IPNI–International Plant Name Index

IR–Inverted Repeat

ITS–Internal Transcribed Spacer

IUCN–The International Union for Conservation of Nature

LB–Late Burst model

LPP–Local Posterior Probability

LSC–Large Single Copy

MAP–Mean Annual Precipitation

MCMC–Markov Chain Monte Carlo

ML–Maximum Likelihood

MSL–Milchunas-Sala-Lauenroth

MYA–Million Years Ago

NGS–Next-generation Sequencing

OU–Ornstein-Uhlenback model

matK–Megakaryocyte-Associated Tyrosine Kinase gene

ndhF–NADH dehydrogenase F gene

nrDNA–Nuclear DNA

PACMAD–Panicoideae-Aristidoideae-Chloridoideae-Micrairoideae-Arundinoideae-Danthonioideae clade

PC–Principal Component

PCA–Principal Component Analysis

PCR–Polymerase Chain Reaction

PDryQ─Precipitation of Driest Quarter

PHYB─Phytochrome B gene

PGI─Glucose-6-phosphate Isomerase

POWO Plants of the World Online

PP (Chapter 3)─Posterior Probability

PP (Chapter 5)─Pedicelled Spikelet

PPi─Pyrophosphate

PS─Precipitation Seasonality

psbA─Photosystem II Reaction Center Protein A gene

QS─Quartet Support

R─Raceme

rbcL─Ribulose-bisphosphate Carboxylase gene

RNA─Ribonucleic Acid

rpl16─Ribosomal Protein L16 gene

rpl22─Ribosomal Protein L22 gene

rpoC1─the β-subunit of RNA polymerase gene

rps15─Ribosomal Protein S15 gene

rps19–Ribosomal Protein S19 gene

SE─Standard Error

SNP─Single Nucleotide Polymorphism

SP─Spikelet Pair

SRA─Sequence Read Archive

SSC─Small Single Copy

SYM─Symmetrical model

S-T─state-and-transition

T─Triad

TDWG─Biodiversity Information Standards

trnF─tRNA-Phe gene

trnL─tRNA-Leu gene

trnT─tRNA-Thr gene

TS─Temperature Seasonality

WGSRPD The World Geographical Scheme for Recording Plant Distributions

CHAPTER 1

1.1 GENERAL INTRODUCTION

Biodiversity is an outcome of evolutionary processes, ecological mechanisms, and complex interplay between multiple historic factors (Swenson, 2011). The grass family Poaceae is one of the largest and globally most important and diverse angiosperm lineages worldwide. Undoubtedly, Poaceae is one of the most studied plant families in multifaceted biodiversity research including taxonomy, evolution, and ecology (Hodkinson, 2018). In the Anthropocene, transformative global environmental changes affect the health of grass ecosystems causing changes in vegetation compositions and loss of biodiversity in these ecosystems (Stevens & al., 2022). Thus, there is a need to understand the history and drivers of Poaceae biodiversity for future research and applications.

Andropogoneae is the most diverse tribe of C_4 Poaceae and main understorey in savannas (Lehmann & al., 2019), comprises lineages shaped by distinct evolutionary history and processes (Arthan & al., 2017; Estep & al., 2014; Welker & al., 2020). In the core Andropogoneae (Arthan et al., 2021), *Heteropogon* and *Themeda* represents diverse macroecological patterns, ecological functions, and morphological variations at the population level. However, *Heteropogon* and *Themeda* have received little attention in terms of phylogenetic history and relationships, which hinders broad understanding in their biodiversity and evolution. Previous phylogenetic studies indicated that *Heteropogon* and *Themeda* are closely related genera and late-diverging Andropogoneae lineages (Arthan & al., 2017; Teerawatananon & al., 2002; Welker & al., 2020). With increased taxon sampling and use of molecular markers, phylogenetic analyses revealed new phylogenetic placements (Arthan & al., 2015) and suggested that hybridization and polyploidization are common evolutionary processes in *Heteropogon* and *Themeda* (Dunning & al., 2017; Estep & al., 2014). However, insight into phylogenetic relationships and history is not comprehensive due to incomplete taxon sampling, insufficient molecular data to yield robust results and explain evolutionary processes, and knowledge gaps in some aspects (e.g., phylogenetic dating or biogeography).

Heteropogon and *Themeda* species are frequently found in savanna systems across Africa, America, Asia, and Australia (Ratnam & al., 2016, Snyman & al., 2013). Their geographical ranges vary between species from endemic to pantropical species (POWO, 2022). Extent of geographic distributions and habitat types imply that climatic preferences of *Heteropogon* and *Themeda* species could be distinct (Lehmann & al., 2011, 2019). According to Fierro (2014), habitat suitability models indicated that climatic factors encompassed by distribution patterns of *Themeda* species are characterized by different sets of precipitation and temperature variables. Climatic factors (e.g., precipitation) greatly influence vegetation and physical compositions of savannas (Lehmann & al., 2014, 2019; Murphy & Bowman, 2012, Ratnam & al., 2020), so investigating climatic occupation of these C_4 grasses is a key initial step to understand ecological functions and interactions of plant groups. However, there is lack of similar framework for *Heteropogon* and interspecific comparative climatic niche analyses.

Climatic conditions are usually effective predictors of plant functional traits (Violle & al., 2007). Different climatic envelopes shape functional traits and adaptation strategies in plants (Kühn et al., 2021). In grasses, precipitation and temperature variables yielded significant correlations with functional traits such as plant height and leaf traits (Bouchanak-Khelladi & al., 2020, Jardine & al., 2021, Moles & al., 2009). Diverse climatic backgrounds (Fierro, 2014) and forms found in *Heteropogon* and *Themeda* represents a good system for species-level studies. This could yield insight in species ecological functions, finer-scale relationships between functional traits and climates, and climatic niche and trait history in the lineages.

Accumulation of novel biodiversity data, especially phylogenetic and ecological data, has revolutionized practices and caused changes in the angiosperm systematics (Brosch & al., 2015). This is particularly true for the systematics of *Heteropogon* and *Themeda* that is dynamic and should be updated due to gaps and changes in biodiversity knowledge. Morphological species concepts have been mainly used in generic and infrageneric classifications of *Heteropogon* and *Themeda* (Deshpande, 1988; Veldkamp & al., 2016). However, strict morphology-based concepts have caused taxonomic debates over species status of *Heteropogon* and *Themeda* due to unclear or overlapping morphological criteria. For example, are *Themeda quadrivalvis* and *T. triandra* the same species or sister species? or, can we separate *Heteropogon contortus* and *H. allonii* as they represent glabrous and hairy forms? These issues/questions should be addressed with combined concepts applying various evidence as being investigated in the preceding paragraphs. Such gaining new ecological and phylogenetic data will lead to more extensive taxonomic revision and reclassifications.

This thesis focuses on evolution, climatic niche, functional traits, and taxonomic revision of *Heteropogon* and *Themeda*. Here are the objectives and scope of this thesis.

1. To study evolutionary history and phylogenetic relationships of *Heteropogon* and *Themeda* (Chapter 3).

2. To explore climatic niche characteristics and history of *Heteropogon* and *Themeda* (Chapter 4).

3. To explain the associations between functional traits and macroecological patterns and climatic regimes of *Heteropogon* and *Themeda*. (Chapter 4).

4. To revise the systematics of *Heteropogon* and *Themeda* based on ecological, morphological, and phylogenetic evidence. (Chapter 5).

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CHAPTER 2

LITERATURE REVIEW

In the traditional classification, Clayton and Renvoize (1986) placed *Heteropogon* and *Themeda* as closely related genera in the subtribe Anthistiriinae, but their evolutionary relationships were still understudied. Increase in phylogenetic evidence supports that *Heteropogon* and *Themeda* are sister genera, which facilitates complete systematics of both genera and also reflects shared evolutionary relationships and history including biogeographic patterns, underlying macroecological mechanisms, and evolution of functional traits. However, evolutionary relationships at species level are not completely understood, and that impedes understanding in respective aspects. Here, taxonomic, phylogenetic, and ecological work regarding these genera is reviewed to provide the background for thesis questions laid out in Chapter 1.

2.1 Taxonomic and Morphological Background of Genus *Themeda* and *Heteropogon*

2.1.1 Genus *Themeda* Forssk.

Themeda occurs throughout the tropics and is considered to be native to the tropical and subtropical zones of Africa, Asia and Oceania (Van Oudtshoorn, 2012; Veldkamp, 2016; Plants of the World Online, 2018). *T. triandra* Forssk. is the type species and the most broadly-distributed species in the genus, which dominates grassland biomes in Africa, Asia, Australia and New Zealand (Forsskåhl, 1775; Rutherford et al., 2006; Snyman et al., 2013; Morales, 2014; Linder et al., 2017).

Currently, 27 *Themeda* species are accepted (The Plant List, 2013; Molares, 2014; Kellogg, 2015). According to georeferenced data by Morales (2014), 15 species have been recorded in India, which can be referred as the centre of biodiversity of the genus and might be the origin of the genus.

For taxonomic history of the genus, Forsskåhl (1775) proposed the genus name with a single species, *Themeda triandra*. Before that time, *Themeda arguens* had been already recognized but went by the other validated name, *Stipa arguens* L. (Linnaeus, 1762). Later, Naezén (1779) published '*Anthistiria* L. f.' without the consideration of Forsskåhl's work. *'Themeda'* had been ignored as an accepted taxonomic name by the taxonomists. Afterwards, several species had been discovered and described under *Anthistiria* (Sprengel, 1824; Kunth, 1829). After that superfluous generic names, including *Perobachne* Presl, *Androscepia* Brong., *Heterelytron* Jungh. and *Aristaria* Jungh., were respectively made according to distinct perspectives of the taxonomists on the morphology, especially in inflorescence structure (Presl, 1830; Brongniart, 1831; Junghuhn, 1840). In 1889, '*Themeda*' was resurrected as Hackel (1889) realised that it was the first name of the organism. He also made a new revision for *Themeda*, which is the taxonomic classification that subsequent works extensively follow (Hackel, 1889).

The number of species and classification system of *Themeda* within the genus have been unstable. For example, up to 31 species of *Themeda* and 13 *T. triandra* varieties were recognized by Zhoa (1998). In addition, an infrageneric classification was proposed by some taxonomists (Camus, 1920a, 1920b; Roberty, 1960). *T. triandra* and *T. australis* is the notable case for species confusion.

Morphologically, *Themeda* is highly recognizable by paniculate inflorescences comprising more than one raceme. The raceme includes a spatheole subtending a cluster of spikelets composed of involucral homogamous spikelets, fertile spikelet pairs and a terminal triad (Clayton and Renvoize, 1986; see Figure 2.1). The raceme organization can resemble a fan or spindle depending on the exsertion of the involucral homogamous spikelets and the density of spikelets in the raceme (Clayton and Renvoize, 1986; Chen and Zhuang, 1989). There are also appendage organs or awns project from the fertile lemma and possessing hygroscopic properties. Adams and Tainton (1990) found that the hygroscopic properties in *Themeda triandra* enabled seeds to move along the soil surface.

The basic chromosome number of *Themeda* is x = 10 in which higher polyploidy from triploid to hexaploid have been recorded for some species (Hayman, 1960; Carnahan and Hill, 1961; Liebenberg, 1986; Fossey and Liebenberg, 1987; Liebenberg et al., 1993).

Apomixis is pronounced in polyploid *Themeda* as shown in *T. quadrivalvis* and *T. triandra* (Brown and Emery, 1957, 1958; Evans and Knox, 1969; Birari, 1980; Liebenberg, 1990). 4-nucleate aposporous embryo sacs of *T. triandra* were detected by Brown and Emery (1957, 1958) and Liebenberg (1990). The process began with the degeneration of megaspore mother cells. Next, unreduced embryo-sac initials were generated and formed aposporous embryo sacs. After two cell divisions, the 4 nuclei were detected within each embryo sac containing one egg, one polar nucleus and two synergids. (Brown and Emery, 1957; Koltunow, 1993; Hand and Koltunow, 2014). The association of ploidy levels and degree of apomictic expression was explained (Birari et al., 1980; Asker and Jerling, 1992; Carman, 1997; Roche et al., 2001; Whitton et al., 2008). Obligate apomixis was observed in octa- and enneaploids of *T. triandra*. The intermediate state of tetraploids and hexaploids represented facultative apomicts, where both unreduced and reduced embryo sacs occur. (Birari et al., 1980; Liebenberg et al., 1993). Perhaps, apomixis might mitigate the adverse consequences from being highly polyploid via asexual reproduction (Gustafsson, 2010). Simultaneously, the expansion of genetic diversity and mutation in polyploids could substitute for the lack of recombination in asexual apomicts (Comai, 2005; Ozais-Akins and van Dijk, 2007).

Figure 2.1. *Themeda triandra* inflorescence and raceme structures, from Shouliang & Phillips (2006); 1. Panicle inflorescence 2. Raceme subtended by spatheole at the base 3. Triad comprising one sessile spikelet and two pedicelled spikelets 4. Involucral homogamous spikelets 5. Upper lemma

2.1.2 Genus *Heteropogon* Pers.

Similar to *Themeda*, the geographic distribution of *Heteropogon* covers the tropics and subtropics of Africa, Asia, Australia and some parts of Oceania, such as the Hawaiian Islands and South America (Bews, 1929; Bor, 1960; Clayton and Renvoize, 1986; Wagner et al., 1990; Goergen and Daehler, 2001; Shouliang and Phillips, 2006). The biodiversity hotspot of the genus is India where all species can be found (Deshpande, 1988). However, no reports have proved about the potential centre of origin of the genus.

Heteropogon was first designated as a genus by Persoon (1807) with *H. glaber* as the type species. Prior to the delineation of *H. glaber*, Linnaeus (1753) had already assigned *Andropogon contortus* L. Roemer and Schultes (1817) compared *Andropogon contortus* and *Heteropogon hirsutus* (now illegitimate name) specimens with *H. glaber* one. They subsequently applied a new combination and changed the name into *Heteropogon contortus* (L.) P. Beauv. ex Roem. By priority, *H. contortus* substituted for *H. glaber* as the type species whereas *H. glaber* was eventually recognized as the synonym of *H. contortus*. Also, Hackel (1883) considered *H. hirsutus* and *H. glaber* as varieties of *H. contortus*. Later, *H. glaber* was selected as the lectotype of *H. contortus* by Hitchcock (1920).

Several names had been proposed under *Heteropogon*; however, most of them were considered synonyms. This is the case in *H. contortus*, *H. melanocarpus* and *H. triticeus*. They have wide distribution ranges and morphological variations in which invoke the recognition of redundant species. For example, *H. hirtus* and *H. glaber* were also reduced to the synonyms of *H. contortus*. In the present, there are six accepted *Heteropogon* species (Chavan and Mehta, 1960; Clayton and Renvoize, 1986; Shouliang and Phillips, 2006; The Plant List, 2013; Kellogg, 2015). Most of them are transferred from *Andropogon* L. Among the six species, the species delimitation of *H. polystachyos* Schult. is inconclusive. It was first proposed as *Andropogon polystachyos* by Roxburgh (1820) who distinguished *A. polystachyos* from *A. contortus* by the habit. Based on Roxburgh's description, Schultes (1824) legitimately applied the name *H. polystachyos* to the species. However, Deshpande (1988) collapsed it into the subspecies of *H. contortus*.

Morphologically, a solitary raceme is common inflorescence structure in genus *Heteropogon*. Within the raceme, at least one pair of well-developed homogamous spikelets appear at a position in the lower 23 of the inflorescences (Deshpande, 1988). Above that position, fertile spikelet pairs occur by dissimilar sessile and pedicelled spikelets. According to LeRoux and Kellogg (1999), *H. contortus* is monoecious. All pedicelled spikelets are staminate. Non-homogamous sessile spikelets in the distal part of the inflorescence are pistillate as anthers failed to develop. However, there are no evidence on how the inflorescence develops in other species. At the raceme terminal, awns converge and twist around one another to form a stiff appendage.

According to cytogenetic investigations, *H. contortus* has a wide range of chromosome numbers from diploid (2x) to enneaploid (9x) (Darlington, 1956; Emery and Brown, 1957; Tothill and Hacker, 1976; Nadeem Ahsan et al., 1991). Tothill and Hacker (1976) also proposed the correlation between chromosome numbers, phenology and geographic distribution. Late-flowering tetraploid populations dominate in the Tropics while mixed phenology and ploidy levels were found in temperate populations. A novel early-flowering habit might aid movement towards sub-tropics zones. In addition, chromosome numbers of *H. melanocarpus, H. ritchiei* and *H. triticeus* have been recorded (Deshpande, 1986).

It is likely that apomixis does get involved because of high level of polyploidy. Notable cases were observed in obligately apomictic *H. contortus* (Brown and Emery, 1957;

Carino and Daehler, 1999). In polyploid varieties, the degeneration of megasporocytes took place in the time that apomictic initials started to form aposporous embryo sacs. In each sac, unreduced cells divided to generate a 4-nucleate embryo sac: one egg, one polar nucleus and two synergids. This 4-nucleate sac will normally undergo embryonic and endosperm development. On the other hand, diploid populations are absolutely sexually reproductive and produce normal 8-nucleate embryo sacs (Gustafsson, 1947).

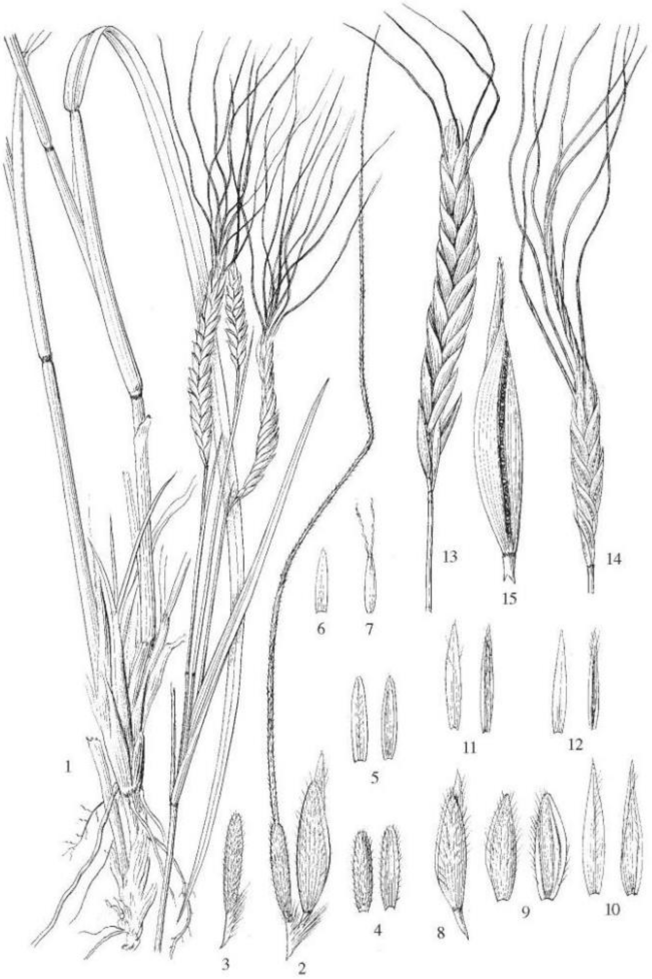

Figure 2.2. *Heteropogon contortus* inflorescence and raceme structures from Shouliang & Phillips (2006); 1. Spike-like inflorescence 2. Fertile spikelet pair composed of one sessile spikelet and one pedicelled spikelet 3. Sessile spikelet 4. Lower glume of sessile spikelet 5. Upper glume of sessile spikelet 6. Lower lemme of sessile spikelet 7. Pistil 8. Pedicelled spikelet 9. Lower glume of pedicelled spikelet 10. Upper glume of pedicelled spikelet 11. Lower lemme of pedicelled spikelet 12. Upper lemme of pedicelled spikelet 13. Solitary raceme of *H. contortus*

2.1.3 Overall view of Andropogoneae Morphology and Anatomy

Phylogenetic analyses of the tribe based on morphology and molecular data (Kellogg and Watson, 1993; Kellogg, 2000; Skendzic et al., 2007; Teerawatananon et al., 2011; Welker et al., 2015; Arthan et al, 2017) have identified morphological key innovations contributing to the rapid diversification of the tribe. Andropogoneae exhibits branched or unbranched inflorescences. These forms could lead to many inflorescence forms such as panicles, digitate racemes and spikes. This depends on how fast and where the branching occurs in the main axis, which is controlled by genetics (Kellogg, 2000 and 2015). Andropogoneae also developed the spikelet pair, consisting of sessile and pedicelled spikelets. Sessile and pedicelled spikelets express different sexual states, bisexual and male or barren or female (rare but seen in *Eriochrysis* P. Beauv.), respectively. Commonly, each spikelet is composed of two florets. In sessile spikelet, the upper floret is bisexual but the lower one is male or barren. Yet, the two florets of the pedicelled spikelet are male or barren (Clayton and Renvoize, 1986; Kellogg, 2000). Awns can be seen in most Andropogoneae except those in subtribe Rottboelliinae (Clayton and Renvoize, 1986). The derivation of the awn in Andropogoneae might be involved in sex expression in spikelet pair as it can be seen in either pistillate or hermaphrodite florets (Kellogg, 2000). In addition, Andropogoneae usually have fragile racemes that break at the nodes and disperse diaspores.

Andropogoneae leaf-blade anatomy and micromorphology was extensively scrutinized by Renvoize (1982). Among 86 species, leaf-blade anatomy is uniform across the tribe. From Figure 2.3 below, the leaf epidermis is composed of long cells, short cells, stomata, silica bodies and the presence of micro hairs on the lower epidermis in an iterative arrangement. Long and short cells alternate over the epidermis by having stomata, silica bodies and micro hairs inserting between these cells.

There are a few differences among leaf transverse sections in tribe Andropogoneae. Leaf outlines are mostly flat but are also V-shaped or U-shaped in some genera such as *Hackelochloa* Kuntze and *Ischaemum* L. (Metcalfe, 1960; Ellis, 1979; Renvoize, 1982; Traiperm et al., 2011; Arthan et al., 2016). In V- or U-shaped anatomy, a group of parenchyma cells can be found at the midrib zone (Traiperm et al., 2011; Arthan et al, 2016). The largest vascular bundle, primary or first-order bundle, is positioned at the midrib. Successive smaller bundles, e.g., second-order or third-order bundles, are organized on two sides of the first one throughout the transverse section. Different vascular bundle orders can be distinguished by cell types, bundle sheath organization and circumference. Hence, the sizes of vascular bundles are continually reduced as the orders increase. In addition, the vascular bundles are associated to sclerenchyma girdles having pointed-capped shape slant towards the epidermis (Ellis, 1976 and 1979). On the upper epidermis, bulliform cells usually occur throughout the outline and can be seen as relatively large irregular and colorless cells (Metcalfe, 1960). For culm anatomy, de Wet (1960) briefly described the characteristics of the Andropogonoid culm /anatomy with relatively small cells in the vascular bundle sheath. However, deep details were reported in some genera of subtribe Ischaeminae and Rottboelliinae by Traiperm et al. (2011) and Arthan et al. (2016). Generally, a few layers of sclerenchyma rings were found under the epidermis of the culm. The outermost circle of vascular bundles was inserted more or less into the sclerenchyma ring. In the special case of the genus *Hackelochloa*, chlorenchymatous instead of sclerenchymatous tissue beneath the epidermis encircled the culm .

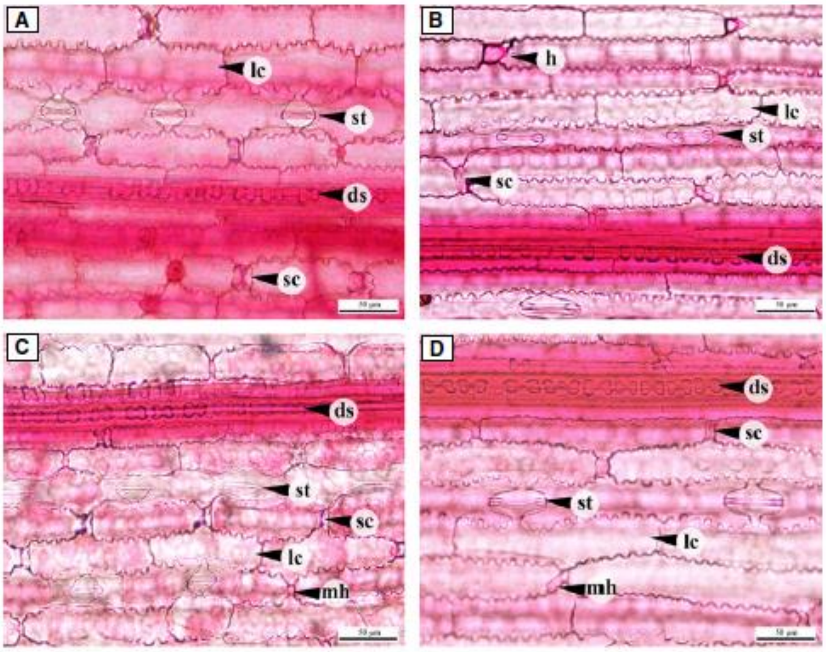

Figure 2.3. Typical Andropogonoid leaf blade anatomy from *Hackelochloa granularis* (left panel; A and C) and *Hackelochloa porifera* (right panel; B and D). The figure illustrates common anatomical structures: 1. long cell (lc) 2. short cell (sc) 3. stoma (st), dumbbell-shaped silica bodies (ds) 4. hair (h) 5. microhair (mh), Adapted from Arthan et al. (2016)

2.1.4 Comparative Macro- and Micromorphology of the genera *Themeda* Forssk. and *Heteropogon* Pers.

The *Themeda* inflorescence is characterized by a cluster of racemes subtended by a spatheole. The raceme(s) can be solitary or densely packed to form a compound panicle. The raceme always bears 7 homogamous spikelets at the base, and then at least one fertile spikelet and triad. The number of fertile spikelets and triads varies among species and is of value for the classification (Morales, 2014; Veldkamp, 2016). Homogamous spikelets can be borne at the same or different levels which determines the raceme shapes. From the morphological point of view, *Themeda* is similar to *Heteropogon* in having homogamous spikelets, but the latter genus only forms terminal solitary racemes.

Root, leaf, and stem anatomy of *Themeda triandra* had been thoroughly investigated by Goossens and Theron (1934). The anatomy showed specific adaptations to dry environments. For example, cells in the outer and middle layers of the root cortex were usually degraded to form air spaces. It was hypothesized that the perforation acts as aerenchyma to provide oxygen for root (Dunn, 1928) or to reserve the water (Goossens and Theron, 1934). Like most plants, the lignification of cell walls is seen in the endodermis and pericycle. This property of cell walls might reduce evaporation and water loss (Scott, 1928; van Fleet, 1961). Goossens and Theron (1934) also observed bulliform cells (previously named as motor cells) on the upper epidermis. One of the interpreted functions of bulliform cells is to help leaf blades respond to arid conditions by sensing water availability with bulliform cells (Shields, 1951; Mauseth, 1988). These cells are swollen and cause the blades to spread if surrounding water is sufficient. When the water is lost through transpiration, they shrink and the blades fold up (Esau, 1965).

Two types of caryopses, one with a concave adaxial side with grooved embryos (type 1) and the other with a flat adaxial side with keeled embryos (type 2), have been observed in spathaceous genera including *Themeda* and *Heteropogon* (Zhang et al., 2014). *Themeda* exhibits both caryopsis types whereas *Heteropogon contortus* displayed only the type 1 caryopsis. In this study, the type 1 caryopsis was hypothesized to be more primitive than the type 2 without further trait evolutionary analyses. However, the neotenic condition in caryopsis was observed in *T. triandra*. The young caryopsis had a concave adaxial side and changed into the flat one when it was mature. Interestingly, *T. anathera* possesses a type 1 caryopsis. The evidence coincides with the molecular dating analyses by Dunning et al. (2017), showing that *T. anathera* an early diverging species and bears pleistomorphy of the group.

In contrast to *Themeda*, *Heteropogon* anatomy has been less studied. Only Renvoize (1982) reported uncommon characteristics in some Andropogonoid genera that do not conform with morphological trends within the tribe. For *Heteropogon*, *Heteropogon melanocarpus* (Elliott) Benth. has glands situated below the vascular bundles on the abaxial side, but the function remains elusive.

Although there are not many investigations on *Themeda* and *Heteropogon* anatomy, the evidence documented above implies that more anatomical data are needed for taxonomic studies. Ellis (1974 and 1979), Goossens and Theron (1934) and Prat (1932) concordantly discovered that leaf transverse sections and epidermis provide adequate characteristics to classify grasses at the generic, species, and variety levels. All in all, past works suggest that anatomical variation may yet reveal synapomorphies in *Themeda* and *Heteropogon*.

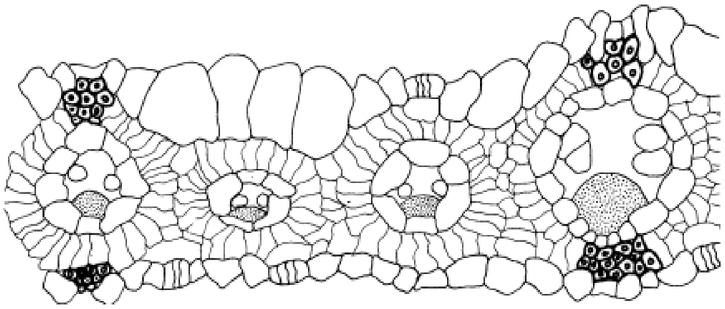

Figure 2.4. Tranverse section of *Themeda triandra* leaf anatomy showing primary vascular bundle (the right most bundle), lower-ranked bundles and secondary bundle (the left most bundle), from Renvoize (1982).

2.2 Phylogenetic Investigations

2.2.1 Nature and Characteristics of Chloroplast and Nuclear Data

Nuclear and plastid DNA sequences (abbreviated as nrDNA and cpDNA, respectively, in the following sections onwards) provide useful sources of data for evolutionary inference (Palmer, 1985; Olmstead and Palmer, 1994; Small et al., 2004). Reviewing the characteristics of these data helps understand and explain phylogenetic phenomena.

Plastid markers are still one of the most chosen DNA data for plant phylogenetic reconstruction plant due to the high copy number of chloroplasts per plant cell, structural stability in terms of conserved gene content and arrangement, uniparental inheritance, and haploidy (Palmer, 1985; Olmstead and Palmer et al., 1994; Dunning et al., 2017). The occurrence of multiple copies facilitates DNA extraction, polymerase chain reaction (PCR) and sequencing. Due to structural stability, universal primer design has been simplified (Small et al., 2004). Apart from the PCR-based approach, high chloroplast copies ensure high coverage of reads from next-generation sequencing (NGS). Plastome assembly from NGS reads can also be carried out almost effortlessly by mapping the plastome of interest to the plastome of its related taxa. From the evolutionary perspective, haploidy and one-sided inheritance guarantees the acquisition of orthologous sequences and the absence of intraspecific variation owing to no recombination. Orthologs are genetic products resulting from when two lineages split from a common ancestor (Jensen, 2001) rather than reticulation or gene duplication (Small et al., 2004), and truly reflect relationships and depict descendant taxa within the lineage. Thus, the phylogenetic interpretation can be simplified by using cpDNA.

In the early years, most plant systematic studies emphasized plastid markers and spacers, especially *rbcL* (Taberlet et al., 1991). Besides *rbcL*, several regions of the chloroplast genome were also tested for nucleotide variations and phylogenetically informative value (Chase et al., 2007; Shaw et al., 2007; Dong et al., 2012; Uncu et al., 2015). These include genes, intergenic spacers and introns that are chiefly employed in evolutionary works, such as *matK*, *atpB* and *ndh*F for the familial level (Hilu and Alice, 2001; Pirie et al., 2008; Edwards and Smith, 2010) and non-coding spacers *trn*T–*trn*L, *trn*L–*trn*F and *atp*B–*rbc*L and introns *rpl16*, *rpo*C1, and *trn*L for the lower ranks due to higher substitution rates (Kelchner & Clark, 1997; Downie et al., 1999; Zhang, 2000; Cerros-Tlatilpa et al., 2011; Saalera et al., 2017).

However, some drawbacks can be found when using chloroplast data. They partly explain hybridization history and polyploidization events because their phylogenies will place taxa on either the maternal or paternal clade. At times, unresolved phylogenetic outcomes at deep divergence events were produced by inadequate information from plastid DNA sequences due to a relatively low rate of nucleotide substitution. Consequently, these drawbacks of the plastid markers were fixed by adding nuclear data as they contain relatively higher substitution rates among genes and sites, and biparental inheritance can be found.

The internal transcribed spacer (ITS) of the18S-5.8S-26S region and the spacers of the 5S arrays were applied in phylogenetic analyses (Hori et al., 1985; Baldwin et al., 1992; Álvarez and Wendel, 2003). Inference through ITS and other nuclear markers has several advantages. Due to biparental inheritance, past events of introgression, hybridization and polyploidization can be unveiled as the key drivers of angiosperm speciation (Paun et al., 2009; Soltis & Soltis, 2009; Kellogg, 2016). According to previous investigations, ITS sequences contain significant variation across species, generic and familial levels. Practically, ITS is therefore informative for phylogenetic resolution. Besides, small target size and high number of copies in the genome facilitate the amplification by PCR and assure ample read coverages in next-generation sequencing (Álvarez and Wendel, 2003).

However, these elements reflect evolutionary lability due to ancient polyploidization, which in turn, paralogs unintentionally mingle in the analysis and misinterpret phylogenetic relationships. Hence, the impact of the ITS evolutionary phenomena should be thoroughly examined before utilized.

ITS sequences scatter and have multiplied from hundreds to thousands of copies in the genome. Concerted evolution has been presumed to homogenize ITS sequences via unequal crossing over and gene conversion. Its strength to make ITS tandem arrays uniform is incomplete (Smith, 1976; Elder and Turner, 1995; Liao, 1999; Ohta, 2010; Poczai and Hyvönen, 2010; Naidoo et al., 2013). The sequences have been pseudogenized and diverged extensively since each copy is capable of evolving independently at different rates from its functional duplicates (Álvarez and Wendel, 2003; Balakirev and Ayala, 2003; Matyášek et al., 2007; Xu et al., 2017). Compared to their functional counterparts, ITS pseudogenes generally show relatively lower stability in secondary structure, higher AT content, indel length variation and substitution rates (Mayol and Rosselló, 2001; Bailey et al., 2003; Feliner

& Rosselló, 2007). Therefore, ITS pseudogene is considered a paralog to its counterpart (Xiao et al., 2010). Apart from pseudogenes, some portions of ITS genetically branched off from one another to form polymorphic sequences. If the concerted evolution partially acts on these elements, again, paralogous sequences are produced (Small et al., 2004). These paralogous ITS data might be sampled in the analysis and complicate the interpretation in tree-based results by giving long branch attraction (Kita and Ito, 2000) and multiple positions of a single taxon on a phylogeny (Kita and Ito, 2000; Muir et al., 2001).

Orthologs and paralogs should be examined and distinguished to obtain reliable sequences (Feliner & Rosselló, 2007). The most basic approach is to estimate sequence similarity and to test through phylogenetic analysis. Theoretically, orthologous and paralogous sequences are sampled from a heterogeneous pool of sequences. Orthologs themselves cluster in their own clade in the tree rather than with their paralogs. However, problems with this approach can arise from an incomplete sampling of whole gene families among taxa due to preferential PCR amplification which then misleads phylogenetic inference. In this case, a more distant ortholog could be interpreted as a paralog. Another issue concerns *in vivo* and PCR-mediated recombination producing chimeric sequences that are phylogenetically meaningless (Cronn et al., 2002).

However, the new idea was developed to overcome adversities in identifying and distinguishing orthologs and paralogs, biased DNA sampling in nrDNA and weak phylogenetic signal from both cpDNA and nrDNA (Sang, 2002; Small et al., 2004). The selection of single-copy genes is the alternative method to reduce drawbacks from ITS sequences and acquire unlimited nuclear information from genes and gene families across the taxonomic hierarchy (Estep et al., 2012; Hawkins et al., 2015; Hu and Li et al., 2017; Sun, 2017). For example, *Adh*, DHAR, G3PDH, GBSSI, GPAT, MADS-box genes, PHYB, and PGI were applied in several analyses (Small and Wendel, 2000; Tank and Sang, 2001; Malcomber, 2002; Järvinen et al., 2004; Small et al., 2004; Fukuda et al., 2005; Rousseau-Gueutin et al., 2009; Welker et al., 2015, 2016). Large-scale screening of candidate nuclear genes by Zhang et al. (2012) from genome comparison yielded 1083 phylogenetically informative nuclear genes. Likewise, Estep et al. (2012) successfully gleaned eleven nuclear markers associated with grass inflorescence architecture by using newly designed degenerate primers.

The effort to search and adopt low-copy genes resolves a variety of problems. Low-copy and single-copy genes have been important as additional proof of past incidents such as hybridization, introgression or lineage sorting when incongruence among cpDNA and nrDNA trees was detected. In the case study by Welker et al. (2015, 2016), a new species of South

American *Saccharum* L. (currently known as *Saccharum intermedium* Welker & Peichoto) was initially screened by four low-copy nuclear genes (*apo1*, *d8*, *Erect panicle2* and *Retarded palea1*). They clearly identified the two *Saccharum* progenitors from South America. This was also supported by morphology and geographic distribution. It is also particularly true in genus *Eriochrysis* P. Beauv. (Welker et al., 2016). According to Rousseau-Gueutin et al. (2009), GBBSSI-2 and DHAR helped discover the evolutionary history of the genus *Fragaria* L. There are three main diploid lineages with independent succeeding polyploidizations into tetraploid species. Thereafter, allopolyploidization among tetraploids themselves and between tetraploids and diploids generated 6X and 8X *Fragaria* species. Apart from tracing polyploidy events, low-copy genes can resolve deep divergence events (Zeng et al., 2014).

2.2.2 Nuclear VS Plastid Data: When Two Genomes Tell Different Stories

There has been high incongruence among different gene trees from single-gene to genome scales (Lihová et al., 2006; Kim and Donoghue, 2008; Pelser et al., 2010; Straub et al., 2012). The incongruence is caused by distinct evolutionary trajectories among different genomes in terms of gene duplication, hybridization, introgression and incomplete lineage sorting (Page and Charleston, 1997; Wendel and Doyle, 1998; Baum, 2007; Zou and Ge, 2008; Twyford and Ennos, 2012).

The phylogenetic patterns of polyploidy via either allopolyploidy or autopolyploidy are illustrated in Figure 2.5 (Kellogg, 2016). For instance, if full sampling can be achieved, an allotetraploid (4x) species will be shown in two different places in a nuclear phylogeny with its two putative progenitors. Unless sampling is adequate, it will appear on the tree without any indication of genome donors. In more complex situations, polyploid species can speciate after auto- or allopolyploidization. Different allopolyploid species will group with one of its progenitors in full sampling. If multiple speciation events occur, two different lineages of allopolyploids can mix up and appear as sister clades when progenitors are not included. This could give rise to an ambiguous or incorrect interpretation from the phylogeny unless the sampling is complete.

In grasses, most phylogenetic disparities were caused by hybridization and introgression. According to Zhang et al. (2012), GBSSII sequences, despite being single-copy, were detected in two copies in some species of Arundinarieae (temperate bamboos). Those copies are located apart in the phylogeny, indicating the occurrence of hybridization in this group. By comparing plastid and GBSSII trees, potential hybrids could be identified as they appeared in more than one position, and their maternal and paternal progenitors could be singled out. In tribe Triticeae, chloroplast and nuclear datasets cooperatively uncovered reticulate history (Mason-Gamer et al., 2010; Escobar et al., 2011; Mason-Gamer, 2013). For example, allotetraploid Asian *Elymus* (StStYY) was affirmed to obtain the St genome from *Pseudoroegneria*. There is still lack of robust proof of the Y genome donor due to insufficient sampling or the extinction of Y genome donor. In addition, the positions of *Elymus* and *Pseudoroegneria* taxa in St-genome clades were not consistent among three nuclear phylogenies at interspecific and intergeneric levels. This points out that introgression may play a crucial role in *Elymus* allotetraploid history. For the genus *Bromus*, the parentage and reticulate origin of section *Genea* were scrutinized by three nuclear markers, ITS1, ITS2 and *Waxy,* and two chloroplast markers, *trnT-trnL* and *trnL-trnF* (Fortune et al., 2008). ITS and chloroplast phylogenies support one another to sort out the maternal lineage. For instance, *B. rubens* (4x) clustered with *B. tectorum* (2x) by ITS data but fell into clade with *B. fasciculatus* (2x) in the chloroplast tree. This prominent proof, analysed with a number of base substitutions in chloroplast and nuclear sequence, implied that the maternal and paternal progenitors of *B. rubens* (4x) shared similar lineage to *B. fasciculatus* (2x) and *B. tectorum* (2x), respectively. Furthermore, *B. rubens* (4x) appeared two times in the *Waxy* tree with *B. fasciculatus* (2x) and *B. tectorum* (2x). Furthermore, the low-copy nuclear gene *Waxy* (Baumel et al, 2002; Ingram and Doyle, 2004; Fortune et al., 2007) could trace the polyploid history of octaploid *B. diandrus* (8x) that occurred thrice with *B. rigidus* (6x) and one time with *B. sterilis* (2x). All in all, the interpretation from various gene trees not only leads to the summary of monophyly or polyphyly of the groups but also the evidence from evolutionary processes, especially hybridization and introgression that are ubiquitous in Poaceae.

Gene trees could deviate from the true species tree by incomplete lineage sorting (Maddison and Knowles, 2006; Degnan and Rosenberg, 2009; Som, 2013). The process stems from ancestral polymorphisms in some genes being retained in two organisms. A relatively short time is not sufficient for specific loci to be fixed by evolutionary forces such as genetic drift (Maddison and Knowles, 2006). Thus, the nucleotide variation of some genes is not separated among two or more different species. This phenomenon is more probable when the population size is large and divergence time is short (Maddison and Knowles, 2006). When more than one gene is analyzed, phylogenetic trees may have different topologies. According to Jakob and Blattner (2006), the observation of 18 polymorphic *trn*L-F haplotypes in *Hordeum* inflated the possibility that incomplete lineage sorting will occur, especially in rapidly speciating descendants that harbour long-surviving haplotypes (4 Mya). Moreover, the loss and survival of certain haplotypes in distinct distribution ranges also causes discordance between ITS and chloroplast analyses.

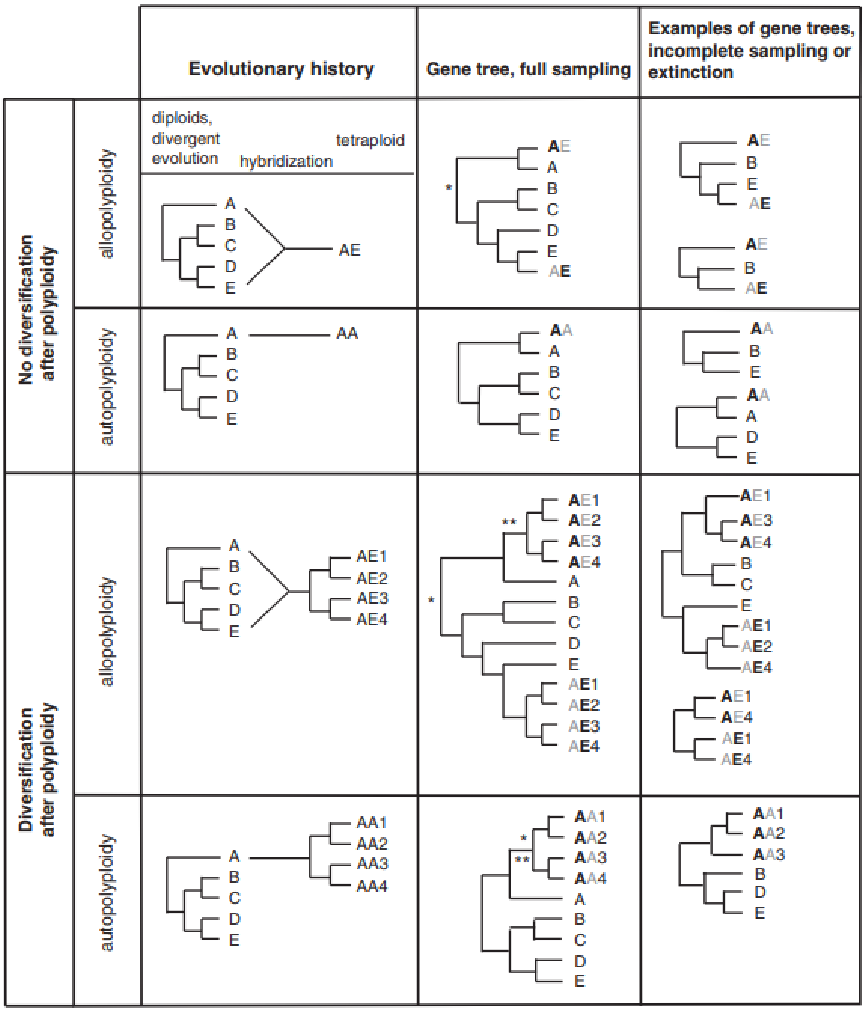

Figure 2.5. Phylogenetic scenerios of autopolyploid and allopolyploid plants under various evolutionary histories and sampling methods, taken from Kellogg (2016).

2.2.3 Sequencing Technologies

A broad sampling of DNA data is required in order to study the complex genetic and evolutionary history of grasses. In 2008, more than 11 Gb of Poaceae sequences were available in GenBank (Buell 2009). Various sequencing technologies have contributed to sufficient nucleotide data to explain a plethora of biological questions such as the origin of a particular taxon, species authentication and evolutionary relationships (Soltis & Soltis, 2003; Yang & Rannala, 2012). Here I describe sequencing methods applied in the field of grass evolution, some of which have been utilized for decades and others have been recently applied.

In the first instance, Sanger sequencing is the foundation to the studies of grass phylogeny, which is still used across subfamilies and in large-scale classifications (Hilu & Alice, 2001; GPWG, 2001; Davis and Soreng, 2007; Skedzic et al., 2007; Teerawatananon et al., 2011; GPWG II, 2012; Morrone et al., 2012; Welker et al., 2015; Soreng et al, 2017). For this method, a few target genes and spacers are amplified by PCR. Specific primers are required to bind with specific sites of PCR product in sequencing process. The DNA sequences from Sanger method can be sequenced in a limited length of less than one kilobase (Heather & Chain, 2015).

To extend sequence length from the original Sanger method, DNA sequences are broken up into numerous small segments. Sequence segments are cloned and sequenced by the Sanger method. Relatively long DNA sequence is produced from the assembly of contiguous sequence *in silico* (França et al., 2002; Kulski, 2016). This methodology is called ‘shotgun sequencing’ that has facilitated whole genome-scale projects (Malé et al., 2014; Tin et al., 2014; Teh et al., 2017). In grasses, complete chloroplast genomes of various crops were successfully constructed by the shotgun approach such as *Agrostis stolonifera* L., *Hordeum vulgare* L., *Oryza sativa* L., *Sorghum bicolor* (L.) Moench and *Triticum aestivum* L. (Matsuoka et al., 2002; Saski et al., 2007) and whole genomes of *Brachypodium distachyon* (L.) P. Beauv. (International Brachypodium Initiative, 2010) and *Sorghum bicolor* (Paterson et al., 2009, 2018).

In pyrosequencing, each nucleotide is sequenced by the activity of polymerase. When correct complementary dNTP pairs with the nucleotide on the template, pyrophosphate (PPi) will be released. Then, ATP sulfurylase converts PPi into ATP. ATP reacts with luciferin catalysed by luciferase. The reaction emits light that will be detected by the machine. Next generation sequencing, such as the 454, Solexa and Illumina (Levy & Myers, 2016) platforms, is based on pyrosequencing. In preparation, each DNA sample is sheared into a number of fragments which are then ligated with a specific adapter. This method allows multiplex DNA samples to run in parallel and augment the amount of DNA sequence. DNA sequences are generated in short reads of approximately 150 to 200 base pairs through emulsion PCR or bridge amplification (Medini et al., 2008; Heather and Chain, 2016).

Several model and non-model grass draft genomes are generated by this method. The application helped delve researchers to into novel functional genes, comparative genomics, and genome duplication events by comparing large amount of DNA data among related species such as *Brachypodium disrachyon* (The International Brachypodium Initiative, 2010), *Oryza sativa* (Yu et al., 2005), *Setaria italica* (L.) P. Beauv. (Zhang et al., 2012), *Sorghum bicolor* (Paterson et al., 2009) and *Zea mays* L. (Schnable et al., 2009). Likewise, full plastome reads were acquired from high-throughput of base calls for millions of DNA fragments with high coverage and accuracy from Illimina sequencing. Currently, a phylogenomic approach based on plastomes has helped disentangle the issues of unresolved and newly-established clades in PACMAD lineages (Cotton et al., 2015; Burke et al., 2016;

Teisher et al., 2017; Arthan et al., 2017; Saarela et al., 2018). Besnard et al. (2013) pinpointed a core-panicoid position of the isolated monotypic genus *Lecomtella* from Madagascar by next generation sequencing (NGS) data, further having a clear-cut taxonomic verification to place it in the separate tribe Lecomtelleae.

Acquisition of phylogenetic information can be impeded by the complexity of nuclear genomes and degraded DNA in old herbarium specimens making the selection of low-copy nuclear loci and whole genome sequencing difficult, respectively. High-throughput sequencing technologies have been developed to resolve these issues and maximize the power of phylogenetic tools. First, target enrichment (or sequence capture) gains a large number of low-copy nuclear loci from hundreds to thousands of copies (Mandel et al., 2014; Weitemier et al., 2014; Nicholls et al., 2015; Hart et al., 2016) in one run. Specifically designed RNA probes from transcriptomics and EST databases are used to hybridize bait sequences at reasonable depth from the genome (Mamanova et al., 2010; Mertes et al., 2011; Cronn et al., 2012; Stull et al., 2013). This reduces background noise from non-target DNA regions. Plants have frequently experienced polyploidizations which cause redundancy in genetic composition (Van de Peer et al., 2009; Jiao et al., 2011; Grover et al., 2012; Zimmer & Wen, 2015). Target enrichment is appropriate and accurate for species-level analyses as orthologs and paralogs can be specified. There are at least three types of target enrichment methods: (1) PCR-based amplification, (2) hybridization-based sequence capture and (3) molecular inversion probe-based amplification (Grover et al., 2012). Many studies extensively adopted the hybridization-based approach coupled with next-generation sequencing (Nicholls et al., 2015; Schmickl et al., 2015; Stephens et al., 2015; Moore et al., 2017). According to Stephens et al. (2015), selective and highly informative data from target enrichment resolved the relationships of recently radiated clades of carnivorous plants, illuminating taxonomic and conservation status.

DNA from aged herbarium and museum specimens is often extremely degraded. Genome skimming primarily focuses on abundant high-copy regions in organellar genomes or repetitive regions with comparatively low coverage, remaining in the old specimens (Straub et al., 2012; Malé et al., 2014; Weitemier et al., 2014; Dodsworth, 2015; Zimmer and Wen, 2015). Genome skimming can achieve minimum depth of 40x and 30x of nrDNA and chloroplast DNA by paired-end and single-end NGS data (Straub et al., 2012). Bock et al. (2013) also utilized complete plastomes, partial mitochondrial genomes and 5S and 35S nrDNA produced by genome skimming to clarify the origin of Artichoke (*Helianthus tuberosus* L.). Additionally, low-copy nuclear genes can be extracted by this method. For example, abundant *d8*, PHYB, *tb1* references from the NCBI database can be mapped to NGS reads to glean and finalize sequences from non-reference samples. Unless they are practically useful, they are still beneficial in probe and primer designing for target enrichment (Straub et al., 2012).

2.2.4 *Themeda* and *Heteropogon* in Evolutionary Framework

Despite an increase in molecular data in disentangling taxonomic questions, few phylogenetic investigations have included sampling of *Themeda* in the analyses. Combined morphological and anatomical data in Kellogg and Watson (1993) yielded the result that the clade of *Themeda*, *Iseilema* Andersson. and *Hyperthelia* Clayton was in close affinity to the clade of *Apluda* L., *Apocopis* Nees and *Pseudanthistiria* (Hack.) Hook. f. On this matter, inflorescence structure can explain the connection among *Themeda*, *Iseilema, Hyperthelia* and *Pseudanthistiria*, but there is still lack of evidence for *Apluda* and *Apocopis*. According to Skendzic et al. (2007), *Themeda triandra* was placed with *Heteropogon contortus*, two representatives of *Iseilema* and two *Chrysopogon* Trin. (including *Vetiveria* Bory) with low support in the ITS tree. However, the analysis failed to describe the relationship of *Themeda* to other genera in the *trn*L-F tree due to polytomies. A combined gene tree from Teerawatananon et al. (2011) showed the monophyly of *Themeda*. Again, it was not possible to interpret the relationship of the *Themeda* clade to the others because of polytomy. In GPWG II (2012), *Heteropogon contortus*, *Iseilema macratherum*, *Themeda avenacea* and *Themeda triandra* showed strong affinity in the plastid tree which is in agreement with morphology (Clayton and Renvoize, 1986). In Estep et al. (2014), *Heteropogon triticeus*, *Themeda arundinacea* (Roxb.) A. Camus, *Themeda triandra* and *Themeda villosa* (Poir.) A. Camus were put in a well-supported clade next to the *Cymbopogon* and the *Bothriochloa-Capillipedium-Dichanthium* clades. Independent allotetraploidy events of *T. triandra* and *T. villosa* are illustrated by a combined single-gene tree. According to Welker et al. (2015), *Themeda arundinacea* and *Heteropogon triticeus* form a sister clade to the *Bothriochloa-Capillipedium-Dichanthium* clade. The *Themeda-Heteropogon contortus* clade was also retrieved in Arthan et al. (2017), and showed close affinity with *Heteropogon triticeus* and *Dichanthium sericeum*, this representing the *Bothriochloa-Capillipedium-Dichanthium* clade.

Dunning et al. (2017) extensively sampled 18 *Themeda* species from wide geographic regions (Fig 2.6). In this study, the analysis supported the conclusion that South Asia is the origin of the genus and *Themeda triandra* itself. According to the molecular dating analyses, *Themeda triandra* dispersed to Australia via mainland Southeast Asia 1.3 mya and has rapidly colonised Africa since 0.9 Mya. *Themeda triandra* is now considered a ferocious invader and has become a major component in grassland biomes in Africa, Australia, and Madagascar.

However, a full picture of *Themeda* evolution has not been reached due to incomplete sampling of *Themeda* species.

Heteropogon may not be monophyletic. *Heteropogon contortus* fell into clades with the genus *Themeda* while *H. triticeus* formed a separate clade when inferred from plastome data (Estep et al., 2014; Arthan et al., 2017). In Hackel et al. (2018), both *H. contortus* and *H. melanocarpus* were included in the analysis but did not form a clade. The placement of *H. melanocarpus* was nested within the *Themeda* clade with high support. From a phylogenetic point of view, *Heteropogon* appears to be a polyphyletic genus but basing this conclusion on only three widespread species (*H. contortus, H. melanocarpus* and *H. triticeus*) may be superficial (Estep et al., 2014; Arthan et al., 2017; Dunning et al., 2017). As mentioned above, there is still lack of insight into *Heteropogon*'s evolution since no publications have examined all species in the same analysis.

Even though nuclear and chloroplast trees have not been incongruent, more analyses are required to understand their taxonomic significance and the potential involvement of more evolutionary mechanisms, such as polyplodization and hybridization, which are partially known in *Themeda* and are barely known for *Heteropogon*. Larger sampling, in terms of diversity and wide distribution range, and simultaneous combined analyses could further disentangle a variety of problems.

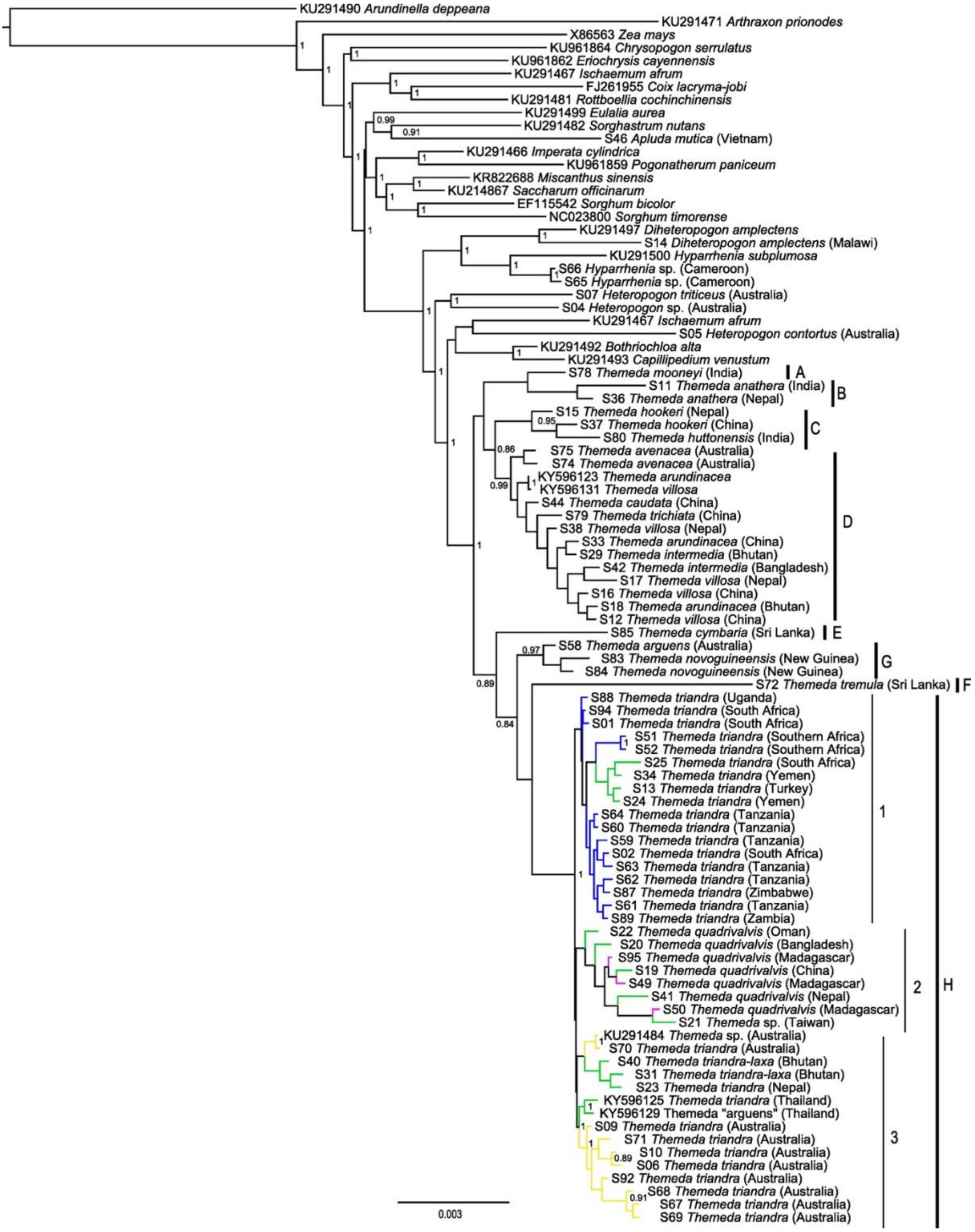

Figure 2.6. *Themeda* phylogenetic tree from Dunning et al. (2017) showing evolutionary relationships among *Themeda* species.

2.3 Grass and Grassland Ecology

2.3.1 Grassland: History and Its Components

Grassland can be simply defined as a habitat in which grasses dominate and natural fire, grazing mammals and drought are three main drivers shaping the grassland structure

(Gibson, 2009; Ratnam et al., 2016). Grasslands in the past have provided key sources of wild plants from which our cultivated plants and those used for recreation or for grazing have been developed (Williams and Diebel, 1996). Grasslands also maintain the stability of ecological and biological processes and biodiversity (Tilman, 1994; Tilman et al., 2006). At the global level, grasslands exist on all continents except Antarctica. The area of grassy ecosystems accounts for around 40% of the terrestrial surface of the earth (Lehmann et al., 2019). Grasslands may be classified into various types, such as savannas, shrublands and temperate grasslands.

It has been postulated that the first grasslands probably had formed by the end of the Eocene (56.0–37.8 Ma) (Strömberg, 2011; Linder et al., 2017) and then expanded from the Miocene (23–5.3 Ma); this is supported by both fossil and molecular evidence (Strömberg, 2011; Estep et al., 2014). The history of grasslands followed a pattern of succession in relation to environmental factors such as the reduction of CO_2, the increase in temperature, and drought (Strömberg, 2011; Linder et al., 2017). In the first stage, C_3 grasses invaded temperate forests in the Early to Middle Miocene (24–11 Ma) (Strömberg, 2011). The displacement of C_3 grasses by C_4 grasses is thought to have taken place during the Late Miocene and Pliocene (3 to 8 Ma). In the Early Oligocene, the major fall in CO_2 concentrations in the atmosphere had taken place (Sage, 2004) and this is thought to have driven the origin of C_4 grasses in the Late Oligocene (Christin et al., 2008; Vicentini et al., 2008; Edwards et al., 2010). The C_4 photosynthetic pathway evolved in the grasses of the PACMAD clade which, by alleviating stress from photorespiration, results in enhanced photosynthetic efficiency (Sage, 2004; Edwards et al., 2010; Edwards and Smith, 2010; Gowik and Westhoff, 2011; Ludwig, 2013). As a result, we see that C_4 grasses tend to outperform C_3 grasses in tropical and subtropical regions. The origin and antiquity of grasslands is not uniform throughout the world but is dependent on disturbance regimes and aridification patterns (Bird et al., 2005; Edwards et al., 2010; Strömberg, 2011; Ratnam et al., 2016).

Natural fire emerged as a driving force by the time that grasslands had expanded around the world and natural fire widely occurs in C_4 grass-related ecosystems. (Bond et al., 2004; Gibson, 2009). Fire regimes can result in the maintenance of grasslands by creating open spaces at the expense of fire-sensitive species and allowing tolerant ones to re-sprout and spread across landscapes (Keeley and Rundel, 2005). Grassland fire can be ignited naturally by lightning and occasionally by volcanic eruptions (Gibson, 2009; Kozlowski, 2012). Fire may also be started anthropogenically, and this probably occurred at the time that humans started using fire for game and land alterations for agriculture (Pyne, 2001; Dove, 2004; Murphy and Bowman, 2007; Kozlowski, 2012). The spread and intensity of fire depends on climate, topography, and the type of fuel (Daubenmire, 1968). As far as climatic factors are concerned, aridity is a prerequisite for fire ignition and is connected to the degree of fire-dependence of the system. (Gibson, 2009). For example, humid zone grasslands are more fire-dependent than less humid ones since high productivity increases plant cover, which then requires more fire to control canopy species such as woody plants. Otherwise, the mesic grassland community cannot be sustained and will be soon replaced by the canopy species (Bond et al., 2003, 2004). By contrast, arid zone grasslands are less fire-dependent because the aridity reduces woody plant productivity and cover, which opens space for grass growth.

Fire not only has effects on physical factors in grasslands, such as soil, but also has an influence on vegetation composition. Burning can lead to both positive and negative impacts, depending on the types of plants present and the characteristics of the fire. For example, perennial plants are susceptible to summer fire as they could be immediately burned out after vegetative growth initiates (Gibson, 2009). Likewise, some woody plants produce highly flammable substances such as terpenoids which can react with fire and kill the plants (Alessio et al., 2007; Bowman et al., 2014). The recovery after fire depends on plant growth form and the position of the perennating buds, which are borne at ground level in hemicryptophytes and below ground in geophytes (Raunkiaer, 1934; Chapman and Crow, 1981) and the seed bank. Some studies also suggested that fire increased species diversity by promoting seedlings from the underground seed bank of exotic plants (Lunt, 1990; Collins et al., 1995). Areas that are burned only occasionally may show more diversity and heterogeneity than frequently burned areas. Furthermore, in some cases non-native, exotic plant species have altered fire regime by changing the types of fuel present, increasing the amount of fuel, and prolonging the burning period, e.g., in Australia, the invasion by *Andropogon gayanus* (Rossiter-Rachor et al., 2008) and *Pennisetum polystachyon* (L.) Schult. (now as *Cenchrus polystachios* (L.) Morrone) (Miller, 2006; Navie and Adkins, 2007).

Grazing by herbivores can also affect the composition of grassland ecosystems, particularly in species diversity (Olff & Ritchie, 1998). Grazing can promote and enhance propagule dispersal and local colonization by introducing new species on their hooves, hairs, feathers, or faeces (Peart, 1989; Gibson, 2009; Laborde and Thompson, 2012). Herbivores may simultaneously create open gaps for colonizers by digging and trampling. They may also prevent local extinction when selective grazing suppresses the performance of dominant species in communities (Milchunas and Noy-Meir, 2002; Hester et al., 2006). The interactions between grazing and other factors which regulate the dynamics of plant diversity were explored by three models: (1) Milchunas-Sala-Lauenroth (MSL) model (Milchunas et al., 1988) (2) state-and transition (S-T) model (Laycock 1991; Westoby et al., 1989) and (3) herbivore optimization hypothesis (Dyer et al., 1982). The MSL model demonstrates the effect of grazing intensity on plant diversity in communities with different grazing history and level of moisture. Changes in species composition and diversity by grazing in subhumid grasslands were larger than the ones in semiarid grasslands in regardless of grazing history. This can be explained by the intermediate disturbance hypothesis (IDH) of Connell (1978). At low levels of disturbance, tall species will be more advantaged by their stature and high soil nutrients and/or moisture that can support high production in these species.

Hence, only a few tall species predominate in such habitats. At the other extreme, when grazing pressure is intense, most species are not able to tolerate such high pressure and only a few tolerant species can persist. The largest number of species can persist in habitats with intermediate levels of disturbance in which no single species dominates overall. Nevertheless, the MSL model overlooks the ecological succession that completely changes one community into another if grazing pressure passes a threshold regime. The S-T model explains that alternate equilibria exist when different grazing regimes act on grasslands. For example, grasslands exposed to intense grazing can be irreversibly altered from a perennial to an annual community. For the herbivore optimization hypothesis, the intermediate grazing level has positive effects on plant fitness. This is evident if grasslands are evolutionarily ancient and have low productivity. In these ecosystems, herbivores help clear litter layers and provide space for new growth.

Drought is determined by the amount and variability of precipitation. Drought decreases grassland productivity (Nippert et al., 2006) and plant survival (Gibson, 2009). It is also correlated with root and leaf morphology. In a case study of the early 1930s, severe drought striking US Midwest prairies reduced foliage height due to water shortage (Weaver and Albertson, 1936). As expected, plants with shallow rooting systems (e.g., *Schizachyrium scoparium*) suffered more under the drought than ones with deeper rooting systems (e.g., *Andropogon gerardii*) (Weaver and Darland, 1949). Later, it was observed that plants developed deeper and more branched root systems. Drought also induces ecological succession, e.g., when the dominant species succumbs to aridity, drought-adapted herbaceous forbs and ruderal plants may benefit from this condition and may eventually replace the former dominant species. When the environment recovers by increased rainfall, a small portion of the original dominant species can rejuvenate and grow vigorously e.g., from the available seed bank.

2.3.2 Savanna Grasslands around the World

Grasslands occur on every continent except Antarctica. According to the Köppen climate classification system (Trewartha, 1943), five climatic zones were proposed for grasslands based on temperature and precipitation. The classification of grassland climates are as follows: tropical moist climates, dry climates, subtropical climates, temperate climates, and highland climates. In this study, the focus is only Savanna grasslands (tropical moist climates) with which *Themeda* and *Heteropogon* are strongly associated.

Generally, savannas can be found in Africa, Asia, Australia, and South America (Figure 2.7) (Huntley and Walker, 1982; Peel et al., 2007; Gibson, 2009; Ratnam et al., 2016). Savannas are composed of specific vegetation comprising Poaceae, Cyperaceae, and woody plants giving some shade but whose canopies do not overshadow the grassy understorey (Sankaran et al., 2005). In the grassy layer, C_4 grasses, especially Andropogoneae, usually dominate (Edward et al., 2010; Ratnam et al., 2011). The appearances of savannas are characterized by canopy height, grass cover and crown cover (Oliveras and Malhi, 2016) from open grassy fields in Africa to densely tree-covered zones in Asia (Sankaran et al., 2005; Hirota et al., 2011; Staver et al., 2011; Lehman et al., 2014). For example, acacia savanna is covered by more than 80% of grasses and the highest tree canopy reaches around 8 m. In contrast, the *cerrado denso* in Brazil is more shaded by crown cover with only 10% of grassy understorey (Oliveras and Malhi, 2016). The coexistence of trees and grasses is a dynamic process in which the balance relies on the interactions between them. If canopies spread and cover most of the area, grasses will be so reduced in number that their flammability is also restricted. Conversely, excess fire from an extensive cover of grasses can inhibit growth in woody plants (Staver et al., 2011a).

Mostly, savannas and forests can best be understood as ecotones or vegetation transitions (Clements, 1905; Torello-Raventos et al., 2013). The ecotone comprises a wide range of savanna types each with unique species and functional traits (Staver et al., 2012; Tomlinson et al., 2012, 2013). This depends on the degree of tree-grass coexistence, geographical locations, climate, water availability, soil type, and disturbances such as fire and grazing (Sankaran et al., 2005; Murphy and Bowman, 2012; Dantas & Pausas, 2013; Scheiter et al., 2013). Staver et al. (2011b) proposed a model of alternative stable states. At high amounts of rainfall, increase in canopy closure results in high surrounding moisture and more shade to the grass layer, which in turn, reduces natural fire due to less fuel substrates. At the other extreme, grasses will dominate the area due to high fuel load and fire leading to woody cover suppression. At an intermediate level of rainfall, disturbances such as fire and herbivory will control the nature of forest-savanna transitions.

In Asia, three savanna types, driven by combinations of factors, were described (Ratnam et al., 2016): (1) Deciduous broadleaf savannas, (2) Fine-leafed and spiny savannas and (3) Pine savannas. These three savanna communities are situated in different geological locations which yield distinct environmental drivers and species composition. Pine savannas are located at high elevation with cool climate, high rainfall, and low soil nutrients, but are maintained by fire. Thus, species composition tends to be fire-tolerant grasses, such as *Cymbopogon*, *Eulalia* and *Themeda*, and cool-tolerant *Pinus* trees (Goldammer and Peñafiel, 1990; Bunyavejchewin et al., 2011; Wanthongchai et al., 2013). Likewise, fire sustains the existence of deciduous broadleaf savannas; however, higher temperature and rainfall determine tree and grass species (Suresh et al., 2011). Instead of pines, dipterocarp, teak or eucalyptus are commonplace in deciduous broad-leaved savannas, and fire-adapted Andropogoneae, such as *Bothriochloa*, *Cymbopogon*, *Dichanthium*, *Heteropogon*, and *Themeda*, can be found within these habitats (Sagar and Singh, 2005; Eiadthong, 2009; Bunyavejchewin et al., 2011). In fine-leaved and spiny savannas, aridity selects for fine-leaved and short-stature plants to survive. Extremely fertile soil enhances the palatability of plants for herbivores and spiny species suffer less from herbivory and may become dominant in such ecosystems (Tomlinson et al., 2013; Ratnam et al., 2016). This evidence demonstrates the interactive effect of climate and abiotic factors on characteristics of savanna ecosystems (Lehmann et al., 2011; 2014).

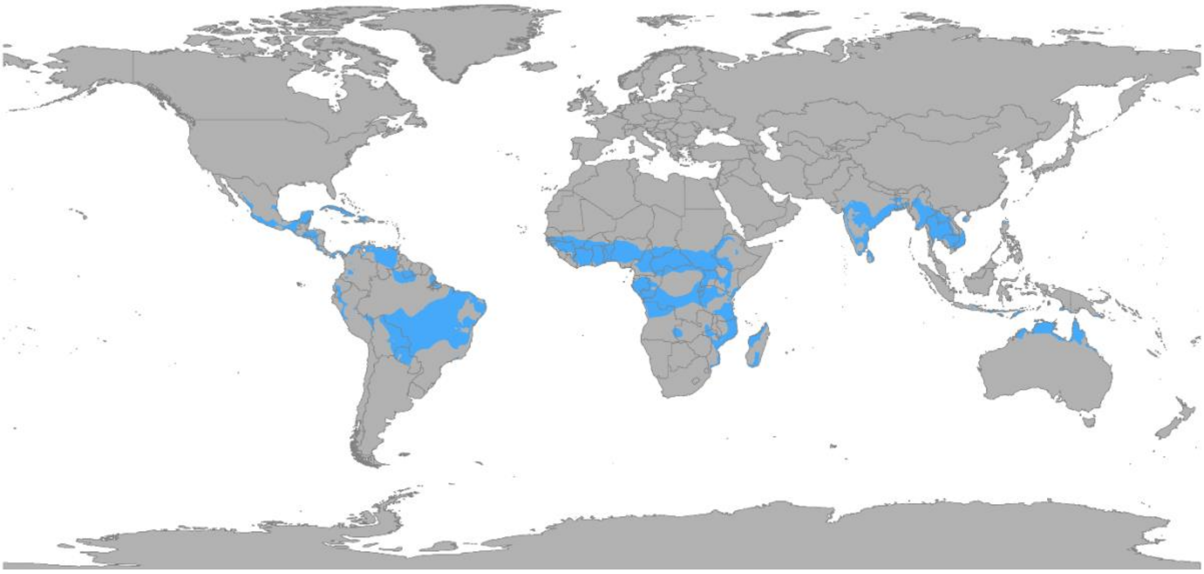

Figure 2.7. The distribution of savannas in Africa, Asia, Australia, and North and South America marked in blue, following the Köppen climate classification system and produced by Peel et al. (2007).

2.3.3 Functional Traits Promoting Dominance in Grasses

Grasses have evolved and adapted their morphology, physiology, and genetic composition to enhance the ability to disperse, establish in new habitats, compete with other species, and transform the environment that favours them in extending their ecological niches and distributions (Linder et al., 2017). Here, I present three aspects that are well-documented in the literature.

A. Morphological Aspects

At the macromorphological level, a number of key innovations were exclusively evolved in the grass family; however, only a few characters have been formally tested for their potential.

Grasses typically allocate most of their biomass to root production, which allows them to survive in almost all types of soil environments (Gould and Shaw et al., 1983). Weaver and Darland (1949) showed that 43% of the root biomass of *Andropogon gerardii* was located in the top 10 cm of the soil, providing access to water and nutrients (February & Higgins, 2010). Grasses exhibit a variety of root architectures which allows them to cope with seasonal fluctuations and drought and nutrient-limited environments (Weaver and Fitzpatrick, 1934; Weaver and Darland, 1949). Furthermore, grasses may also produce rhizosheaths, a mucilaginous structure capturing soil particles (Buckley, 1982), which is more pronounced in grasses growing in sandy soils and arid conditions. It is thought to preserve moisture (Buckley, 1982; Price, 1911; Watt et al., 1994; Linder et al., 2017) or potentially to provide space for a bacterial community to proliferate and fix nitrogen (Bergman et al., 2008).

In fire-prone environments, some perennial grasses produce long rhizomes with below-ground bud banks which can re-sprout (Clarke et al., 2012). Rhizomes may occur down to 10 cm depth in the soil and viable buds can still be found (Lemieux et al., 1993). During burning periods, the buds are protected by scale leaves but also by the soil which has a low thermal conductivity and acts as an insulator for re-sprouting (Choczynska and Johnson, 2009; Clarke et al., 2012). After summer fires, the temperature may rise above 40˚C at 4.5 cm soil depth (Auld and Bradstock, 1996). In soil heating simulations a surface temperature of 700℃ had dropped to 60˚C at 2 cm depth in all soil types (Choczynska and Johnson, 2009). The soil temperature profile is associated with viable bud distribution along the rhizome. According to Choczynska and Johnson (2009), less than 40% of the buds of perennial grasses could tolerate the temperatures at 1 cm depth, but more than 50% survival was observed at 2 cm depth. The characteristics of rhizome combined with soil properties help grasses survive fire.

There is no evidence or data on how floral traits facilitate ecological dominance in grasses or interact with particular environmental factors. However, there are differences in floral characteristics among *Themeda triandra* populations from different geographic regions, e.g., the size of the inflorescence is smaller in high elevation populations (Pers. Obs.). Also, the density of hairs on homogamous spikelets varies among varieties of *T. triandra* (Pers Obs.). However, the association between these characters and environmental factors is unknown.

The awn is involved in photosynthesis and development of the caryopsis (Tambussi et al., 2007). The awn can be hygroscopic, which appears in subfamilies Danthonioideae, Panicoideae and Pooideae (Kellogg, 2015). The hygroscopic awn is generally twisted (Kellogg, 2015) and facilitates seed (caryopsis) dispersal and seedling establishment (Peart, 1979; Peart and Clifford, 1987; Garnier and Dajoz, 2001; Elbaum et al., 2007; Gibson, 2009) by absorbing surrounding moisture and successively altering shape to orient the caryopsis in microhabitats (Peart, 1979; Peart and Clifford, 1987).

B. Physiological Aspects

Physiologically, the evolution of C_4 photosynthetic types is thought to correlate with the migration of C_4 grasses out of the forest (Edwards and Smith, 2010) and facilitate colonization and persistence in humid hot and arid conditions (Sage, 2004; Christin and Osborne, 2014; Forrestel et al., 2014; Linder et al., 2017). According to Watcharamongkol et al. (2018), evolutionary models between photosynthetic pathway type and temperature indicate that C_4 photosynthesis promoted the migration of C_4 grasses into cooler environments. C_4 species might be outcompeted by C_3 ones in cool environments due to lower photosynthetic efficiency and unsuitable leaf anatomy. However, nitogen- and water-use efficiency as well as high net assimilation rate might be advantages for C_4 species to grow in temperate regions (Atkinson et al., 2016). C_4 grasses are adapted to high temperature and drought with several ecophysiological attributes. C_4 grasses increase CO_2 concentration by double carbon fixation in order to avoid O_2 competition in binding to active site of Rubisco at high temperature. This maintains high photosynthetic rate in C_4 plants (Taylor et al., 2014). C_4 grasses have comparatively lower stomatal conductance, which decreases transpiration (Knapp, 1993; Taylor et al., 2011). This implies water conservation in drought conditions. The C_4 pathway has enabled Andropogonoid grasses to survive in dry conditions where large niches had not been occupied (Christin and Osborne, 2014; Forrestel et al., 2014; Spriggs et al., 2014). This is thought to promote the diversification of Andropogoneae, which covers one-tenth of all species in Poaceae (Clayton and Renvoize, 1986; Kellogg, 2015; Soreng et al., 2017).

C. Genetic Aspects

Additionally, polyploidy and apomixis are associated with long distance dispersal and survival (Linder and Baker, 2014). Polyploidy allows grasses to reduce the effect of inbreeding depression and homozygous recessive genes (Comai, 2005). Harbouring more than one genome could reduce negative effects and maintain some levels of genetic diversity within the population (Soltis and Soltis, 2000; Eliášová et al., 2013; Rosche et al., 2017). In an experiment from Stadler (1929), x-ray treatments were applied to induce mutation in *Avenea* and *Triticum* dormant seeds at different ploidy levels. The mutations were observed by tiller colors from white to green in x-rayed seeds. The mutation frequency decreased with increasing chromosome number and reached zero in triploid *Avena* and *Triticum*. Lower mutation levels in higher ploidy species implied that the redundant chromosome number masked the mutation effect. In addition, some polyploid plants also express apomictic characteristics that ensure asexual reproduction that sustains genetic composition optimal to survival ability (te Beest et al., 2012).

2.3.4 Ecological Dominance

There are several different definitions of ecological dominance but in general the term refers to the magnitude of one or more species that is in some ways superior to its competitors and has a greater occurrence in terms of numbers, biomass, and competitive ability (Whittaker, 1965; McNaughton and Wolf, 1970). Ecological dominance of a particular species is the outcome of a set of influences from inter- and intraspecific interactions and environmental factors acting on species in the community (Whittaker, 1965; Dayton, 1975; Tilman, 1984; Hart, 1990; Steneck et al., 1991; Walker et al., 1999; McKane et al., 2002; Hillebrand et al., 2008). As evaluated in brown algal communities (Dayton, 1975), ecological dominance of *Hedophyllum sessile* depended on wave intensity. In moderate waves, it could replace well-adapted fugitive species and maintain the amount of understorey ones in the area. However, it failed to thrive in the presence of two other brown species even in favourable conditions. In plant communities, only a handful of resources are limiting, such as CO_2, light, nutrients, and water (Tilman, 1982). By becoming ecologically dominant, major plant species outperform other minor species by different strategies. For example, resource partitioning (Hutchinson, 1959), in which plants occupy different niches, reduces interspecific competition. McKane et al. (2002) discovered that in arctic tundra the plants with the most aboveground production *Eriophorum vaginatum* (Cyperaceae) had the ability to take up more glycine, which is more prevalent than other nitrogenous substances, than any other species. In another case, dominant plant species possess traits that tolerate fitness-reducing factors such as shade and high temperature (Hart, 1990).

However, it is not always the case that dominant species will occur at equilibrium in the community over the long-term. Dominant species might gain more resources and survive. Minor species in most plant communities may still be present perhaps due to ecological gaps maintained by uncommon factors such as spatially unequal resources or local-scale disturbances (Huston, 1979; Phillips et al, 1994). Such mechanisms in plant communities do not only select for dominance by a single species but also sustain minor or subordinate species (Grime, 1987), leading to species-rich communities (Langenheder et al., 2012). Moreover, the existence of subordinate species benefits the maintenance of communities as proposed by the insurance hypothesis (Yachi, and Loreau, 1999). In this hypothesis, when new disturbances occur in a community, some subordinate species may outcompete the dominant ones, causing the shift in ecological dominance. This scenario could take place when invasive species are introduced and induce competitive dominance to occur (Keddy, 2001). In the case of cheat grass (*Bromus tectorum* L.), it was introduced from Europe and Asia to the Great Basin, USA. Outside its native range, *B. tectorum* is gradually spreading over Californian grasslands by initiating fire ignition that is harmful to native species together with dispersing seed aided by local grazers (Knapp, 1996). Additionally, disturbances and low chance of seed dispersal and rarity of native species intensified invasion by foreign annual grasses in California grasslands (Seabloom et al., 2003a). However, more desirable traits, such as low demand of water and nutrients in native species, represent strong advantages over introduced species. It is observed that the natives could still grow in drier and nutrient-poor regions as seen in the case of *Heteropogon contortus* and *Pennisetum setaceum* (Now as *Cenchrus setaceus*) (Goergen and Daehler, 2001). Seabloom et al. (2003b) tested whether exotic annual grasses are superior competitors to the perennial ones. They found that the annual plants were unable to compete with perennial plants since the perennials exploited soil nutrients and moisture. They also performed seed-addition experiments and discovered that perennial species could invade exotic annual communities and reduce the performance of annual species. However, when disturbances, such as fire and mowing, were applied, this increased the abundance of exotic annuals but decreased cover of the native perennial plants. Hence, they suggested that the annuals are not superior to the native perennials in acquiring resources, but the perennials were limited by recruitment ability. In addition, heavy grazing and drought were hypothesized to be the initial factors that lead to the invasion of annual species. Overall, ecological dominance is a dynamic process in which one or more species could respond to environmental changes and disturbances and through advantageous traits come to dominate habitats.

2.3.5 *Themeda triandra* and *Heteropogon contortus* in Grassland Ecology

Being widespread species across grasslands and savannas in Africa, Asia and Australia, its economic, conservative, and ecological values are well described (Mitchell and Miller, 1990; Snyman et al., 2013). *Themeda triandra* is renowned for its palatability to natural large grazers and livestock production and is an important model species in several studies (Marshall and Bredon, 1967; McNaughton, 1985; Zacharias, 1990; Danckwerts, 1993; Snyman et al., 2013). *Themeda triandra* is a climax or subclimax species (Smit et al., 1992) that substitutes for other species and remains in a climax community when no disturbances are involved. Within its native distribution, *T. triandra* tolerates a wide range of rainfall (300‒6,250 mm), elevation (sea level to > 3,300 m) and soil types (Mucina et al., 2006). Rainfall directly correlates with the amount of soil water which stimulates tiller extension, leaf production and flowering (Snyman et al., 2013). Rainfall triggers the production of leaves and tillers by aiding mobilization of carbohydrates (Nursey, 1971; Danckworth and Gordon, 1990).

In ecological communities, the dynamics of *Themeda triandra*-dominated grasslands are associated with how *T. triandra* responds, in terms of competitiveness, productivity and survival, to a set of environmental factors such as grazing, natural fire, precipitation, soil and temperature (Morgan and Lunt, 1999; Bond et al., 2003). Over the course of the long history of coexistence between grasses and herbivores, grazing has effects on the reproductive fitness of *T. triandra* (O’Connor, 1994). *Themeda triandra* is prone to be more intolerant of grazing than other dominant grasses in the same community (Coughenour et al., 1985; Hodkinson et al., 1989; Mott et al., 1992). According to Hodkinson et al. (1989), *T. triandra* exposed to frequent defoliation regained leaf area more slowly than its competitor *Cenchrus ciliaris* due to a decrease in photosynthetic rate and photosynthetic products in the sink. Leaf production and reproductive parts are somewhat reduced due to a shortage of carbohydrate reserves (Danckwerts, 1993), then leading to decreased seed production (O’Connor and Pickett, 1992). On the other hand, defoliation actively reduces water stress owing to loss of leaf area when *Themeda* plants grow in dry climates (Snyman and Opperman, 1983). Comparatively, tillers germinating below the defoliation zone in *Cenchrus ciliaris* resulted in a 10-fold leaf area expansion, maintaining the regrowth process. Similarly, *T. triandra* is more sensitive to grazing than *Heteropogon contortus* and *Panicum maximum* after the dry season, as only a few buds are left in adult plants for replacement (Mott et al., 1992). At the population level, there is intraspecific variation in defoliation responses. Experimentally, short, medium, and tall populations of *T. triandra* reacted differently to clipping methods (Oesterheld and

McNaughton, 1988). Although each variety could compensate biomass after clipping over the time, the short ecotype showed relatively high recovery.

In the case of burning, plant biomass and production are reduced immediately after fire events (Bennett et al., 2002; Snyman, 2004a). Fire can directly burn out above-ground biomass and alter physical and chemical components such as soil water, soil nutrients and the amount of litter (Cass et al., 1984; Fynn et al., 2003; Snyman, 2004b). Such changes secondarily cause a negative impact on plant production and survival. However, former studies indicated that burning elevated the number of *T. triandra* seedlings because heat, airborne smoke and aqueous extracts help break seed dormancy and induce more vigorous seedlings (Brown and Staden, 1997; Morgan, 2001; Snyman, 2005). Yet, natural fire specifically injures certain vegetative parts such as meristematic tissue, tillers, and roots (Booysen et al., 1963; Snyman, 2004a). In comparative experiments, *T. triandra* was more vulnerable to both selective and non-selective defoliation than the co-occurring species *Aristida junciformis*, which has a stronger root system. However, *T. triandra* outcompeted *A. junciformis* under competitive conditions (Morris & Tainton, 1993). However, repeated burning raised the *T. triandra* population to occupy more space.

The role of *Heteropogon contortus* in grasslands has been documented in a handful of studies. The *H. contortus* community has been extensively utilized as pasture (Morris, 1958; Grice and Mcintyre, 1995; Everitt et al., 2011). Like *T. triandra*, *H. contortus* can only tolerate light grazing. As it normally produces relatively low seed numbers, a prolonged grazing regime tends to decrease or eliminate seeds, consistently in both Queensland, Australia and Southern Africa. O' Connor and Pickett (1992) counted seeds of African perennial grasses in m^2 plot in light and heavy grazing. *H. contortus* produced relatively low seed numbers as compared with competitive *Aristida bipartina*. In heavy condition, *H. contortus* produced 18,097 seeds per square metre whereas *A. bipartina* yields 1,696,802 seeds per square metre. The number of *H. contortus* seeds increased in light condition (52,089 seeds/m^2) but it is less than those of *A. bipartita* (1,973,300 seeds/m^2). The number of *H. contortus* seeds remaining in the seed bank was higher under light grazing (499 seeds/m^2) than in heavy grazing (no seeds). In North America, the anthropogenic shift of land management minimized grazing pressure (Smith, 2009; Tjelmeland, 2011). This allowed ecological space for *H. contortus* to survive, produce seeds and resprout as eventually it became invasive (Orr et al., 2004; Heuzé et al., 2013). The invasiveness of *H. contortus* directly has an influence on species richness as observed by Bielfelt & Litt (2016). When the density of *H. contortus* became larger along a gradient of *H. contortus* cover, the species richness was decreased. When the amount of rainfall (mm) was considered, Orr et al. (2004)

showed a positive correlation between rainfall and inflorescence density in the presence of limited stocking rates and inflorescence density itself determine seed production. It is also found that the greatest seed production was reported at the lowest stocking rate. If this trend holds true, this could imply that grazers might consume reproductive tillers at more intense stocking rates.

Some evidence indicates that fire enhanced the recruitment and dominance of *H. contortus* by favouring seed germination and reducing the basal area of competitive species (Shaw, 1957; Woodhouse, 1964; Tothill, 1969; Orr et al., 1991, 1997a, 1997b, 2009; Daehler and Goergen, 2005). Apart from fire, another factor contributing to its superiority is tolerance to the aftermath from fire. Firstly, chemical compounds in smoke solution stimulate seed germination (Flematti et al., 2004, 2013; Baldos and DeFrank, 2015). Secondly, according to Goergen and Daehler (2001), native *H. contortus* in Hawai outperforms invasive *Pennisetum setaceum* (Forssk.) Chiov. (Now as *Cenchrus setaceus* (Forssk.) Morrone) in low-nutrient and dry environments in that it still could flower and produce more seeds. Lastly, seeds could escape from the destructive effect of fire by burial whereas ground-cover species shed their seeds above the soil surface and were burned out by fire (Tothill, 1969). Accordingly, *H. contortus* is of significant relevance in grassland management, especially when invasive species come into play as in Hawai'i and Australia (Goergen & Daehler, 2001, 2002).

2.4 Methods in Functional Trait Investigations

2.4.1 Plot Methods

Data collection is the initial procedure to acquire the information on species composition, plant cover and distribution for analysing and understanding ecological process. Prior to field collection, it is necessary to design sampling methods corresponding to biological questions (Kenkel et al., 1989). In plant communities of interest, vegetation is surveyed, and variables are thoroughly recorded in different ways, in this case, plot-based and transect-based methods will be detailed. In plot-based sampling, square or circle stakes are set out in a line at constant distances to one another, for example, 20 m or 30 m between the stakes. The appropriate size of plots should be taken in the consideration, depending on vegetation types. For example, plots for assessing tree density should be larger than those for understorey species density (Barbour et al., 1987; Cox, 1990; Fidelibus and Aller, 1993). For species richness observations, plots are initialized by set a centre plot as a buffer zone with a radius and extended by transect lines from the centre with an equal angle to each other. Within each transect line, circle stakes are placed at equal distances and all target species are recorded within the boundary (Stohlgren et al., 1995; Bull et al., 1998). A plot-based approach is very comprehensive and effective for ecological research related to species richness since it can be designed to cover appropriate areas (Vorontsova et al., 2015). For transect-based methods, points are positioned along the line and data are only collected at each point. The extension of this method, called the point-centered-quarter method, is to intersect extra lines with the previous one to form four quarters. Next, plants situating near the transect points will be collected.

2.4.2 Trait Evolution

In comparative evolution, a phylogeny depicts a broad picture of relationships among lineages and divergence points of transitional events where two lineages diverge from a common ancestor under predicted hypotheses or models. At each transitional stage, there are changes, at least, in adaptive morphological traits or phenotypes developed in the ancestor and successively passed on to the descendants. Theoretically, if some traits that emerged from the common ancestor are found in related lineages, there will be a significant likelihood that the traits are shared between two lineages and the rate of evolutionary changes cause differences in the traits (Felsenstein, 1985). Through evolutionary time, morphological transformation is associated with multiple character states and one of them precedes the others. In a comparative approach, an ancestral state must be clarified for each node in phylogenetic trees to trace changes and trends among lineages (Schluter et al., 1997). Such trends reflect what traits contributed to the diversification of lineages (Maynard Smith and Szathmáry, 1995). For example, the evolution of the flower has facilitated the angiosperms to speciate in large numbers, compared to gymnosperms (Stebbins, 1981). In this case, the flower is called ‘the key innovation’.

Methodologically, a collection of trait information is gathered corresponding to observations, specific terms or references which can be discrete or continuous data (Pagel, 1999; O’Meara, 2006; Maddison et al., 2007). To establish the ancestral state, the evolutionary rates and models are put into consideration. Each model is designated to predict the fate of traits from the beginning to certain point of the phylogeny. Ancestral state reconstruction is generally conducted by maximum likelihood or Bayesian approaches, calculating the probability that each specific model predicts particular morphological changes. For discrete data, equal rates (ER), symmetrical (SYM), and all rates different models (Lewis, 2001; Revell, 2012) specify different patterns of rates for all character states. In the case of continuous data, there are four widely used models, Brownian Motion (BM), Early Burst (EB/AC), Late Burst (LB) and Ornstein-Uhlenback (OU). For Brownian Motion, the evolution of traits is analogized to the course of events in which the traits evolve by walking randomly through time intervals with specific rates, resulting in distinct scenarios due to genetic drift or adaptive evolution (Felsenstein, 1985; Lynch and Walsh, 1998; Butler and

King, 2004; O'Meara et al., 2006). Alternatively, in the early burst (EB) model, as its name implies, the maximum variance can be observed at the earliest divergence of the group of interest and will shrink over time due to a slower rate of evolution or morphological constraints (Stegen & Swenson, 2009; Harmon et al., 2010; Ingram et al., 2012). This model is accordance with Simpsonian theory about adaptive radiation. Namely, once species occupy new niches, they will diversify, and the rate will be reduced when niches are filled (Simpson, 1953). In contrast to the EB model, the Late Burst model indicates that the rate of evolution increases through time, leading to higher variance than that of the divergence point. In the Ornstein-Uhlenback model, species tend to evolve towards optimal states or adaptive peaks resembling disruptive selection (Ingram et al., 2012). Under simulations, the model allows random walks to occur in constrained trait space; however, only some phenotypes in the lineages will be reached at adaptive peaks that are favoured by natural selection and remain at equilibrium state (Hansen, 1997; Butler and King, 2004; Mahler et al., 2013). After model selection, all models are tested to choose the best model for the inference, using, for instance, the Akaike Information Criterion (AIC) or hierarchical likelihood ratio.

According to Christin et al. (2013), the analyses of continuous data of foliar anatomy focused on the outer and inner bundle sheath cells functioning in double carbon fixation. It revealed that the OU model best explained that the increase in %OS [OS area/ (OS area + M area)] is fixed in the common ancestors of the BEP and PACMAD clades. It implied that the width of the outer bundle sheath cells was enlarged whereas distances between bundle sheath were reduced. This mechanism facilitated C_4 evolution by diminishing the distance between mesophyll and bundle sheath cells and enhancing the concentration of CO_2 in bundle sheath cells in favour of CO_2-reduced condition (Dengler et al., 1994; Muhaidat et al., 2007). At the same time, those types of cells were selectively reduced in size in BEP taxa, and they eventually lost their ability to become C_4 plants.

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CHAPTER 3

COMPLEX EVOLUTIONARY HISTORY OF TWO ECOLOGICALLY SIGNIFICANT GRASS GENERA, *THEMEDA* AND *HETEROPOGON* (POACEAE: PANICOIDEAE: ANDROPOGONEAE)

3.1 INTRODUCTION

The emergence of C_4 grasslands in the Late Miocene, between 3 and 8 Mya, is considered to be one of the major global vegetation transformations (Cerling et al., 1997; Edwards et al., 2010). This change was facilitated by adaptations of the dominant C_4 grasses to fire, grazing, lower precipitation and increased seasonality (Strömberg, 2011; Linder et al., 2018). In Poaceae subfamily Panicoideae, diverse grasses from the C_4 tribe Andropogoneae form the main understorey in the tropical savannas of South America, Africa and Asia (Arthan et al., 2016; Lehmann et al., 2019). Two of the genera, *Heteropogon* Pers. and *Themeda* Forssk., make a significant contribution to present-day ecosystems, where they are often dominant (Snyman, Ingram & Kirkman, 2013; Ratnam et al., 2016; Fig. 3.1E–G). Due to the ecological importance of these genera, understanding their evolutionary history is crucial for documenting the origin and dynamics of the savanna biome in the tropics. *Heteropogon* and *Themeda* were both placed in Andropogoneae subtribe Anthistiriinae by Clayton & Renvoize (1986). Later, Anthistiriinae were included in subtribe Andropogoninae, based on molecular data (Kellogg, 2015; Soreng et al., 2017). Currently, five *Heteropogon* and 29 *Themeda* species are accepted and distributed mainly in the tropics (Clayton et al., 2006). Two species, *H. contortus* Pers. and *T. triandra* Forssk. are distributed throughout the tropics and from Africa to East Asia, respectively, and are keystone species in many grasslands where they are found (Goergen & Daehler, 2001; Wang et al., 2016). The remaining species have variable range distributions from restricted to regionally widespread, mainly distributed throughout South Asia, South-East Asia and Australia (Deshpande, 1988; Veldkamp, 2016; POWO, 2019).

Heteropogon and *Themeda* are morphologically distinct, especially in inflorescence structure that has been used to define them (Clayton & Renvoize, 1986; Fig. 3.1A–D). Both genera have sterile homogamous spikelets in the lower part of the inflorescence and fertile spikelets in the upper part. In most species an appendage called an awn emerges from the fertile lemma (Clayton & Renvoize, 1986). The term ‘inflorescence’ is used here informally to indicate a unit at the apex of a single flowering culm traditionally named a ‘raceme’, even though developmentally the correct term for these complex structures is a synflorescence

(Kellogg, 2015; Fig. 3.1A–D). All *Heteropogon* species have solitary inflorescences with awns converging and twisting around one another to form a group of stiff appendages. At least three or more pairs of well-developed homogamous spikelets appear in the lower two-thirds of the inflorescence (Deshpande, 1988). In *Themeda*, a single inflorescence is subtended by a spatheole (bract) and has a compact cluster of only two pairs of homogamous spikelets, a few fertile spikelet pairs and a triad (a group of one sessile and two pedicellate spikelets) (Clayton & Renvoize, 1986). Some *Themeda* have an aggregation of several inflorescence branches that forms a more complex structure.

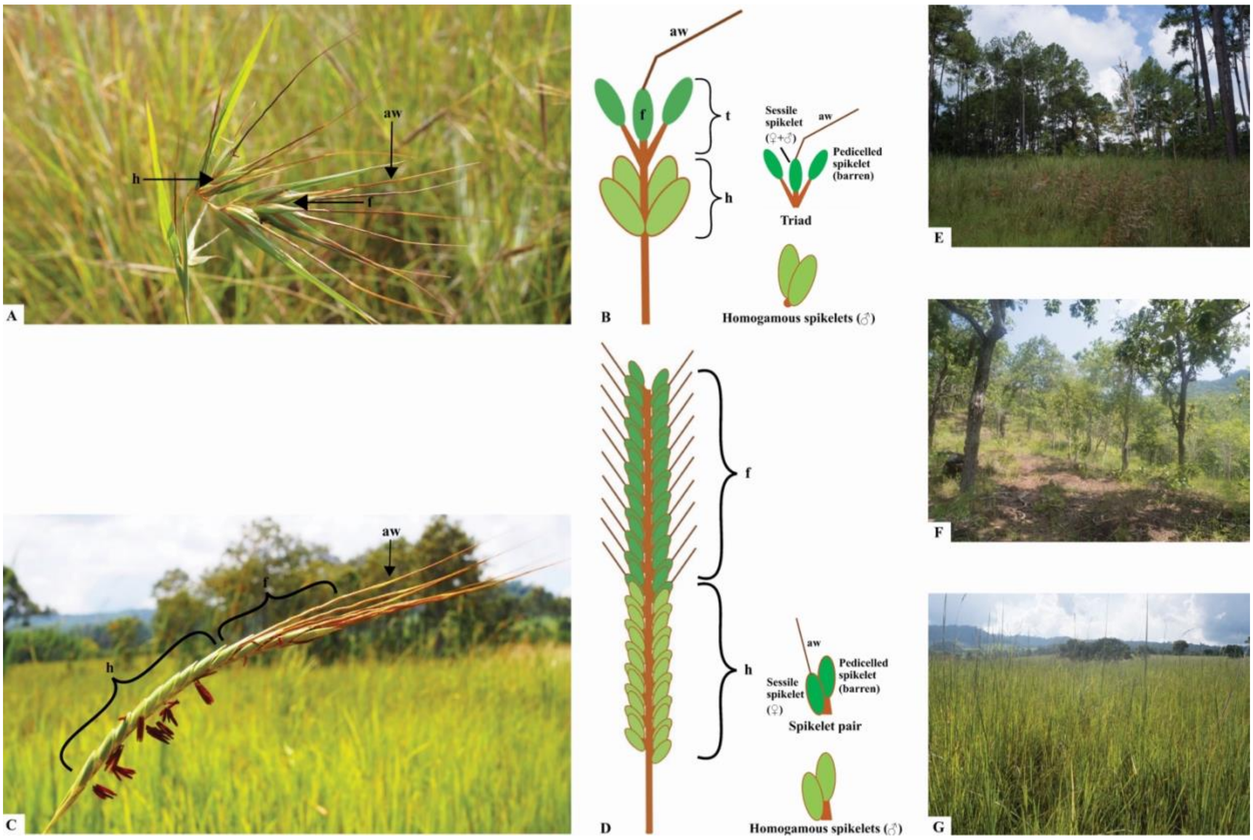

Figure 3.1. Typical inflorescence structure and floral diagram of *Themeda*, exemplified by *T. triandra*(A and B) and *Heteropogon*, exemplified by *H. triticeus* (C and D) and the characteristics of some savanna environments in Southeast Asia in which *Heteropogon* and *Themeda* are typically found: low-elevation pine savanna in Thung Salaeng Luang National Park, Thailand (E), broad-leaved savanna in Phu Soi Dao National Park, Thailand (F) and tall-grass savanna in Thung Salaeng Luang National Park, Thailand (G). Abbreviations: f = fertile spikelet, h = homogamous spikelet, t = triad and aw = awn. All photographs: Watchara Arthan.

Heteropogon and *Themeda* are sister genera, but to date their evolutionary relationships have been investigated with only limited taxon sampling. Early single-locus phylogenetic trees (ITS and *trnL-F*) placed *H. contortus* and *T. triandra* as sister groups

(Skendzic, Columbus & Cerros-Tlatilpa, 2007; Teerawatananon, Jacobs & Hodkinson, 2011). The broadly sampled phylogenetic tree by GPWG II (2012) showed that *Heteropogon* and *Themeda* had strong affinities with *Iseilema* Andersson, as might be expected given the morphological similarities between *Themeda* and *Iseilema*. Nuclear single-copy genes suggested that *Heteropogon* and *Themeda* are sister to *Bothriochloa* Kuntze, *Capillipedium* Stapf and *Dichanthium* Willemet (the BCD clade; Estep et al., 2014; Welker et al., 2015; Bianconi et al., 2020). The first plastome analysis also retrieved the *Heteropogon–Themeda* sister relationship (Arthan et al., 2017). The plastome analysis also revealed an unexpected position of *H. triticeus* (R.Br.) Stapf ex Craib close to *Cymbopogon flexuosus* (Nees) W.Watson. Phylogenetic relationships in *Themeda* were investigated by Dunning et al. (2017) who identified seven clades but did not fully sample *Heteropogon*. Dating analyses by Dunning et al. (2017) showed that *Themeda* originated around the same time as the global C_4 grassland expansion. They hypothesized that the pantropical species *T. triandra* dispersed from its South-East Asian origin during the last 1.5 Mya. Similar age estimates for the sister genus *Heteropogon* and the similarly widespread *H. contortus* are lacking.

Previous studies on *Themeda* and *Heteropogon* were based on limited species sampling and in most cases limited genomic information, hindering our ability to draw conclusions on the origin, diversification and polyphyly of these important grass genera. The aims of this study are: (1) to reconstruct the evolutionary history of *Heteropogon* and *Themeda* using plastome and nuclear data; (2) to estimate divergence times among species of both genera and (3) to review the taxonomic implications of the relationships.

3.2 MATERIALS AND METHODS

3.2.1 Taxon Sampling

Taxon sampling (Table 3.1) was based on previous phylogenetic studies (Estep et al., 2014; Arthan et al., 2017; Dunning et al., 2017; McKain et al., 2018) with further samples selected on the basis of published taxonomic and morphological data (Clayton & Renvoize, 1986; Kellogg, 2015). All accessible species of *Heteropogon* and *Themeda* were sampled; samples of *H. contortus* and *T. triandra* were selected to cover the whole of their distribution ranges. Leaf material was collected from 61 herbarium specimens from the Royal Botanic Gardens, Kew (K), the Natural History Museum, London (BM) and Chinese National Herbarium, Institute of Botany, Chinese Academy of Sciences (PE) and used to produce genome skims. Genome-skimming data for 15 accessions from Arthan et al. (2017) and Dunning et al. (2017, 2019) were also included in this study. Ingroups included 32 *Heteropogon* and 29 *Themeda* accessions, representing five and 14 accepted *Heteropogon* species and *Themeda* species, respectively. Different accessions of *H. contortus* and *T. triandra* were sampled to cover their distribution ranges and morphological variation. We added 20 specimens from the closely related genera *Agenium* Nees, *Bothriochloa*, *Capillipedium*, *Cymbopogon* Spreng., *Dichanthium*, *Eremopogon* Stapf, *Iseilema* and *Pseudanthistiria* (Hack.) Hook.f. to test the monophyly of *Heteropogon* and *Themeda*. In the plastome analyses, other Andropogoneae besides these genera from GenBank were included (Table 3.1), and *Arundinella deppeana* Nees, *Garnotia tenella* (Arn. ex Miq.) Janowski and *G. thailandica* Gould were selected as the outgroup. For the nuclear analysis, only *A. deppeana* was available as outgroup.

Table 3.1. List of GenBank plastome sequences and newly sequenced plastomes and nuclear data used in this study. P and N indicate that the accessions are present (+) or absent (–) in plastome (P) or nuclear (N) analysis.

Species	**Country**	**Collector name**	**Collector number**	**Herbarium**	**Plastome size (bp)**	**Accession number**	**Reference**	**P**	**N**
Agenium leptocladum (Hack.) Clayton	Paraguay	E. Hassler	12427	K	137,726	MT504963	This study	✓	✓
Agenium villosum (Nees) Pilg.	Bolivia	M. Nees & M. Saldias	36425	K	137,731	MT504964	This study	✓	✓
Andropogon abyssinicus R. Br. ex Fresen.	Kenya	Pasquet	1097	MO	138,738	NC035030	Arthan et al. (2017)	✓	✗
Andropogon burmanicus Bor	Thailand	W. Arthan	071	BKF	140,898	NC035038	Arthan et al. (2017)	✓	✗
Andropogon chinensis (Nees) Merr.	Thailand	W. Arthan	042	BKF	138,817	NC035012	Arthan et al. (2017)	✓	✗
Andropogon distachyos L.	Thailand	W. Arthan	050	BKF	139,098	NC035041	Arthan et al. (2017)	✓	✗
Andropogon fastigiatus Sw.	Thailand	W. Arthan	009	BKF	138,658	NC035010	Arthan et al. (2017)	✓	✗
Apluda mutica L.	Unknown	USDA	PI 219568	Unknown	140,299	NC036684	Gallaher et al. (2019)	✓	✗
Arthraxon hispidus (Thunb.) Makino	Thailand	W. Arthan	023	BKF	140,507	NC035048	Arthan et al. (2017)	✓	✗
Arthraxon lanceolatus (Roxb.) Hochst.	Thailand	W. Arthan	001	BKF	140,381	NC035017	Arthan et al. (2017)	✓	✗
Arthraxon microphyllus (Trin.) Hochst.	Thailand	P. Traiperm	537	BKF	139,858	NC035050	Arthan et al. (2017)	✓	✗
Arthraxon prionodes (Steud.) Dandy	Unknown	Unknown	Unknown	Unknown	-	-	Burke et al. (2016)	✗	✓

Table 3.1. List of GenBank plastome sequences and newly sequenced plastomes and nuclear data used in this study. P and N indicate that the accessions are present (+) or absent (–) in plastome (P) or nuclear (N) analysis (continued).

Species	**Country**	**Collector name**	**Collector number**	**Herbarium**	**Plastome size (bp)**	**Accession number**	**Reference**	**P**	**N**
Arundinella deppeana Nees	Mexico	L. Clark et al.	1680	XAL	140,804	NC030620	Burke et al. (2016)	✓	✓
Bothriochloa alta (Hitchc.) Henrard	USA	M. R. Duvall	s.n.	DEK	137,645	NC030621	Burke et al. (2016)	✓	✓
Bothriochloa decipiens (Hack.) C.E. Hubb.	Australia	E. A. Kellogg	TK086	Unknown	138,381	NC040131	Burke et al. (2016)	✓	✗
Capillipedium venustum (Thwaites) Bor	Unknown	Unknown	PI 11713	Unknown	138,257	KU291493	Burke et al. (2016)	✓	✓
Chrysopogon gryllus (L.) Trin.	Republic of Macedonia	E. A. Kellogg	PI 250984	A	140,034	NC035035	Arthan et al. (2017)	✓	✗
Chrysopogon orientalis (Desv.) A. Camus	Thailand	P. Traiperm	578	BKF	140,712	NC035047	Arthan et al. (2017)	✓	✗
Chrysopogon zizanioides (L.) Roberty	USA	E. A. Kellogg	Vet-MRL-001	MO	139,971	NC035034	Arthan et al. (2017)	✓	✗
Coix lacryma-jobi L.	Thailand	W. Arthan	072	BKF	140,863	KY596160	Arthan et al. (2017)	✓	✗
Cymbopogon citratus (DC.) Stapf	Unknown	Jeff	90Cc	Unknown	-	-	Dunning et al. (2019)	✗	✓
Cymbopogon densiflorus Stapf	Tanzania	M. McCallum	T73	K	140,062	MT504965	This study	✓	✓
Cymbopogon flexuosus (Nees) Will. Watson	Thailand	W. Arthan	027	BKF	139,715	NC035040	Arthan et al. (2017)	✓	✓
Cymbopogon obtectus S.T.Blake	Australia	M. Lazarides	4370	K	139,704	MT504966	This study	✓	✓

Table 3.1. List of GenBank plastome sequences and newly sequenced plastomes and nuclear data used in this study. P and N indicate that the accessions are present (+) or absent (–) in plastome (P) or nuclear (N) analysis (continued).

Species	**Country**	**Collector name**	**Collector number**	**Herbarium**	**Plastome size (bp)**	**Accession number**	**Reference**	**P**	**N**
Cymbopogon pospischilii (K.Schum.) C.E.Hubb.	China	R. J. Soreng	5561	K	140,219	MT504967	This study	✓	✓
Cymbopogon schoenanthus Spreng.	Sudan	G. E. Wickens	Unknown	K	139,648	MT504968	This study	✓	✓
Cymbopogon sp.	Unknown	Unknown	Unknown	Unknown	-	-	Dunning et al. (2017)	✗	✓
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark		J. M. Saarela	666	CAN	-		Burke et al. (2016)	✗	✓
Dichanthium annulatum (Forssk.) Stapf	Unknown	Unknown	SUPG011	Unknown	136,805	NC042145	Bhatt & Thanker (unpublished)	✓	✗
Dichanthium sericeum (R. Br.) A. Camus	Thailand	P. Traiperm	571	BKF	138,271	KY596128	Arthan et al. (2017)	✓	✗
Diheteropogon amplectens var. *catangensis* (Chiov.) Clayton	Unknown	Unknown	PI12585	Unknown	139,700	KU291497	Burke et al. (2016)	✓	✓
Dimeria ornithopoda Trin.	Thailand	P. Traiperm	575	BKF	140,629	NC035020	Arthan et al. (2017)	✓	✗
Elymandra androphila (Stapf) Stapf	Liberia	J. G. Adam	24797	MO	139,731	MH181166	McAllister et al. (2018)	✓	✗
Elymandra subulata Jacq.-Fél.	Guinea	Jacques-Felix	7306	K	139,800	MH181214	McAllister et al. (2018)	✓	✗

Table 3.1. List of GenBank plastome sequences and newly sequenced plastomes and nuclear data used in this study. P and N indicate that the accessions are present (+) or absent (–) in plastome (P) or nuclear (N) analysis (continued).

Species	**Country**	**Collector name**	**Collector number**	**Herbarium**	**Plastome size (bp)**	**Accession number**	**Reference**	**P**	**N**
Eremochloa ciliaris (L.) Merr.	Thailand	P. Traiperm	524	BKF	138,970	NC035028	Arthan et al. (2017)	✓	✗
Eremochloa eriopoda C.E. Hubb.	Thailand	P. Traiperm	591	BKF	138,995	NC035023	Arthan et al. (2017)	✓	✗
Eremopogon delavayi (Hack.) A.Camus	China	R. J. Soreng et al.	5236	K	139,855	MT504969	This study	✓	✓
Eremopogon foveolatus Stapf	United Arab Emirates	T. M. Heller	Unknown	K	139,797	MT504970	This study	✓	✓
Eremopogon tuberculatus (Hack.) A.Camus	India	J. F. Duthie	10595	K	139,986	MT504971	This study	✓	✓
Eriochrysis cayennensis P. Beauv.	Brazil	C. A. D. Welker	365	ICN	140,426	NC029882	Welker et al. (2016)	✓	✗
Eriochrysis laxa Swallen	Brazil	C. A. D. Welker	489	ICN	140,135	NC029883	Welker et al. (2016)	✓	✗
Eriochrysis pallida Munro	Zambia	Pasquet	1162	MO	140,382	NC042751	Welker et al. (2019)	✓	✗
Eulalia aurea (Bory) Kunth	Unknown	Unknown	PI12153	Unknown	140,220	KU291499	Burke et al. (2016)	✓	✓
Eulalia contorta (Brongn.) Kuntze	Thailand	P. Traiperm	573	BKF	140,738	NC035026	Arthan et al. (2017)	✓	✗
Eulalia siamensis Bor	Thailand	P. Traiperm	557	BKF	140,642	NC035031	Arthan et al. (2017)	✓	✗
Eulaliopsis binata (Retz.) C.E. Hubb.	Thailand	P. Traiperm	567	BKF	141,091	NC035049	Arthan et al. (2017)	✓	✗
Exotheca abyssinica (Hochst. ex A. Rich.) Andersson	Kenya	Pasquet	1102	MO	139,230	MH181196	McAllister et al. (2018)	✓	✗

Table 3.1. List of GenBank plastome sequences and newly sequenced plastomes and nuclear data used in this study. P and N indicate that the accessions are present (+) or absent (–) in plastome (P) or nuclear (N) analysis (continued).

Species	Country	Collector name	Collector number	Herbarium	Plastome size (bp)	Accession number	Reference	P	N
Garnotia tenella (Arn. ex Miq.) Janowski	Thailand	P. Traiperm	552	BKF	139,629	NC035051	Arthan et al. (2017)	✓	✗
Garnotia thailandica Gould	Thailand	P. Traiperm	535	BKF	139,668	NC035042	Arthan et al. (2017)	✓	✗
Germainia capitata Balansa & Poitr.	Thailand	W. Arthan	028	BKF	139,817	NC035046	Arthan et al. (2017)	✓	✗
Hemisorghum mekongense (A. Camus) C.E. Hubb.	Thailand	P. Traiperm	569	BKF	140,765	NC035022	Arthan et al. (2017)	✓	✗
Heteropogon contortus Beauv. ex Roem. & Schult.	Angola	T. Harris & F. Murray-Hudson	781	K	135,095	MT504972	This study	✓	✓
	Australia	M. Evans	3209	K	134,979	MT504973	This study	✓	✓
	Bolivia	J. R. I. Wood	10831	K	134,991	MT504974	This study	✓	✓
	China	R. J. Soreng, P. M. Peterson & Sun Hung 5724	5724	K	134,979	MT504975	This study	✓	✓
	Eritrea	S. Edwards & G. E. Tewoldeberhan	3888	K	135,078	MT504976	This study	✓	✓
	Haiti	H. H. Bartlett	17487	K	134,987	MT504978	This study	✓	✓
	Hawaii	Degener	33424	K	134,979	MT504977	This study	✓	✓

Table 3.1. List of GenBank plastome sequences and newly sequenced plastomes and nuclear data used in this study. P and N indicate that the accessions are present (+) or absent (–) in plastome (P) or nuclear (N) analysis (continued).

Species	Country	Collector name	Collector number	Herbarium	Plastome size (bp)	Accession number	Reference	P	N
	India	R. P. Celarier	A-3230-I	K	135,112	MT504979	This study	✓	✓
	Italy	P. Marchi & M. Iberite	15808	BM	135,092	MT504980	This study	✓	✓
	Madagascar	-	NOP166	K	134,988	MT504982	This study	✓	✓
	Madagascar	-	SLC102	K	134,885	MT504983	This study	✓	✓
	Mexico	R. V. Moran	7100	K	134,991	MT504984	This study	✓	✓
	New Caledonia	H. S. McKee	41421	K	134,980	MT504985	This study	✓	✓
	Nicaragua	R. W. Pohl	12376	K	134,979	MT504986	This study	✓	✓
	Oman	P. N. Allison	28	K	135,001	MT504987	This study	✓	✓
	Pakistan	C. Wright	99	BM	134,988	MT504988	This study	✓	✓
	Paraguay	K. Fiebrig	5769	BM	134,979	MT504989	This study	✓	✓
	Sierra Leone	E. A. Cole	17	K	134,983	MT504990	This study	✓	✓
	South Africa (Johannesburg)	M. S. Vorontsova	2356	K	135,073	MT504992	This study	✓	✓
	South Africa (Kromdraai)	M. S. Vorontsova	2329	K	135,098	MT504993	This study	✓	✓
	Sri Lanka	D. Clayton	5936	K	135,040	MT504981	This study	✓	✓
	Tanzania	P. J. Greenway & Kanuri	14454	K	134,988	MT504991	This study	✓	✓
	Thailand	W. Arthan	035	BKF	134,982	NC035027	Arthan et al. (2017)	✓	✓
Heteropogon fischerianus Bor	India	E. T. Bourne	2099	K	135,014	MT504994	This study	✓	✓

Table 3.1. List of GenBank plastome sequences and newly sequenced plastomes and nuclear data used in this study. P and N indicate that the accessions are present (+) or absent (–) in plastome (P) or nuclear (N) analysis (continued).

Species	Country	Collector name	Collector number	Herbarium	Plastome size (bp)	Accession number	Reference	P	N
Heteropogon melanocarpus Benth.	Ecuador	W. H. Camp	3206	K	139,830	MT504995	This study	✓	✓
	Oman	T. A. Cope	619	K	139,851	MT504996	This study	✓	✓
Heteropogon ritchiei (Hook. f.) Blatt. & McCann	India	H. Santapau	22007	K	139,424	MT504997	This study	✓	✓
Heteropogon triticeus	Thailand	W. Arthan	034	BKF	140,120	KY596142	Arthan et al. (2017)	✓	✗
	Thailand	W. Arthan	017	BKF	140,046	KY596153	Arthan et al. (2017)	✓	✓
	Thailand	P. Traiperm	534	BKF	140,127	KY596159	Arthan et al. (2017)	✓	✗
	Thailand	W. Arthan	046	BKF	140,091	KY596176	Arthan et al. (2017)	✓	✗
	Australia	E Addicott	EPA3355	Unknown	138,972	KY707769	Dunning et al. (2017)	✓	✓
Hyparrhenia diplandra (Hack.) Stapf	Thailand	W. Arthan	012	BKF	139,175	NC035037	Arthan et al. (2017)	✓	✗
Hyparrhenia rufa (Nees) Stapf	Thailand	W. Arthan	045	BKF	139,269	NC035011	Arthan et al. (2017)	✓	✗
Hyparrhenia subplumosa Stapf	Unknown	Unknown	PI12665	Unknown	139,138	NC030625	Burke et al. (2016)	✓	✓
Imperata cylindrica (L.) Raeusch.	Unknown	S. V. Burke	21	DEK	140,831	KU291466	Burke et al. (2016)	✓	✓
Ischaemum afrum (J.F. Gmel.) Dandy	Unknown	Unknown	PI364924	Unknown	141,097	KU291467	Burke et al. (2016)	✓	✓

Table 3.1. List of GenBank plastome sequences and newly sequenced plastomes and nuclear data used in this study. P and N indicate that the accessions are present (+) or absent (–) in plastome (P) or nuclear (N) analysis (continued).

Species	**Country**	**Collector name**	**Collector number**	**Herbarium**	**Plastome size (bp)**	**Accession number**	**Reference**	**P**	**N**
Iseilema anthephoroides Hack.	India	Satyavathi	IAW5	K	139,777	MT504998	This study	✓	✓
Iseilema hubbardii Uppuluri	India	Satyavathi	IAW3	K	139,716	MT504999	This study	✓	✓
Iseilema laxum Hack. ex Duthie	India	L. J. G. van der Maesen	2833	K	139,580	MT50500	This study	✓	✓
Iseilema macratherum Domin	Unknown	Unknown	PI257760	Unknown	139,643	NC030611	Burke et al. (2016)	✓	✓
Iseilema membranaceum (Lindl.) Domin	Australia	M. E. Trudgen & M. Trudgen	12750	K	139,582	MT505001	This study	✓	✓
	Australia	Jeff	07lm	Unknown	-	-	Dunning et al. (2019)	✗	✓
Iseilema prostratum (L.) Andersson	India	V. R. K. Murty	H4043/66	K	139,806	MT505002	This study	✓	✓
Iseilema vaginiflorum Domin	Australia	M. L.	3131	K	139,635	MT505003	This study	✓	✓
Kerriochloa siamensis C.E. Hubb.	Thailand	P. Traiperm	580	BKF	138,335	NC035009	Arthan et al. (2017)	✓	✗
Miscanthus sinensis Andersson	Unknown	Unknown	Unknown	Unknown	141,372	NC028721	Nah et al. (2016)	✓	✗
Mnesithea helferi (Hook. f.) de Koning & Sosef	Thailand	P. Traiperm	574	BKF	140,801	NC035036	Arthan et al. (2017)	✓	✗

Table 3.1. List of GenBank plastome sequences and newly sequenced plastomes and nuclear data used in this study. P and N indicate that the accessions are present (+) or absent (–) in plastome (P) or nuclear (N) analysis (continued).

Species	**Country**	**Collector name**	**Collector number**	**Herbarium**	**Plastome size (bp)**	**Accession number**	**Reference**	**P**	**N**
Monocymbium lanceolatum C.E. Hubb. ex Hutch. & Dalziel	Guinea	J. G. Adam	6762	K	139,056	MH181170	McAllister et al. (2018)	✓	✗
Parahyparrhenia siamensis Clayton	Thailand	P. Traiperm	583	BKF	140,355	KY596155	Arthan et al. (2017)	✓	✗
Pogonatherum paniceum (Lam.) Hack.	USA (cultivated)	L. G. Clark	s.n.	MO	139,205	NC029881	Welker et al. (2016)	✓	✗
Polytoca digitata (L. f.) Druce	Thailand	W. Arthan	054/060	BKF	140,892	NC035044	Arthan et al. (2017)	✓	✗
Pseudanthistiria umbellata Hook. f.	Sri Lanka	G. Davidse	7828	K	137,900	MT505004	This study	✓	✓
Pseudosorghum fasciculare (Roxb.) A. Camus	Thailand	W. Arthan	067	BKF	140,474	NC035024	Arthan et al. (2017)	✓	✗
Rottboellia cochinchinensis (Lour.) Clayton	USA	L. G. Clark et al.	1698	ISC	140,336	KU291481	Burke et al. (2016)	✓	✓
Saccharum officinarum L.	Unknown	Unknown	IJ76-514	Unknown	141,176	NC035224	Evans & Joshi (2016)	✓	✗
Saccharum spontaneum L.	Unknown	Unknown	SES234B	Unknown	141,168	NC034802	Evans & Joshi (2016)	✓	✗
Schizachyrium brevifolium (Sw.) Nees ex Buse	Thailand	W. Arthan	010	BKF	138,027	NC035013	Arthan et al. (2017)	✓	✗
Schizachyrium exile (Hochst.) Pilg.	Thailand	W. Arthan	047	BKF	138,519	NC035029	Arthan et al. (2017)	✓	✗

Table 3.1. List of GenBank plastome sequences and newly sequenced plastomes and nuclear data used in this study. P and N indicate that the accessions are present (+) or absent (–) in plastome (P) or nuclear (N) analysis (continued).

Species	**Country**	**Collector name**	**Collector number**	**Herbarium**	**Plastome size (bp)**	**Accession number**	**Reference**	**P**	**N**
Schizachyrium imberbe (Hack.) A. Camus	Argentina	C. A. D. Welker & M. C. Peichoto	564	ICN	139,759	NC035045	Arthan et al. (2017)	✓	✗
Schizachyrium sanguineum (Retz.) Alston	Thailand	W. Arthan	022	BKF	139,272	NC035015	Arthan et al. (2017)	✓	✗
Schizachyrium scoparium (Michx.) Nash	USA	E. A. Kellogg	V46	MO	139,274	NC035032	Arthan et al. (2017)	✓	✗
Schizachyrium spicatum (Spreng.) Herter	Uruguay	C. A. D. Welker	627	ICN	139,205	NC035039	Arthan et al. (2017)	✓	✗
Schizachyrium tenerum Nees	Argentina	C. A. D. Welker & M. C. Peichoto	604	ICN	138,555	NC035043	Arthan et al. (2017)	✓	✗
Sorghastrum nutans (L.) Nash	Unknown	W. P. Wysocki	s.n.	DEK	141,061	NC030498	Burke et al. (2016)	✓	✓
Sorghum bicolor (L.) Moench.	Unknown	Cultivar	BTx623	Unknown	140,754	NC008602	Saski et al. (2007)	✓	✗
Themeda anathera (Nees) Hack.	Nepal	Stainton, Sykes & Williams	Unknown	K	138,941	MT505005	This study	✓	✓
Themeda arguens (L.) Hack.	Australia	G. Chippendale	7795	K	138,790	MT505006	This study	✓	✓
Themeda arundinacea (Roxb.) A. Camus	Thailand	W. Arthan	064	BKF	139,742	NC035014	Arthan et al. (2017)	✓	✓
Themeda cymbaria Hack.	Sri Lanka	F. W. Gould	13491	K	139,036	MT505007	This study	✓	✓
Themeda huttonensis Bor	India	N. L. Bor	6717	K	139,655	MT505008	This study	✓	✓

Table 3.1. List of GenBank plastome sequences and newly sequenced plastomes and nuclear data used in this study. P and N indicate that the accessions are present (+) or absent (–) in plastome (P) or nuclear (N) analysis (continued).

Species	**Country**	**Collector name**	**Collector number**	**Herbarium**	**Plastome size (bp)**	**Accession number**	**Reference**	**P**	**N**
Themeda minor L. Liu	China	Unknown	Unknown	PE	139,649	MT505009	This study	✓	✓
Themeda mooneyi Bor	India	H. F. Mooney	4034	K	139,865	MT505010	This study	✓	✓
Themeda quadrivavis	Madagascar	M. S. Vorontsova	350	K	138,961	NC035492	Dunning et al. (2017)	✓	✓
Themeda sabarimalayana Sreek. & V.J.Nair	India	K. M. Matthew & K. T. Mathew	51031	K	Partial plastome sequences		This study	✓	✓
Themeda strigosa (Buch. -Ham. ex Hook. f.) A. Camus	India	H. H. Haines	4514	K	139,085	MT505011	This study	✓	✓
	India	S. Mokim	1516b	K			This study	✗	✓
Themeda tremula (Nees) Hack.	Sri Lanka	D. Clayton	5686	K	138,665	MT505012	This study	✓	✓
Themeda triandra Forssk.	Angola	T. Harris	867	K	138,900	MT505013	This study	✓	✓
	Australia	E. Addicott	DCRYAN1218	unknown	-		Dunning et al. (2017)	✗	✓
	Australia	P. M. Peterson	14430	K	138,850	MT505014	This study	✗	✓
	Australia	T. Handasyde	unknown	unknown			Dunning et al. (2017)	✗	✓
	China	R. J. Soreng	5205	K			This study	✗	✓
	Ethiopia	H. F. Mooney	4844	K	138,816	MT505015	This study	✓	✓
	India	R. P. Celarier	A-2699	K	138,998	MT505016	This study	✓	✓
	Philippines	Dionora, Salazar & Quick	Tt-PHIL-16-02	unknown			This study	✗	✓

Table 3.1. List of GenBank plastome sequences and newly sequenced plastomes and nuclear data used in this study. P and N indicate that the accessions are present (+) or absent (–) in plastome (P) or nuclear (N) analysis (continued).

Species	**Country**	**Collector name**	**Collector number**	**Herbarium**	**Plastome size (bp)**	**Accession number**	**Reference**	**P**	**N**
	South Africa	C. E. R. Lehmann	TheCradle1	unknown			Dunning et al. (2017)	✗	✓
	South Africa	K. Simpson	KS	unknown			Dunning et al. (2017)	✗	✓
	South Africa	L. Smook	3023 AD	K	138,910	MT505019	This study	✓	✓
	Tanzania	P. Peterson	23898	K	138,833	MT505017	This study	✓	✓
	Thailand	W. Arthan	070	BKF	138,865	NC035016	Arthan et al. (2017)	✓	✓
	Uganda	P. A. Christin & M. R. Lundgren	PAC2015-10	unknown	138,891	KY707771	Dunning et al. (2017)	✓	✓
	Yemen	J. R. I. Wood	3457	K	138,883	MT505018	This study	✓	✓
Themeda unica S.L. Chen & T.D. Zhuang	China	M. B. Deng	92103	PE	138,735	MT505020	This study	✓	✓
Themeda villosa (Poir.) A. Camus	Thailand	W. Arthan	065	BKF	139,589	NC035021	Arthan et al. (2017)	✓	✓
Tripsacum dactyloides (L.) L.	China	-	-	-	141,050	NC037087	Wang et al. (2017)	✓	✗
Zea mays L.	Unknown	Unknown	Unknown	Unknown	140,384	NC001666	Maier et al. (1995)	✓	✗

3.2.2 Sequencing and Assembly

Sixty-one new genome-skimming datasets were generated (Table 3.1). DNA extraction was performed as described in Besnard et al. (2013). At least 50 ng of DNA per sample was sent to the Get-PlaGe core facility (Castanet-Tolosan, France). Libraries were prepared with the Truseq Nano DNA sample prep kit. Paired-end reads of 150 bp were produced by bridge amplification with the high-throughput Illumina HiSeq 3000 sequencing platform.

Plastome assembly was performed from genome-skimming data (0.85–5.85 Gb of 150 bp paired-end reads per sample), using the GetOrganelle v.1.6.4d tool (https://github.com/Kinggerm/GetOrganelle) (Jin et al., 2020) that used SPAdes (Bankevich et al., 2012), Bowtie2 (Langmead & Salzberg, 2012), BLAST+ (Camacho et al., 2009) and Bandage (Wick et al., 2015). GetOrganelle was run with a search for k-mers of 21, 45, 65, 85 and 105 bp and extending contigs for 15 rounds. Complete circular sequences were produced for all datasets except from *Themeda sabarimalayana* Sreek. & V.J.Nair due to low sequencing coverage (c. 10×). All sequences for each accession were annotated using GeSeq (Tillich et al., 2017) with reference plastomes of *C. flexuosus*, *H. contortus*, *Iseilema macratherum* Domin and *T. triandra* from NCBI. The gene arrangement of annotated plastomes was examined in Geneious R9 (Biomatters Ltd, Auckland). Plastomes were rearranged manually by using the reference plastomes as mentioned above. For *T. sabarimalayana*, partial plastid sequences were extracted from the reads by using methods described in Dunning et al. (2019). The reads were mapped to a *T. triandra* reference plastome with Bowtie2 (Langmead & Salzberg, 2012) and filtered with SAMtools (Li et al., 2009) to discard low-quality reads ($Q < 20$). The resulting mpileup file was then used to manually call nucleotide positions using custom bash scripts from Olofsson et al. (2016). For each position the minimum read depth was three and the SNP call depth was two. All plastomes have been deposited in NCBI (accession numbers in Table 3.1).

3.2.3 Nuclear Gene Extraction

The raw data for the genome-skimming datasets was then cleaned as in Dunning et al. (2019) before extracting nuclear genome information. NGS QC Toolkit v.2.3.3 (Patel & Jain, 2012) was used to remove sequencing adaptors, low-quality reads (> 80% of bases with $Q < 20$), reads with ambiguous bases and low-quality bases ($Q < 20$) from the 3′ end of reads. Bowtie2 v.2.3.5.1 (Langmead & Salzberg, 2012) was then used to map the cleaned paired-end reads to the *Sorghum bicolor* reference genome obtained from Ensembl Plants (Bolser et al., 2017). For each sample, we then generated sequences for 3269 single-copy genes identified in the *S. bicolor* genome using BUSCO v.2 (Simão et al., 2015). Finally, we extracted sequence information using the same methods as described previously for the *T. sabarimalayana* plastid genome, removing sequences with < 200 bp and discarding genes with < 50% of samples represented. All raw sequence reads were deposited in the Sequence Read Archive (SRA) with accession numbers SAMN15683809–SAMN15683869.

3.2.4 Alignment and Phylogenetic Analyses

MAFFT v.7.402 (Katoh & Standley, 2013) was used through the CIPRES Science Gateway v.3.3 (Miller, Pfeiffer & Schwartz, 2010) to align the set of 136 whole plastome sequences. jModelTest2 v.2.1.6 (Darriba et al., 2012) estimated GTR+Γ+I as the best-fit model of nucleotide substitution based on BIC. The plastid alignment was then analysed with maximum likelihood (ML) and Bayesian inference (BI) by using RAxML v.8.2.12 (Stamatakis, 2014) and MrBayes v.3.2.7a (Ronquist et al., 2012), respectively. Under ML, 500 bootstrap pseudoreplicates were specified to test node support. For BI, two independent Markov Chain Monte Carlo runs with four chains, 50 000 000 generations each, 1000 generation sampling and 10% burn-in were set. Consensus trees were visualized with FigTree v.1.4.4 (http://tree.bio.ed.ac.uk/software/figtree).

The 2464 single-copy nuclear genes were aligned in reference to the *S. bicolor* genome and were subsequently analysed using a coalescent based species tree approach. ML gene trees were generated using PhyML v.21031022 (Guindon & Gascuel, 2003) with 100 bootstrap pseudoreplicates, using the best substitution model as selected by Smart Model Selection SMS v.1.8.1 (Lefort, Longueville & Gascuel, 2017). Nodes with < 10% bootstrap support were collapsed before inferring a multigene coalescence species tree from the individual gene trees using ASTRAL-III v.5.6.2 (Zhang et al., 2018).

3.2.5 Dating Analyses

The plastome alignment was analysed with BEAST2 v.2.6.1 (Bouckaert et al., 2014) in the CIPRES Science Gateway. Due to the scarcity of fossils in our group, we used divergence time of *Zea mays* L. from the rest of Andropogoneae, estimated at 15.26 Mya by Christin et al. (2014) under a younger, non-phytolith scenario as calibration point, implemented as a normal prior with a standard deviation of 0.0001. A GTR+Γ model with four gamma categories, a relaxed log-normal clock (Drummond et al., 2006) and a Yule model were set. Four independent runs with 100 000 000 generations and sampling every 1000 generations were executed in BEAST2. The four runs were assessed for convergence and effective sample size (ESS) by Tracer v.1.7.1 (Rambaut et al., 2018). ESS values for most parameters were > 200. Tree files were combined using LogCombiner v.2.6.1 implemented in the BEAST2 package. The maximum clade credibility tree was searched with TreeAnnotator v.2.6.0 and annotated with median node heights, after discarding a burn-in of 40%.

3.3 RESULTS

3.3.1 Plastomes

The newly sequenced plastomes, including the first plastomes for *Agenium*, *Eremopogon* and *Pseudanthistiria* range in length from 134 885 bp in an accession of H. contortus to 141 765 bp in *Iseilema hubbardii* Uppuluri, with mean coverage ranging from 57.13 to 563.82 when excluding *T. sabarimalayana*. Inverted repeat (IR) boundaries are conserved across the dataset, i.e. rps19-psbA and rpl22-rps19 for the IR–LSC and rps15-ndhF and ndhH-rps15 for the IR–SSC boundary. For *T. sabarimalayana*, only 26 905 bp of plastome sequence could be assembled.

3.3.2 Phylogenetic Analyses

The original alignment of 136 plastomes has a total length of 166 902 bp. After discarding one IR, the alignment has a final length of 137 619 bp, which includes 15.5% gaps and 0.6% Ns. Both ML and BI yielded nearly identical, well-resolved tree topologies as shown in Figure 3.2, and in the Supporting Information, Appendix I and II. Bootstrap (BS) values of 100 and posterior probabilities (PP) of 1 supported most nodes, although low support was observed among some early diverging lineages, such as the split of the *Mnesithea* Kunth–*Eremochloa* Buse clade from the rest of Andropogoneae (BS = 66, PP = 0.95). Maximum support was observed where the DASH clade [an acronym for the clade comprising *Diheteropogon* (Hack.) Stapf, *Andropogon* L., *Schizachyrium* Nees and *Hyparrhenia* Andersson ex E.Fourn. (Arthan et al., 2017)] splits from Anthistiriinae (Fig. 3.2). A clade of *Agenium*, *Bothriochloa*, *Capillipedium*, *Dichanthium*, *Eremopogon*, *Iseilem*a and *Pseudanthistiria* was strongly supported as the sister lineage of *Heteropogon* and *Themeda*.

Our study retrieved close relationships between most *Heteropogon* and *Themeda* species. *Heteropogon* is polyphyletic (Fig. 3.2). The sister relationship of *H. triticeus* and *Cymbopogon* (BS = 96, PP = 1) was recovered as in Arthan et al. (2017). *Heteropogon melanocarpus* (Elliott) Benth. is nested in *Themeda*; *H. ritchiei* (Hook.f.) Blatt. & McCann shows strong affinity with *T. huttonensis* Bor, *T. minor* and *T. mooneyi* Bor. (BS = 96, PP = 0.97). *Heteropogon fischerianus* Bor is nested in the *H. contortus* clade (BS = 100, PP = 1). *Heteropogon contortus* is sister to the *Themeda* clade (Fig. 3.2; BS = 85, PP = 0.99). Most relationships in *H. contortus* have short branch lengths and weak support.

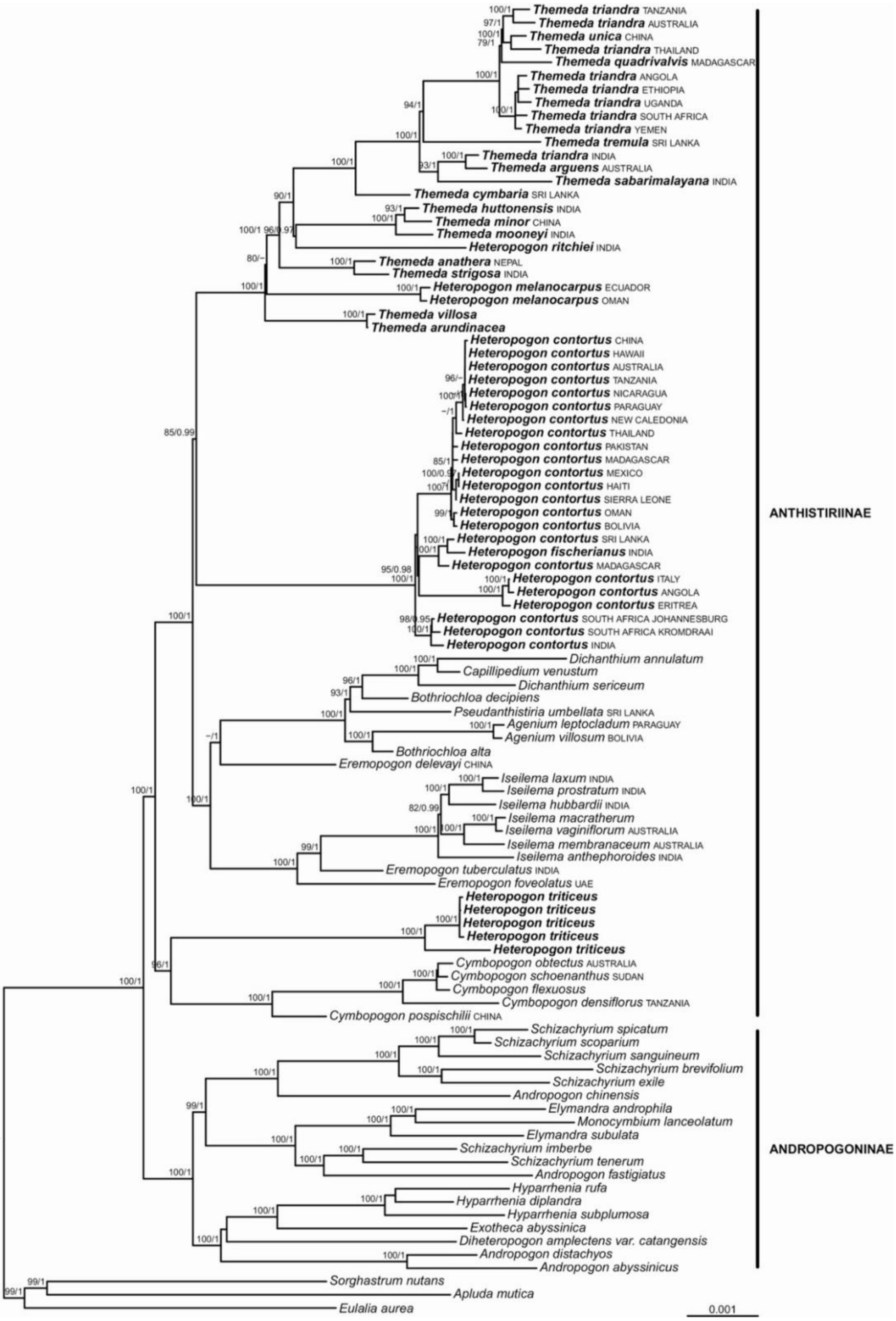

Figure 3.2. A partial maximum likelihood phylogenetic tree showing subtribes Andropogoninae and Anthistiriinae, based on plastomes under GTR+Γ+I model showing close-up the Andropogoninae (DASH clade) and Anthistiriinae clades with the clade, comprising *Apluda mutica*, *Eulalia aurea* and *Sorghastrum nutans*, as the outgroup. Only nodes supported by ML

bootstrap > 70% and posterior probability and > 0.95 were labelled in the tree. See Supporting Information for full ML and BI trees based on 136 plastomes of Andropogoneae.

Themeda is paraphyletic, including some *Heteropogon*. The tree topology conforms to that of Dunning et al. (2017). A clade formed by *T. arundinacea* (Roxb.) A.Camus –*T. villosa* (Lam.) A.Camus is sister to the other *Themeda* spp. (Fig. 3.2; BS = 100, PP = 1) plus *H. melanocarpus* and *H. ritchiei*. Most relationships in *Themeda* are well resolved except some recent divergences in *T. triandra*.

For the nuclear coalescent analysis, 2464 gene trees were used, most of which (2460) have missing taxa. As taxon sampling of the nuclear tree was not the same as that of the plastome topology, only *Heteropogon* and *Themeda* and their closely related clades (e.g., *Iseilema* and BCD clades) can be compared (Fig. 3.3). Most parts agree with the plastome tree, but there are a few discordances. The sister relationship between *H. triticeus* and the *Cymbopogon* clade was not recovered in the nuclear tree, and *H. triticeus* was instead placed as sister to *H. contortus* with a local posterior probability (LPP) of 1, but weak quartet support (QS) of 44.89 (only 44.89% of concordant gene tree quartets supporting the branch; Fig. 3.3). The coalescent analysis placed *H. ritchiei* with *H. melanocarpus* inside *Themeda* rather than as isolated lineage in *Themeda* in the plastome tree (Fig. 3.2). The nuclear tree also placed *T. arguens* (L.) Hack. sister to *T. triandra* (LPP = 1 and QS = 55.58), whereas the plastome tree places *T. tremula* (Nees) Hack. as the sister species (Fig. 3.2).

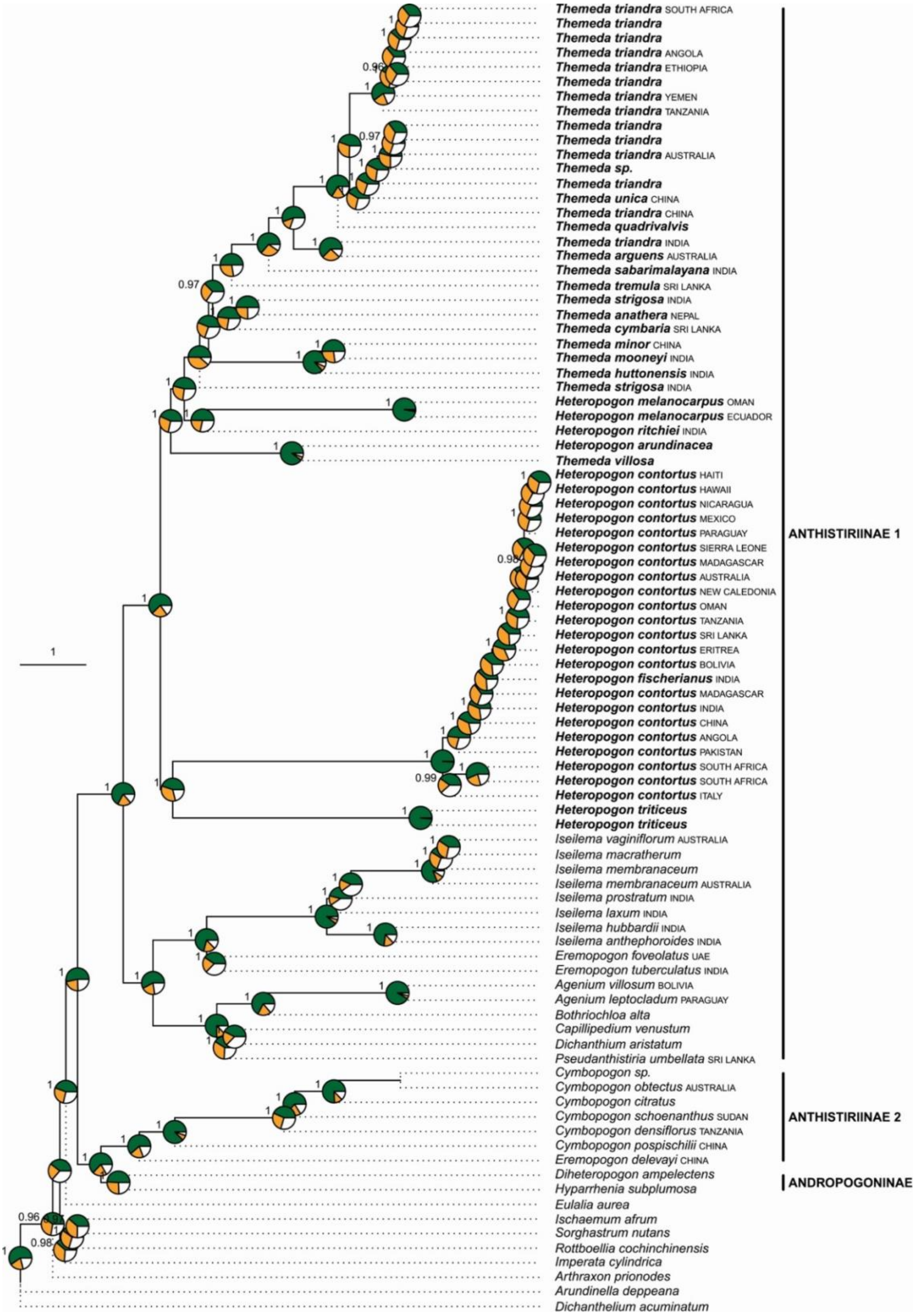

Figure 3.3. Coalescent tree based on 2464 single-copy nuclear genes analysed with ASTRAL-III. Pie charts at the nodes represent the proportion of concordant gene tree quartets from the main topology (dark green section), the first alternative (orange section) and the second alternative (white section). Local posterior probabilities of the main topology are labelled above the pie charts.

3.3.3 Dating Analyses

A maximum clade credibility tree of plastome data (Fig. 3.4) found a topology nearly identical to the ML and BI trees (Fig. 3.2). *Heteropogon triticeus* diverged from *Cymbopogon* 8.84 Mya (95% highest posterior density interval: 7.4–10.3 Mya), and the divergence between *H. contortus* and *Themeda* occurred c. 7.6 (6.1–8.8) Mya. *Heteropogon contortus* populations started to diverge from 1.6 (1.1–2.3) Mya. The *T. arundinacea–T. villosa* lineage diverged from other *Themeda* 5.80 (4.8–7.2) Mya, but the split between the two species occurred recently, 0.2 (0.04–0.3) Mya. Among *T. triandra* accessions, African populations diverged from populations from Asia and Australia 1.15 (0.82–1.58) Mya.

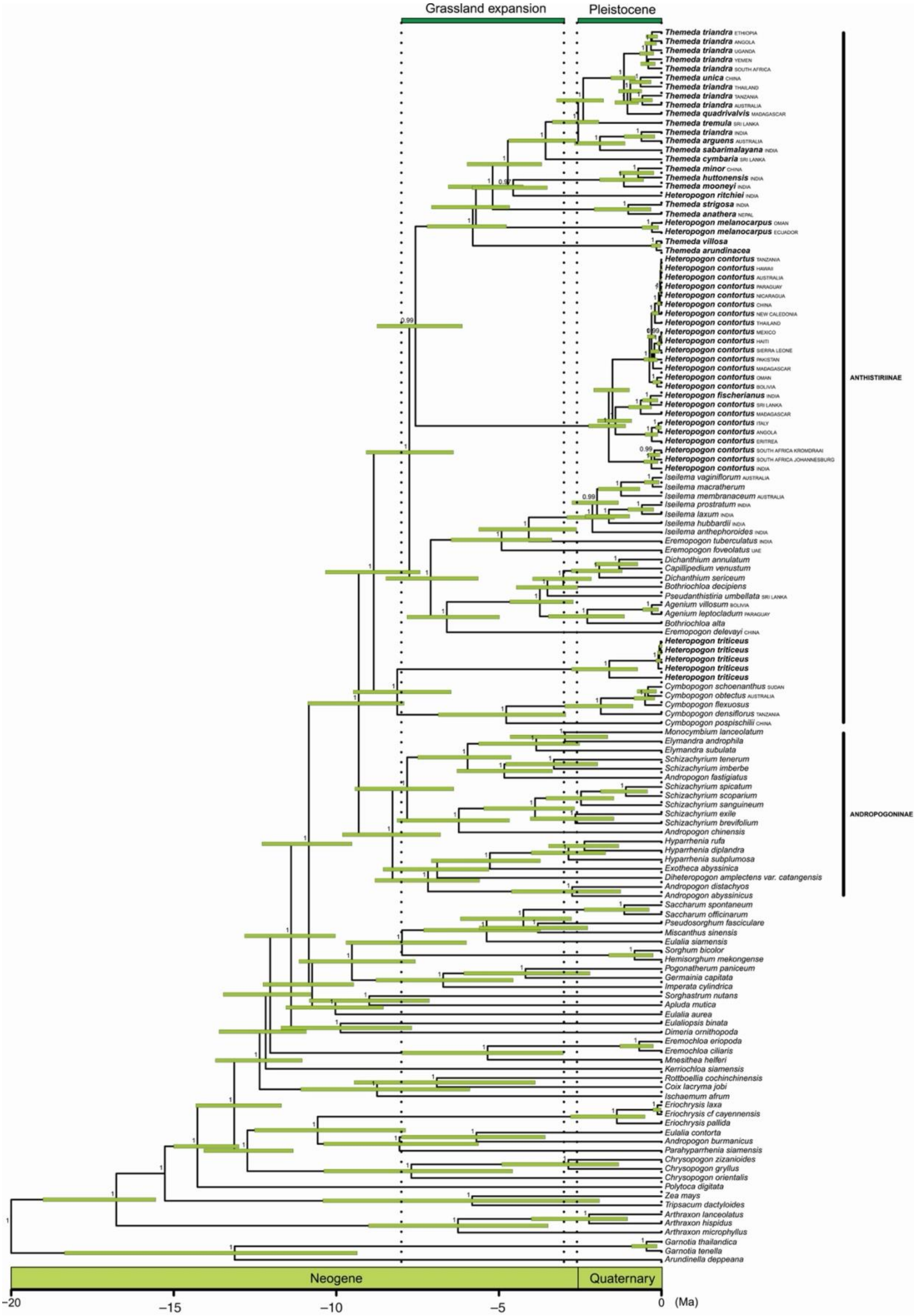

Figure 3.4. Dated tree produced from plastome data with a single calibration point fixed at 15.26 Mya, based on the divergence time between *Zea mays* and the rest of the crown Andropogoneae.

Posterior probabilities (PP) > 0.95 are shown at the nodes. 95% of HPD of estimated dates are shown as error bars. Dark green boxes above the tree and dotted lines represent timeframes covering estimated grassland expansion in the Late Miocene (8–11 Mya) and the Pleistocene, respectively.

3.4 DISCUSSION

With comprehensive sampling of plastome and nuclear genome-wide trees, we show that *Themeda* and *Heteropogon*, as currently defined, are not monophyletic (Figs 3.2, 3.3). Both genera therefore need revision to represent natural groups. The necessary taxonomic changes will be made in a separate manuscript. *Themeda* is paraphyletic but forms a monophyletic taxon supported by both plastome and nuclear data if *H. ritchiei* and *H. melanocarpus* are included. *Heteropogon* is clearly polyphyletic; in a strict sense, it would only include the type species *H. contortus* and (pending further study) *H. triticeus*.

The position of *H. ritchiei* differs between the nuclear and plastome trees, although there is nuclear and plastome agreement that *H. melanocarpus* and *H. ritchiei* are embedded in *Themeda*. The result is a morphologically diverse group: both *H. melanocarpus* and *H. ritchiei* have *Heteropogon*-type inflorescences, in which two to four pairs of non-involucral homogamous spikelets are present. Such inflorescence structure is not seen in typical *Themeda* species that have a strict arrangement of two pairs of involucral homogamous spikelets. However, the number of homogamous spikelets in both species is fewer than that observed in other *Heteropogon* (usually more than four pairs; Deshpande, 1988). A decrease in the number of homogamous spikelets may follow inflorescence reduction trends documented in Poaceae (Vegetti & Anton, 1995) and may be an early stage of a transition towards a *Themeda*-type inflorescence. The arrangement of homogamous and fertile spikelets could become denser to form a *Themeda*-type inflorescence.

For *Themeda* as a whole, trends in the number of spikelet pairs can be interpreted. Only a triad is retained in the racemes of *T. arguens*, *T. quadrivalvis* (L.) Kuntze, *T. sabarimalayana*, *T. tremula* and *T. triandra*. This is also true for *T. novoguineensis* (Reeder) Jansen, which Dunning et al. (2017) placed close to that clade. In contrast, species in the rest of the genus [e.g., *T. anathera* (Nees) Hack., *T. mooneyi* Bor and *T. strigosa* (Ham. ex Hook.f.) A.Camus] produce at least one spikelet pair and a triad in a raceme. In some species, inflorescence branches are gathered in a cluster (in *T. triandra*), but in the others a solitary inflorescence is observed (in *T. huttonensis*; Clayton et al., 2006; Veldkamp, 2016). Different combinations in the numbers of spikelet pairs, the presence of triads and the complexity of inflorescence architecture among species may reflect tradeoffs in the production of spikelets and the fitness of the plants (Valladares, Skillman & Pearcy, 2002). Increase in inflorescence branches in the species lacking spikelet pairs could compensate for the low numbers of bisexual spikelets. No explanation for a potential selective advantage of triads over spikelet pairs or vice versa has been proposed so far.

A novel result in this study is that *T. unica* S.L.Chen & T.D.Zhuang belongs to the *T. triandra* clade, in addition to two other morphologically similar species, *T. laxa* (Andersson) A.Camus and *T. quadrivalvis*. These names may need to be placed in synonymy under *T. triandra*, which our data show is more diverse morphologically than previously recognized. It has been documented that *T. quadrivalvis* and *T. triandra* form a single clade and species complex encompassing extensive genetic and morphological variation (Keir & Vogler, 2006). *Themeda quadrivalvis* lacks a spikelet pair within the raceme, which is also seen in *T. triandra*, and *T. unica* is distinct by its arrangement of homogamous spikelets on different levels (Chen & Phillips, 2006). Habit is another labile character (Heidel et al., 2016): whereas *T. triandra* is considered perennial, *T. quadrivalvis* is annual (Clayton et al., 2006). In *Themeda*, an annual habit is otherwise only known in *T. helferi* Hack., the phylogenetic position of which is unknown. This species was once treated as *T. quadrivalvis* var. *helferi* (Munro ex. Hack.) Bor and shares the annual habit, but genetic data are needed to properly assess its position. The closest relative of *T. triandra* differs between the nuclear (*T. arguens*) and plastome (*T. tremula*) trees, indicating possible hybridization before the origin of *T. triandra*.

Discordant positions of *H. triticeus* between nuclear and plastome trees make its classification difficult. It is sister to *Cymbopogon* in the plastome trees (Fig. 3.2) but sister to *H. contortus* in the nuclear trees (Fig. 3.3). We included multiple samples of both *H. triticeus* and *Cymbopogon* species, and therefore the discrepancy is not due to a single aberrant individual or a mix-up of samples. The nuclear tree did not fully support sister relationships between *H. triticeus* and the *Cymbopogon* clade. Almost half of nuclear genes yielded the topology where *H. contortus* and *H. triticeus* are sisters, with the remaining genes supporting the alternative position of *H. triticeus* (see Fig. 3.3, the common ancestor of *H. contortus* and *H. triticeus*). It is possible that *H. triticeus* acquired genome components from both the *Cymbopogon* and *H. contortus* lineages. Allopolyploidy is another possible explanation as a high ploidy in *H. triticeus* (2n = 60) has been documented (Tothill & Hacker, 1976). However, retracing the events that shaped the genome of this species will require further investigation with more samples and appropriate analyses and markers (Estep et al., 2014). In particular, phasing paralogous gene copies, which was not possible with our sequencing approach, will be critical for such a complex genome. Pending such analyses and given its morphological similarity to that of *H. contortus*, *H. triticeus* should for the moment be retained in *Heteropogon*.

Both nuclear and plastome trees place *H. fischerianus* in *H. contortus* (Figs 3.2, 3.3), which is also consistent with morphology. According to Deshpande (1988), distichous leaves (dense two-ranked phyllotaxy in one plane) are the only character that distinguishes *H. fischerianus* from *H. contortus*. Even though phyllotaxy is highly conserved across the Poaceae (Kellogg, 2000), intraspecific phyllotactic variation can emerge naturally via a single mutated gene (abph1) (Greyson & Walden, 1972; Jackson & Hake, 1999; Fleming, 2005). Therefore, *H. fischerianus* should be considered a synonym of *H. contortus*.

A final result with implications for taxonomy is the support, with both nuclear and plastome data, for a clade corresponding to the former subtribe Anthistiriinae sensu Clayton & Renvoize (1986), subsumed under Andropogoninae by Kellogg (2015) and Soreng et al. (2017). Although several genera (e.g. *Anadelphia* Hack., *Clausospicula* Lazarides, *Elymandra* Stapf, *Exotheca* Andersson, *Hyperthelia* Clayton, *Monocymbium* Stapf and *Parahyparrhenia* A.Camus) were previously included in Anthistiriinae (Clayton & Renvoize, 1986; Soreng et al., 2015), most of them were phylogenetically proven to belong to different lineages (Arthan et al., 2017; McAllister et al., 2018; Welker et al., 2020). Although type species of some genera have not been included in our analyses, we propose that an emended Anthistiriinae would be composed of the genera *Agenium*, *Bothriochloa*, *Capillipedium*, *Cymbopogon*, *Dichanthi*um, *Eremopogon*, *Heteropogon*, *Iseilema*, *Pseudanthistiria* and *Themeda*, separate from Andropogoninae. Inflorescence structure and spikelet morphology vary across these genera with no clear synapomorphy for the clade. The presence of basal homogamous spikelets is common, but this character also occurs in *Diheteropogon* and *Hyparrhenia* in Andropogoninae. Most genera of Anthistiriinae, except for members of *Cymbopogon*, only have a single raceme that may be quite short as in *Iseilema* and *Themeda*. At the species level, phylogenetic relationships suggest possible taxonomic changes in *Heteropogon* and *Themeda*. Necessary nomenclatural adjustments will be made in a separate publication.

The divergence of *Themeda* from *H. contortus* was estimated here at 7.56 Mya, at the start of the Miocene grassland expansion (Edwards et al., 2010). Speciation of *Themeda* started from 5.80 Mya in the Late Miocene until the early Pleistocene c. 2.40 Mya. The *T. arundinacea*–*T. villosa* clade diverged in the Late Miocene (Fig. 3.4). The latter is the only clade except *T. triandra* distributed in South-East Asia, and the divergence of this lineage from the rest of *Themeda* (5.4 Mya) in South-East Asia coincides with the development of savannas in the region (Ratnam et al., 2016). The divergence of the endemic Indian *Themeda*, *T. anathera* and *T. strigosa*, in the Early Pliocene (Figs 3.2, 3.4) could be correlated with a shift from C_3 grasslands to monsoonal C_4 ones in northern India during the Late Miocene (Quade et al., 1995; Srivastava et al., 2018).

The diversification of the widespread *T. triandra* and *H. contortus* was here estimated to the Pleistocene. This supports the results of Dunning et al. (2017) for *T. triandra* and suggests that both species became widespread only after the Miocene grassland expansion. Aridification in the Plio-Pleistocene may have shaped the Old-World savannas (Kaya et al., 2018) and favoured the spread of these now common savanna grass species. Further phylogeographic inferences are not possible here due to the lack of resolution within species. Another challenge is the potential confounding effect of recent anthropogenic introductions (Oviedo Prieto, Herrera Oliver & Caluff, 2012; Clayton et al., 2016; Mata et al., 2018). A comparative, genome-wide population genetic study of both species would be highly informative.

3.5 CONCLUSION

Phylogenetic analysis of the nuclear and the plastid genome show that neither *Themeda* nor *Heteropogon*, as currently understood, is monophyletic. *Themeda* includes *H. melanocarpus* and *H. ritchei*, whereas *Heteropogon* should be restricted to *H. contortus* (including *H. fischerianus*) and *H. triticeus*. The analysis also supports the recognition of Anthistiriinae. The *Themeda–Heteropogon* clade, in the strict sense, diversified during the Miocene grassland expansion, and the widespread *T. triandra* and *H. contortus* spread during the Pleistocene.

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CHAPTER 4

HETEROPOGON-THEMEDA GRASSES EVOLVE TO OCCUPY EITHER TROPICAL GRASSLAND OR WETLAND BIOMES

4.1 INTRODUCTION

Understanding associations between climatic niche, habitats, and functional traits of plant species can provide insights into their macroevolutionary patterns and trait evolution. A variety of combinations of environmental factors (e.g., precipitation, temperature, and disturbance) govern biome formations across the planet (Woodward et al., 2004). The environment exerts substantial control on the sorting of plant form and function via life-history strategies (Bazzaz, 1991). Life-history strategies in practice reflect ensembles of plant functional traits that combine to determine plant growth, survival, and reproduction (Westoby & Wright, 2006; Caruso et al., 2020). Functional traits are defined as morpho-physio-phenological traits that impact fitness indirectly via their effects on growth, reproduction, and survival (Violle et al., 2007) and environment sorts enable plants to acclimate to suitable climatic niches in different locations (Crisp et al., 2009; Aubin et al., 2016). However, plants are capable of dispersing along climatic gradients, which are associated with trait changes over time and the emergence of new functional traits (Donoghue & Edwards, 2014; Funk et al., 2017).

Phylogenetically, both climatic characteristics and functional traits can be viewed in a species- or clade-specific context (Pearman et al., 2008; Donoghue & Edwards, 2014) and can be interpreted to infer evolutionary history. Two opposing ecological theories, niche conservatism (Wiens & Graham, 2005) and niche divergence (Donoghue & Edwards, 2014), have been tested as potential drivers of species distribution patterns, ecological speciation, and trait evolution (Ackerly, 2003; Pyron et al., 2015). Niche conservatism emphasizes the tendency of closely related species to retain the same climatic niche and responsive functional traits as their ancestors (Wiens & Graham, 2005; Liu et al., 2012). The process of niche conservatism results in subpopulations or species tracking and maintaining similar climatic niche in adjacent areas even if speciation occurs (Pyron et al., 2015). In contrast, niche divergence is viewed as a less prevalent but high-impact phenomenon (e.g., biome shifts; Donoghue & Edwards, 2014) as sister species undergo trait transitions that are slightly or completely different from their ancestors, to adapt to novel environments (Crisp et al., 2009; Gavrilets & Losos, 2009). Currently, a growing number of comparative studies have been conducted on different plant lineages (e.g., Crisp & Cook, 2012) that help infer the macroecological processes and plant adaptations that affect species distributions and how life histories and traits evolve and diversify in different environments (Woodward & Williams, 1987; Kelly et al., 2021).

Wetlands and grasslands/savannas dominate tropical C_4 grassy biomes, and they are shaped by precipitation, seasonality, seasonal inundation, fire, and grazing (Sankaran & Ratnam, 2013; Joyce et al., 2016; Lehmann & Parr, 2016). Grasslands and savannas cover a broad climatic range of rainfall and dry seasons of 4–9 months per year (Lehmann et al., 2011). Wetlands and seasonally inundated grasslands are generally characterized by higher rainfall than grasslands and savannas (Finlayson, 2005; Gopal, 2013) and are sensitive to changes in flooding and precipitation seasonality (PS) (Erwin, 2009; Joyce et al., 2016). In terms of geographic distribution, tropical savannas and grasslands occupy a greater land surface area than tropical wetlands: ~20% versus ~2%–6%, respectively, of the global land surface (Barrow, 1994; Scholes & Hall, 1996). However, savannas and wetlands are structured as mosaics (examples presented in Mantlana et al., 2008; Melack & Hess, 2010; Souza-Neto et al., 2016). Differences in climatic regimes and geographic proximity of wetlands and savannas provide the potential for biome shifts and niche divergence of species in savannas and wetlands (Donoghue & Edwards, 2014). Forrestel et al. (2015) demonstrated that shifts from grasslands to wetlands in the genus *Lasthenia* Cass. (Asteraceae) are evolutionarily labile and under selection due to changes in hydrological regimes. However, investigations of climatic niche evolution in savanna and wetland grasses are scarce despite these ecosystems being globally widespread.

Grass species proliferate, tolerate, and adapt to open ecosystems via a set of functional traits that represent life-history strategies. Distinct grass lineages have been found to have correlations between size-related traits, especially height and leaf area, and climatic factors (Liu et al., 2012; Jardine et al., 2020). In C_4 grassy biomes, wetland and savanna grass species have a set of functional traits correlated with both seasonal dryness and inundation or combinations of the two. With seasonal inundation, grasses must mitigate water saturation and anoxic conditions alongside the need to avoid shading due to rapid growth and high productivity (Moor et al., 2017). Wetland species are hypothesized to have specialized traits to cope with inundation such as larger stature, rapid growth, and adventitious roots (Bortherton & Joyce, 2015; Moor et al., 2017). In contrast, savanna and grassland species must tolerate periods of limited water availability, exposure to solar radiance, fire, and grazing (Skarpe, 1996; Sankaran, 2009). Further, fire and flooding have often been associated with different seed dispersal mechanisms that can aid in seed burial for plant establishment and fire escape (Peart & Clifford, 1987; Linder et al., 2018). Grass awns that are pivotal in dispersal show high variability in function and morphology (Cavanagh et al., 2019). Geniculate awns are functionally active and respond to moisture by twisting and moving on the soil surface (hygroscopic), while many species have passive awns or even no awns (Peart & Clifford, 1987; Cavanagh et al., 2019).

The *Heteropogon* Pers.-*Themeda* Forssk. clade is an ecologically and morphologically diverse lineage of the grass tribe Andropogoneae, a major group in C_4 grassy biomes (Kellogg, 2015; Welker et al., 2020). The clade is relatively young (~8–10 million years), originating and diversifying during the time of the Miocene C_4 grassland expansion (Arthan et al., 2021), and comprises approximately 31 species (POWO, 2019). The ecological success of the clade is represented by two globally significant species: *Heteropogon contortus* (L.) P.Beauv. ex Roem. & Schult. and *Themeda triandra* Forssk. (Snyman et al., 2013; POWO, 2019). Both species share a broad distribution range across Africa, Asia, Australia, and North America (Barkworth et al., 2003; POWO, 2019), but only *H. contortus* occurs in South America (Goergen & Daehler, 2001). *Heteropogon triticeus* (R.Br.) Stapf ex Craib, *Themeda arundinacea* (Roxb.) A. Camus, *Themeda caudata* (Nees ex Hook. & Arn.) A. Camus, and *Themeda villosa* (Lam.) A. Camus are only found in mesic environments of Southeast Asia (Ratnam et al., 2016; POWO, 2019). Species with even more restricted distributions include *Themeda anathera* (Nees ex Steud.) Hack. in the Himalaya mountains and *Heteropogon ritchiei* (Hook.f.) Blatt. & McCann endemic to southern India. Morphological variation (e.g., plant height and size-related leaf traits; Clayton et al., 2006 onwards) presumably represents adaptation to different climatic niches and habitat types.

Diversity in geographic range, habitats, and phenotypes of the clade lead to questions about relationships between climatic niche, habitats, and responsive functional traits and provides an opportunity to explore macroevolution and trait evolution within C_4 grassy biomes at the species level. Here, we examine the *Heteropogon-Themeda* clade and seek to build on the most recent phylogenetic work of the *Heteropogon-Themeda* clade to understand relationships between the climate and key functional traits of the clade, to answer the following questions: (1) What is the interspecific bioclimatic variation of *Heteropogon* and *Themeda* species and how does bioclimatic variation explain their distribution patterns? In this aspect, we also focus on two widespread species, *H. contortus* and *T. triandra*, to examine differences in climatic niches. (2) Do wetland and grassland/savanna species occupy distinct bioclimatic and functional trait spaces? (3) How do functional traits evolve between grassland/savanna and wetland species?

4.2 MATERIALS AND METHODS

4.2.1 Species Occurrence Records and Selection of Bioclimatic Data

Species occurrence records for all *Heteropogon* and *Themeda* species were obtained from two main databases: Global Biodiversity Information Facility (GBIF) (www.gbif.org) using the "rgbif" package (Chamberlain et al., 2020) in R software (R Core Team, 2021) and the Botanical Information and Ecology Network (BIEN) databases (Enquist et al., 2016). Additional records were obtained from the Tropicos database (www.tropicos.org), plant specimen labels deposited in Bangkok Forest (BKF), Kew (K), Leiden (L), and Paris (P) herbaria, data collected by Morales-Fierro (2014), and fieldwork data from Thailand in 2018. Species records from regions not covered by these databases were compiled from floras (Shouliang & Phillips, 2006a, 2006b). Here, species occurring in a single locality are defined as endemic. All occurrence data sets were cleaned using R scripts and the "CoordinateCleaner" package (Zizka et al., 2019) by erasing records from the sea and out of range.

Nineteen climatic variables were extracted from the cleaned occurrence points at a resolution of 10 min from the WorldClim database (Hijmans et al., 2005) using the "raster" package (Hijmans & van Etten, 2012). Boxplots were used to inspect data patterns and outliers, which were then deleted. Principal component analysis (PCA) was performed using the "FactoMineR" package (Lê et al., 2008). All variables were standardized and centered. To avoid overparameterization, highly correlated variables ($r^2 \geq 0.75$) were dropped from the data set by considering the first two principal components of PCA and Pearson's coefficients (Appendix IIIA, IIIB). The PCA was used to select four bioclimatic driver variables also known to be significant regulating factors of C_4 grassy biomes (Lehmann et al., 2011; Bocksberger et al., 2016): temperature seasonality (TS), mean annual precipitation (MAP), precipitation seasonality (PS), and precipitation of driest quarter (PDryQ).

4.2.2 Trait Selection and Habitat Classification

Simple size-related functional traits (e.g., leaf length, width, or area) are accessible from databases and herbarium specimens and effective in explaining some ecological functions of plants (Pérez-Harguindeguy et al., 2016). Six vegetative and six reproductive traits were compiled from GrassBase (Clayton et al., 2006 onwards), Morales-Fierro (2014), measurements from herbarium specimens (K, BKF), and the literature (Deshpande, 1988; Shouliang & Phillips, 2006a, 2006b; Veldkamp, 2016). The traits were selected based on their ecological importance in grassy ecosystems as described in Table 4.1. Vegetative traits include five quantitative traits: culm height, leaf length, leaf width, leaf area, and leaf width to length ratio, and one qualitative trait, the presence of stilt roots, was recorded. Maximum culm height, recorded from floras as the typical maximum distance between the ground level and the apex of the inflorescence, is used as the maximum plant height (Clayton et al., 2006 onwards). Leaf length is measured from the base to the apex of the blade, and leaf width is the widest part of the blade. Reproductive traits include five quantitative traits: sessile spikelet length, caryopsis length, caryopsis width, callus length, and awn length, and one qualitative trait, awn type (geniculate, straight, or awnless). Spikelet measurements include the whole spikelet, but not the callus or pedicel. The measurement of caryopses follows Zhang et al. (2014). Awn is measured from the point of the attachment to the lemma to the apex. Maximum, minimum, and mean values were calculated for each trait across species (Appendix IV, V).

Table 4.1. Grass functional traits and their ecological importance

Functional traits	Ecological importance	Citations
Culm height	Competition: light acquisition	Liu & Osborne (2014), Moles et al. (2009)
Leaf length	Competition: productivity	Wright et al. (2004)
Leaf width	Drought avoidance	Wright et al. (2017)
Leaf area	Competition: productivity Reduce hydrological stress Solar irradiance	Linder et al. (2018), Pan et al. (2020) Li et al. (2020), Pan et al. (2020), Wright et al. (2004) Gallaher et al. (2019)
Leaf width to length ratio (Leaf ratio)	Drought avoidance	Gallaher et al. (2019), Wright et al. (2014)
Spikelet length	Dispersal	Linder et al. (2018)
Callus length	Seed establishment	Silberbauer-Gottsberger (1984)
Caryopsis length	Seed establishment and dormancy	Cayssials & Rodríguez (2013), Linder et al. (2018)
Caryopsis width	Seed establishment and dormancy	Cayssials & Rodríguez (2013), Linder et al. (2018)
Awn length	Seed establishment and dispersal	Peart & Clifford (1987), Linder et al. (2018)
Awn type	Seed establishment and dispersal mode	Cavanagh et al. (2019), Peart & Clifford (1987)
Presence of stilt root	Mitigate water saturation	Moor et al. (2017), Pan et al. (2020)

Habitat data for each *Heteropogon* and *Themeda* species were compiled from the literature (Table 4.2; Deshpande, 1988; Shouliang & Phillips, 2006a, 2006b;

Veldkamp, 2016), labels from herbarium specimens, and online herbarium databases from K (apps.kew.org), L (bioportal.naturalis.nl), and P (science.mnhn.fr) herbaria. Data on local community composition, seasonality, soil types, and geology were also obtained in habitat categorization to help identify major habitats: grassland and savanna, or wetland. Terminology was standardized for grassland and savanna, for example, woodland and savanna are interchangeable terms that refer to a habitat where C_4 grasses are the main ground cover and sparse trees are present within the area (Table 4.2). Some habitats not described in the literature as grasslands/savannas or wetlands, such as coastal areas or rock outcrops (Goergen & Daehler, 2001), were excluded from the habitat classification.

Table 4.2. Summary of habitat classifications and key references of *Heteropogon-Themeda* species

Species	**Sample size**	**Habitat types**	**Key references to the habitat classification**	**Phylogenetic analyses**
Heteropogon contortus	7,069	Savanna & Grassland	Grice & McIntyre (1995) Daehler & Carino (1998) Ratnam et al. (2016)	✓
Heteropogon fischerianus	1	Savanna & Grassland	Deshpande (1988)	✓
Heteropogon melanocarpus	544	Savanna & Grassland	Vesey-Fitzgerald (1970) Srivastava (2004) Strohbach (2013) Nanjarisoa et al. (2017)	✓
Heteropogon ritchiei	6	Savanna & Grassland	Puri & Patil (1960) Lekhak & Yadav (2012) Rahandale & Rahandale (2014)	✓
Heteropogon triticeus	3244	Savanna & Grassland	Kirkpatrick et al. (1987) Scott et al. (2009) Ens et al. (2015) Sookchaloem et al. (2015)	✓
Themeda anathera	55	Savanna & Grassland	Muhammad et al. (2012) Shaheen et al. (2015) Amjad et al. (2016)	✓
Themeda arguens	516	Savanna & Grassland	Kirkpatrick et al. (1988) Neldner et al. (1997) Djufri & Wardiah (2017) Sutomo (2020) Sutomo et al. (2020)	✓
Themeda arundinacea	56	Wetland	Yadava (1990) Lehmkuhl (1994) Dangol & Maharjan (2012) Pala et al. (2012) Ratnam et al. (2016) Naskar & Bera (2018)	✓
Themeda avenacea	581	Savanna & Grassland	Kennedy et al. (2001) Lang (2008) Lewis et al. (2008)	✓

Table 4.2. Summary of habitat classifications and key references of *Heteropogon*-*Themeda* species (continued)

Species	Sample size	Habitat types	Key references to the habitat classification	Phylogenetic analyses
Themeda caudata	72	Wetland	Bhatia (1958) Xiwen & Walker (1986) Ghosh (2012) Biswas et al. (2016)	✓
Themeda cymbaria	23	Savanna & Grassland	Kothandaraman et al. (2020) Mondal & Sukumar (2015) Pulla et al. (2016) Sankaran (2009) Subashree & Sundarapandian (2017)	✓
Themeda gigantea	24	Wetland	Marler & Ferreras (2017) Veldkamp (2016) Li et al. (2011) Xiwen & Walker (1986)	✗
Themeda helferi	6	Savanna & Grassland	Kumar et al. (2018) Shouliang & Phillips (2006b)	✓
Themeda hookeri	33	Savanna & Grassland	Li et al. (2016) Liu et al. (2019) Veldkamp (2016) Xiwen & Walker (1986) Zhao et al. (2020)	✓
Themeda huttonensis	4	Savanna & Grassland	Shouliang & Phillips (2006b)	✓
Themeda idjenensis	7	Wetland	Veldkamp (2016)	✗
Themeda intermedia	52	Wetland	Gressitt (1982) Paijmans (1983) Manner & Lang (2006) Mylliemngap & Barik (2019)	✓
Themeda minor	1	Savanna & Grassland	Chen-feng et al. (2004) Liu et al. (2004)	✓
Themeda mooneyi	5	Savanna & Grassland	Mahata et al. (2019) Murthy (2003)	✓

Table 4.2. Summary of habitat classifications and key references of *Heteropogon-Themeda* species (continued)

Species	**Sample size**	**Habitat types**	**Key references to the habitat classification**	**Phylogenetic analyses**
Themeda novoguineensis	18	Wetland	Eden (1974) Gillison (1983) Gressitt (1982)	✓
Themeda pseudotremula	1	Savanna & Grassland	Potdar et al. (2003)	✗
Themeda quadrivalvis	1,457	Savanna & Grassland	Shukla et al. (2010) Patzelt (2011) Keir & Vogler (2006) Vogler & Owen (2008)	✓
Themeda sabarimalayana	1	Savanna & Grassland	Sreekumar & Nair (1987)	✓
Themeda saxicola	1	Savanna & Grassland	Karthikeyan et al. (1989) Bor (1951)	✗
Themeda strigosa	2	Savanna & Grassland	Bor (1960) Karthikeyan et al. (1989)	✓
Themeda tremula	37	Savanna & Grassland	Amarasinghe & Pemadasa (1982) Pemadasa (1990) Pemadasa & Mueller-Dombois (1979)	✓
Themeda triandra	46,703	Savanna & Grassland	Snyman et al. (2013) Morgan & Lunt (1999) Lunt (1995) Trollope (1982) Mott & Tothill (1984) O'Connor (1997)	✓
Themeda trichiata	3	Savanna & Grassland	Shouliang & Phillips (2006b)	✓
Themeda unica	1	Savanna & Grassland	Shouliang & Phillips (2006b)	✓
Themeda villosa	245	Wetland	Ratnam et al. (2016) Biswas et al. (2016) Dutta & Sarma (2018) Rawat (2005) Mylliemngap & Barik (2019)	✓
Themeda yunnanensis	0	Savanna & Grassland	Chao (2009) Tain et al. (2007) Shouliang & Phillips (2006b)	✗

4.2.3 Statistical Analyses of Climatic Niche and Traits among *Heteropogon-Themeda* Species

A. Climatic Niche and Trait Analyses among Habitat Groups

PCA was used to analyze and illustrate bioclimatic niche groupings, based on the four selected bioclimatic variables, between habitat groups using the “FactoMineR” package (Lê et al., 2008). To understand trait groupings, factor analysis of mixed data (FAMD) was performed in “FactoMineR” package by using continuous (plant height, leaf area, leaf ratio, maximum sessile spikelet length, and maximum awn length) and discrete characters (habit, presence of stilt root, presence of awn, and awn type). Missing data were addressed using the function “imputePCA” in the “missMDA” package (Josse & Husson, 2016). To test statistical differences, all bioclimatic and functional trait mean values from all species were scaled and centered. The Kruskal–Wallis test was chosen as the statistical test for continuous traits, given the size of the data set of 29 species. Dunn's and Wilcoxon's tests were performed as post hoc analyses to compare between habitat groups.

B. Climatic niche and trait analyses between widespread species, *Heteropogon contortus*, and *Themeda triandra*

The climatic space occupied by *H. contortus* and *T. triandra* was compared. Occurrence records of each species were divided into continents according to The World Geographical Scheme for Recording Plant Distributions (WGSRPD) (Brummit, 2001). The Tropics of Capricorn and Cancer (between 23.44 and −23.44 latitude) were used to separate tropical and temperate regions. Records from islands were discarded, but records from Madagascar were combined with those from Africa. This resulted in five tropical data sets for *H. contortus* from Africa, America, Asia, Australia, and the Middle East along with three tropical data sets for *T. triandra* from Africa, Asia, and Australia. A data set of *Themeda quadrivalvis* (L.) Kuntze sampled from the Middle East was included in this analysis as it is nested in the *T. triandra* clade despite its annual habit (Dunning et al., 2017; Arthan et al., 2021). The temperate data set was separated from the tropical data set and compared with each other to determine the differences in climatic niche. The similar bioclimatic data from the previous section (TS, MAP, PS, and PDryQ) were used in the PCA to compare the climatic niche space of *H. contortus* and *T. triandra*. Similar settings of niche equivalency and similarity tests described above were used to compare bioclimatic niche occupancy between *H. contortus* and *T. triandra* + *T. quadrivalvis* populations. Analysis of variance was used to test statistical differences among traits, and PCA was used to group these two widespread species by traits using the “FactoMineR” package (Lê et al., 2008).

“ENMTools” (Warren et al., 2021) and “ecospat” package222s (Di Cola et al., 2016) were used to compute the climatic niche overlap between species. The PCA-env method (Broennimann et al., 2011) was implemented in the “ecospat” package to quantify niche overlap between species estimated by Schoener's D (Schoener, 1970) and Warren's I matrices (Warren et al., 2021). Higher D and I values indicate greater overlap between species pairs. Species with fewer than five occurrence records were not included in equivalency and similarity tests.

Observed niche overlap values in the previous step were statistically compared with a null distribution of niche overlap values calculated from background points. Niche equivalency tests the similarity of two species in their climatic space and hence any potential for functional equivalence and mutual replacement. Niche similarity tests take climatic differences into account to test if the two species are more different than expected by chance. Both tests were performed according to Warren et al. (2021), using background points within a 5 km buffer radius and nonparametric tests with 1000 pseudoreplicates to create null distributions. The null distribution of sampled D and I values from the background environment was set to compare with empirical D and I values. The two species considered as significantly different have distinct climatic niche occupations. These analyses were repeated with all possible pairs of species and species grouped by habitat types.

4.2.4 Phylogenetic Comparative Methods

A. Phylogenetic Reconstruction

Andropogoneae plastome alignment from Arthan et al. (2021) was combined with four other *Themeda* accessions, *Themeda avenacea* (F. Muell.) T. Durand & B. D. Jacks., *Themeda intermedia* (Hack.) Bor, *Themeda novoguineensis* (Reeder) Jansen, and *Themeda trichiata* S. L. Chen & T. D. Zhuang, from Dunning et al. (2017) to produce a phylogenetic tree. The phylogenetic tree includes 25 ingroup species, representing 81% of the 31 species in the genera *Heteropogon* and *Themeda* (Table 4.2). Bayesian analyses were run using MrBayes v.3.2.7a (Ronquist et al., 2012) in CIPRES (Miller et al., 2010). The GTR + Γ + I was the best model estimated from jModelTest v.2.1.6 (Darriba et al., 2012). Two Markov Chain Monte Carlo (MCMC) runs were set with 100 000 000 generations each, 2000 generation samplings, and 25% burn-in. Dating analyses followed Arthan et al. (2021) using BEAST2 v.2.6.1 (Bouckaert et al., 2014), with the divergence time between *Zea mays* L. and the other Andropogoneae at 25 Ma. Effective sample size values for most parameters were more than 200 as explored by Tracer v.1.7.1 (Rambaut et al., 2018).

B. Continuous Trait Analyses—Bioclimatic Variables and Functional Traits

We investigated how the four climate variables and functional traits evolved in the context of habitat preferences of species in the *Heteropogon-Themeda* clade. The evolution of climatic occupancy was analyzed by PCA values of the four climatic variables from Section 2.3 with the function “fastanc” in the “phytools” package (Revell, 2012). For functional traits, the phylogenetic signal was estimated using Blomberg's K (Blomberg et al., 2003) and Pagel's (Pagel, 1999) values with maximum likelihood estimation with 1000 simulations in the “phytools” package (Revell, 2012) with the “phylosig” function. The maximum clade credibility tree was pruned to include only the *Heteropogon-Themeda* clade. The phylogenetic tree was painted with habitat types by all-rate-different (ARD) with the “make.simmap” function from “phytools” packages with 500 simulations. Each simulated tree reconstructed shifts in habitat type at different positions along the branches. All trait values were log-transformed before fitting trait evolution models, except for maximum awn length, which was squared-root transformed as it contained zero values (awnless species). The “OUwie” package (Beaulieu et al., 2012) was then used to test six different Brownian motion (BM) and Ornstein Uhlenbeck (OU) models on the simulated trees: BM (simple Brownian motion), BMS (different evolutionary rates between habitat groups), OU1 (one optimum across habitat groups), OUM (more than one optimum across habitat groups and with a single pull strength), OUMA (more than one optimum across habitat groups; multiple pull strengths; a single evolutionary rate), and OUMV (more than one optimum across habitat groups; a single pull strength; multiple evolutionary rates). Trait optimum value (θ), strength of selection (α), and rates of evolution (σ) were estimated from the analyses. The OU model is a model of macroevolution. Note that the strength of selection explained by the statistic describes current trait value evolution towards the optimum value (θ) over time (Butler & King, 2004). The statistic is derived from the OU model predicting and simulating changes in trait values along the branches of the phylogeny over large timescales (Butler & King, 2004; Cooper et al., 2016) as opposed to more conventional measures such as $R = h^2S$ making use of genetic data between generations (Stinchcombe et al., 2017).

C. Discrete Trait Analyses—Awn Evolution Analyses

Awn type transitions and rates were analyzed using BayesTraits v.3.0.2 (Pagel et al., 2004). Character coding in this study treats the geniculate state as 0. The nonhygroscopic straight state and the awnless state are coded with 1 and 2 as derived characters, respectively. A set of 1000 post-burn-in Bayesian trees was sampled from the phylogenetic analyses to account for phylogenetic uncertainty. The trees included ingroups and additional outgroups, *Andropogon distachyos* L., *Hyparrhenia subplumosa* Stapf, and *Schizachyrium sanguineum*

(Retz.) Alston. The multistate mode and the MCMC method in BayesTraits were selected to run with nine different transition models. 100,000,000 generations, 10,000,000 burnin, tree sampling every 1,000 generations, and exponential hyperprior of 10 were set for the MCMC analyses. Median log-likelihood values (−InL) were calculated from each transition model. Likelihood ratio tests were used for model comparisons to find the best transition model.

To reconstruct the probabilities and patterns of change along the phylogenetic tree, the best model estimated for the MCMC analyses was applied to the same set of 1,000 post-burnin trees. We tested the best model against three other models, ARD, equal rates, and symmetrical rates, to confirm that the previous model was the best model. The function "make.simmap" from the "phytools" package (Revell, 2012) was used in stochastic mapping. Simulations were run with 100 replicates per tree, which yielded 100,000 simulated trees in total. All trees were summarized using the "describe.simmap" function, yielding an average number of shifts and probabilities between states at nodes. The summary tree was visualized using pie charts to represent the probabilities of each awn state at the nodes.

4.3 RESULTS

4.3.1 Summary of Species Occurrence Records and Habitat Categorization

A total of 60,585 occurrence records were obtained, of which 46,703 were for *Themeda triandra*. Within the study group, we recognize six endemic species: *Heteropogon fischerianus* Bor, *Themeda minor* L. Liou, *Themeda pseudotremula* Potdar et al., *Themeda sabarimalayana* Sreek. & V. J. Nair, *Themeda saxicola* Bor, and *Themeda unica* S. L. Chen & T. D. Zhuang having a single record each (Table 4.2).

Twenty-four species exist in a variety of savannas including dipterocarp deciduous forest, Acacia woodlands, Eucalyptus woodlands, Melaleuca savanna, and Miombo woodland. Seven wetland species were identified from the literature by indicative descriptions such as "seasonally flooded," "riverine forest," "alluvial grassland," "flood plain," "waterlogged depressions," or "river basin" (Gopal, 2013; Joyce et al., 2016).

4.3.2 Climatic Niche and Functional Traits Separation among Habitat Groups

The bioclimatic envelopes of the wetland species were characterized by higher MAP and PDryQ and lower seasonality than the grassland/savanna group ($P < 0.05$; Figs. 4.1A–D; Table 4.3). According to the PCA, 88.8% of variance explained the separation between the wetland and the grassland/savanna groups (Fig. 4.1E; Appendix VI). The wetland species exist in the area with high rainfall that was sufficient to create a seasonally inundated area or wetland (Joyce & Wade, 1998). Average lower PS in wetlands suggested a shorter dry season in the habitat as compared to grasslands/savannas. Most grassland/savanna species have high rainfall seasonality values of more than 50 (Fig. 4.1C), with dry seasons lasting more than 5 months. Standing water of wetlands is maintained during the dry phase as rainfall during the “dry” season is not very low (Fig. 4.1D).

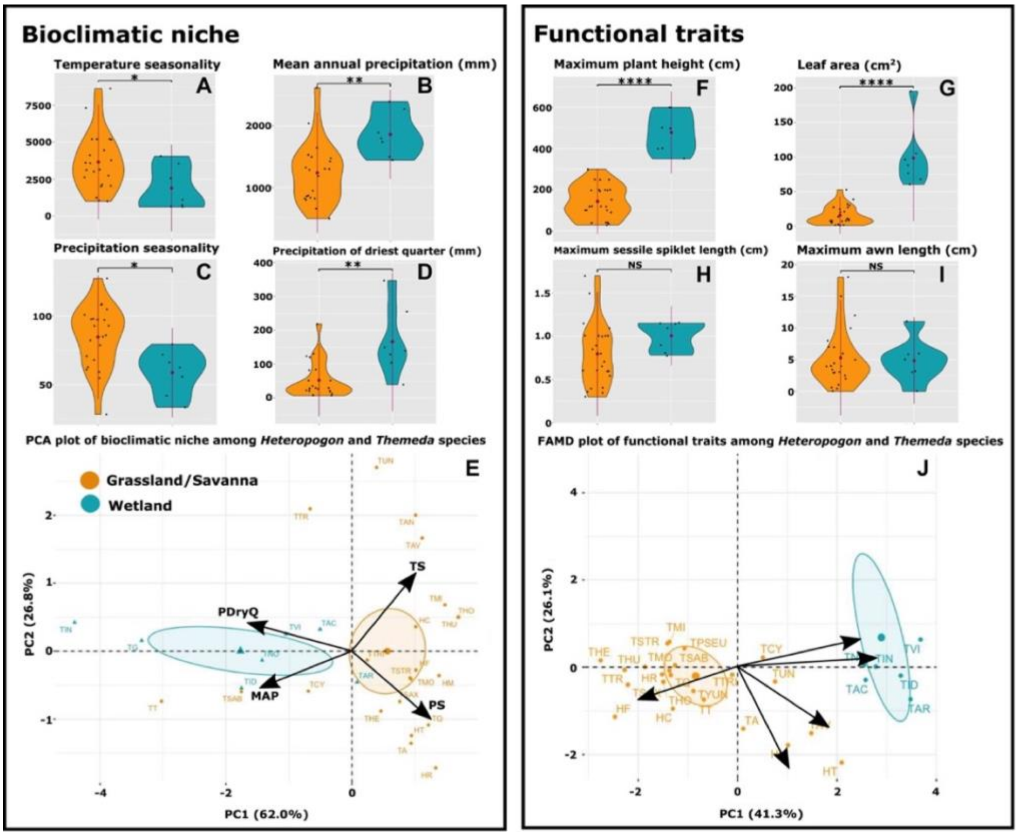

Figure 4.1. Box plots representing bioclimatic ranges (**A–D**) and functional traits (**F–I**) between grassland/savanna (orange) and wetland (blue) and principal component analysis (PCA) of bioclimatic variables € and functional traits (**J**) of *Heteropogon* and *Themeda* species distinguishing bioclimatic overlap and trait space between grassland/savanna and wetland groups. Asterisks above the plots represent statistical significance between the groups.

HC = *Heteropogon contortus*, HF = *Heteropogon fischerianus*, HM = *Heteropogon melanocarpus*, HR = *Heteropogon ritchiei*, HT = *Heteropogon triticeus*, TAN = *Themeda anathera*, TA = *Themeda arguens*, TAR = *Themeda arundinacea*, TAV = *Themeda avenacea*, TC = *Themeda caudata*, TCY = *Themeda cymbaria*, TG = *Themeda gigantea*, THE = *Themeda helferi*, THO = *Themeda hookeri*, TID = *Themeda idjenensis*, TIN = *Themeda intermedia*, TMI = *Themeda minor*, TMO = *Themeda mooneyi*, TNO = *Themeda novoguineensis*, TPSEU = *Themeda pseudotremula*, TQ = *Themeda quadrivalvis*, TSAB = *Themeda sabarimalayana*, TSAX = *Themeda 115axicola*, TT = *Themeda triandra*, TTR = *Themeda tremula*, TUN = *Themeda unica*, TVI = *Themeda villosa*, TYUN = *Themeda yunnanensis*.

The wetland species are spread out by the variance of MAP and precipitation of the driest quarter along the PC1. Broad precipitation ranges can be found within single species such as

Themeda villosa that ranges from 670 to around 2500 mm/year. One wetland species, *Themeda arundinacea*, is positioned close to the grassland/savanna group in climatic space (Fig. 4.1E) as it occupies lower precipitation envelopes than other wetland species.

Table 4.3. Statistical differences in functional traits between the grassland/savanna and wetland species tested by the Kruskal–Wallis test and post hoc comparisons using Dunn’s and Wilcoxon’s tests

	Grassland/ Savanna [Mean (SE)]	Wetland [Mean (SE)]	Kruskal-Wallis test	Dunn’s test	Wilcoxon test	Significance difference
Bioclimatic variables						
Temperature seasonality	3650 (413)	1897 (554)	5.03	-2.24	121	$P < 0.05$
Mean annual precipitation	1239 (104)	1862 (136)	8.44	2.91	20	$P < 0.005$
Precipitation seasonality	84.8 (4.80)	58.9 (6.16)	6.24	-2.50	126	$P < 0.05$
Precipitation of driest quarter	52.2 (11.4)	166 (38.7)	9.67	3.11	16	$P < 0.005$
Functional traits						
Maximum plant height (cm)	144 (16.2)	479 (37.6)	15.9	-2.24	121	$P < 0.001$
Leaf length (cm)	40.2 (5.12)	129 (21.4)	15.1	3.89	2.5	$P < 0.001$
Leaf area (cm^2)	15.3 (2.75)	98.2 (17.2)	15.8	3.97	0	$P < 0.001$
Leaf width to length ratio	0.027 (0.003)	0.014 (0.001)	6.67	-2.58	138	$P < 0.05$
Maximum sessile spikelet length (cm)	0.796 (0.073)	1.000 (0.065)	3.60	1.90	44	$P > 0.05$
Maximum awn length (cm)	5.31 (0.927)	4.86 (1.29)	0.01	0.09	82	$P > 0.05$

In the PCA of functional traits, some vegetative traits were highly correlated; thus, we chose one of them to explain functions in the grasslands/savannas and wetlands. The vegetative traits did not correlate with reproductive ones in the PCA (Appendix VIIA−VIIB), while no significant differences were detected among reproductive traits (data not shown). The wetland species have taller culms (479 ± 37.6 cm) than the grassland/savanna species (144 ± 16.2 cm). Likewise, the wetland species also have greater leaf area (98.2 ± 17.2 cm2) than the grassland/savanna species (15.3 ± 2.75 cm2) ($P < 0.05$; Figs. 4.1F–G; Table 4.3). In contrast, the maximum length of the spikelet and the awn did not differ significantly between the two habitat types ($P > 0.05$; Figs. 4.1H–I). The FAMD biplot showed that 67.40% of the morphological variance explained the grassland/savanna versus wetland groupings (Fig. 4.1J), demonstrating that distinct sets of functional traits represent the grassland/savanna versus wetland species, but the grassland/savanna species encompass greater trait variation than the wetland group.

4.3.3 Climatic Niche and Functional Traits Separation between Two Widespread Species *Heteropogon contortus* and *T. triandra*

The bioclimatic envelope of *H. contortus* is typified by greater seasonality than *T. triandra* (Figs. 4.2A–D; Table 4.4). *Themeda triandra* occupies a significantly narrower climatic niche than *H. contortus*, especially in terms of seasonality (Figs. 4.2A, 4.2C). PCA of climate variables explained 85.96% of variance separating *H. contortus* from *T. triandra* (Fig. 4.2E). *Themeda triandra* is generally greater in stature and produces longer leaves than *H. contortus* (Figs. 4.2F–G; Table 4.4), but the leaf area does not significantly differ between the species (Fig. 4.2H). The leaf width to length ratio showed that *H. contortus* had a higher leaf ratio than *T. triandra* (Fig. 4.2I). Trait space distinguished *H. contortus* from *T. triandra* by 90.60% of the trait variation included in this study (Fig. 4.2J).

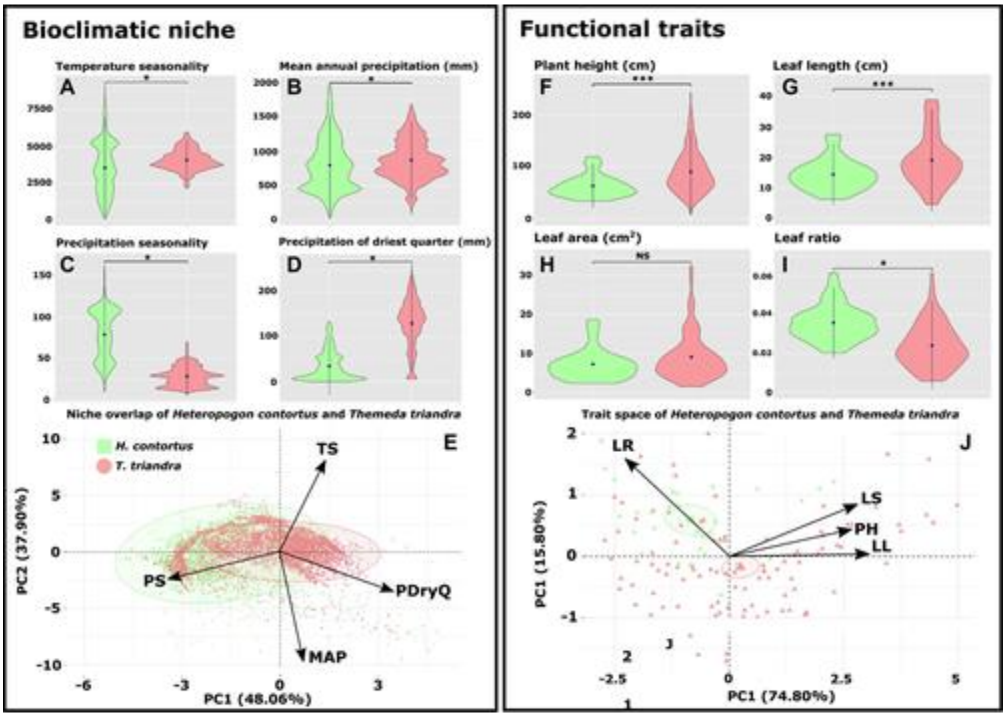

Figure 4.2. Box plots showing significant differences in bioclimatic factors (**A–D**) and height- and size-related leaf traits, except leaf area (**F–I**) of two widespread species *Heteropogon contortus* and *Themeda triandra*. Bioclimatic niche space (**E**) and trait space (**J**) of two species were

shown by principal component analyses. Bioclimatic niche: MAP = mean annual precipitation, PDryQ = precipitation of driest quarter, PS = precipitation seasonality, and TS = temperature seasonality; functional traits: LL = leaf length, LR = leaf ratio, LS = leaf size, and PH = plant height.

Table 4.4. Statistical differences in bioclimatic characteristics and functional traits between *Heteropogon contortus* and *Themeda triandra* tested by analysis of variance (ANOVA) and post hoc comparisons using the Tukey's honest significant difference test

	***H. contortus* [Mean (SE)]**	***T. triandra* [Mean (SE)]**	**ANOVA test F-value**	**Tukey HSD test**	**Significance difference**
Bioclimatic variables					
Temperature seasonality	3593 (20.2)	4115 (3.31)	2040	522.455	$P < 0.05$
Mean annual precipitation	797 (4.46)	869 (1.33)	351.2	71.940	$P < 0.05$
Precipitation seasonality	78.9 (0.351)	28.6 (0.056)	63892	-50.307	$P < 0.05$
Precipitation of driest quarter	34.8 (0.399)	130 (0.249)	20206	95.441	$P < 0.05$
Functional traits					
Maximum plant height (cm)	63.6 (3.64)	91.3 (1.64)	15.5	0.301	$P < 0.05$
Leaf length (cm)	14.4 (0.793)	21.0 (1.40)	10.29	0.299	$P < 0.001$
Leaf area (cm^2)	7.26 (0.624)	9.13(0.708)	2.02	0.167	$P > 0.05$
Leaf width to length ratio	0.036 (0.001)	0.026 (0.002)	21.75	-0.432	$P < 0.001$

4.3.4 Comparisons of Climatic Niche Overlap, Equivalency, and Similarity among Species

Low to intermediate D and I values ranged from 0 to 0.56 and from 0 to 0.74, respectively, following the criteria from Broennimann et al. (2011). The highest climatic niche overlap from niche equivalency tests was found between *Themeda arguens* (L.) Hack. and *Themeda quadrivalvis* ($D = 0.54$, $I = 0.74$, $P < 0.05$). *H. contortus* and *Heteropogon ritchiei* shared the most and the least similar bioclimatic envelopes with other species, respectively (Table 4.5).

Table 4.5. Matrix of background or similarity tests between species pairs of the *Heteropogon-Themeda* clade[†] in two directions.

	HC	TT	TAV	HM	TQ	HT	TA	THO	TAN	TCY	TTR	HR	THE	TMO	TVI	TC	TIN	TAR	TG	TNO	TID
HC	■	▨	□	□	▨	▨	▨	□	□	▨	▨	▨	□	□	□	▨	▨	□	▨	▨	▨
TT	▨	■	▨	▨	▨	▨	▨	▨	□	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
TAV	□	▨	■	▨	▨	▨	▨	▨	□	▨	▨	▨	▨	▨	□	▨	▨	▨	▨	▨	▨
HM	□	▨	▨	■	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
TQ	▨	▨	▨	▨	■	□	▨	▨	▨	▨	▨	▨	▨	□	▨	▨	▨	□	▨	▨	□
HT	▨	▨	▨	▨	□	■	▨	▨	▨	▨	▨	▨	□	▨	▨	▨	▨	▨	▨	▨	▨
TA	▨	▨	▨	▨	□	▨	■	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	□
THO	□	□	□	□	▨	▨	▨	■	▨	▨	▨	▨	▨	▨	□	▨	▨	□	▨	▨	▨
TAN	□	▨	□	□	▨	▨	▨	▨	■	▨	▨	▨	▨	▨	□	□	▨	▨	▨	▨	▨
TCY	▨	□	▨	□	▨	▨	▨	▨	▨	■	▨	▨	▨	▨	▨	□	□	□	▨	▨	▨
TTR	□	▨	▨	▨	▨	▨	▨	▨	▨	▨	■	▨	▨	▨	□	□	▨	▨	□	▨	▨
HR	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	■	▨	▨	▨	▨	▨	▨	▨	▨	▨
THE	□	□	□	▨	▨	▨	▨	▨	▨	▨	▨	▨	■	▨	□	□	▨	□	▨	□	▨
TMO	▨	▨	▨	□	□	▨	▨	▨	▨	▨	▨	▨	▨	■	▨	□	▨	▨	▨	▨	▨
TVI	□	▨	▨	▨	□	▨	▨	□	▨	□	▨	▨	▨	▨	■	□	□	□	□	□	□
TC	□	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	□	■	▨	□	▨	□	▨
TIN	□	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	□	□	■	□	▨	▨	▨
TAR	□	□	▨	▨	▨	▨	▨	▨	▨	□	▨	▨	▨	▨	□	□	□	■	▨	▨	▨
TG	□	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	□	□	□	□	■	▨	▨
TNO	□	▨	▨	▨	□	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	□	□	▨	▨	■	□
TID	▨	▨	□	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	□	□	□	□	□	□	■

Savanna and wetland species are labeled by orange and blue boxes, respectively. Nonparametric tests were analyzed with 1000 pseudoreplicates by comparing with empirical *D* (upper diagonal) and *I* (lower diagonal) values. White and gray boxes indicate that the species pairs are significantly similar ($P > 0.05$) or dissimilar ($P < 0.05$), respectively; [†]Some species are discarded from the analyses as they provide less than five presence records that ENMTools package does not allow in the analyses; HC = *Heteropogon contortus*, HM = *Heteropogon melanocarpus*, HR = *Heteropogon ritchiei*, HT = *Heteropogon triticeus*, TAN = *Themeda anathera*, TA = *Themeda arguens*, TAR = *Themeda arundinacea*, TAV = *Themeda avenacea*, TC = *Themeda caudata*, TCY = *Themeda cymbaria*, TG = *Themeda gigantea*, THE = *Themeda helferi*, THO = *Themeda hookeri*, TID = *Themeda idjenensis*, TIN = *Themeda intermedia*, TNO = *Themeda novoguineensis*, TQ = *Themeda quadrivalvis*, TT = *Themeda triandra*, TTR = *Themeda tremula*, TVI = *Themeda villosa*.

Bioclimatic niche overlap between the wetland and grassland/savanna groups was overall low, with a D value of 0.190 and an I value of 0.410 (Appendix VIII). Niche equivalency and similarity tests rejected the null hypothesis, indicating that the group climatic niche spaces are not identical or similar. Wetland species pairs showed greater bioclimatic niche overlap compared to the grassland/savanna species in niche equivalency and similarity tests (Table 4.5). For example, the bioclimatic niche of *Themeda caudata* was shared with most wetland species (Table 4.5). However, the bioclimatic niche also differed among some wetland species; for instance, *T. arundinacea* and *T. villosa* had very low D values (Table 4.5).

Variations in the bioclimatic envelopes occupied by the *Heteropogon-Themeda* clade partly explained distribution patterns at interspecific levels. Low D and I values were obtained between endemic species or between endemic and wide-ranging species, showing that the most narrow-ranging species occupy a unique climate space (Table 4.5). The climate space of *Themeda anathera* is dissimilar to that of the other species as shown by the significantly low D and I matrices in niche similarity tests (Appendix IX). This is also particularly true for other narrow-ranging species, *H. ritchiei*, *Themeda cymbaria* Hack., *Themeda helferi* Hack., *Themeda hookeri* (Griseb.) A. Camus, and *Themeda idjenensis* Jansen. However, most D and I values are significantly different from null distributions in equivalency tests (Appendix IX).

Overall, climatic niche analyses of *H. contortus* and *T. triandra* quantified a low, but significantly different climatic niche overlap of 0.29 and 0.39 for D and I values, respectively. When the continents are considered separately, the PCA explained 81.40% and 87.40% of the variance between *H. contortus* and *T. triandra* populations (Fig. 4.3). African *T. triandra* shares the most similar bioclimatic niche with South American *H. contortus* ($D = 0.67$, $I = 0.79$, $P > 0.05$; Appendix X, XI). Asian and Australian *T. triandra* have lower overlap with the South American *H. contortus* when compared to the African *T. triandra* ($D = 0.38$ and 0.33, $I = 0.61$ and 0.48, $P < 0.05$; Appendix X, XI). Asian and Australian groups are positioned in the more mesic and arid portions of the PCA surface (Fig. 4.3). High inter- and intraspecific overlaps between the temperate and tropical populations of both species showed no statistical differences (Appendix XII).

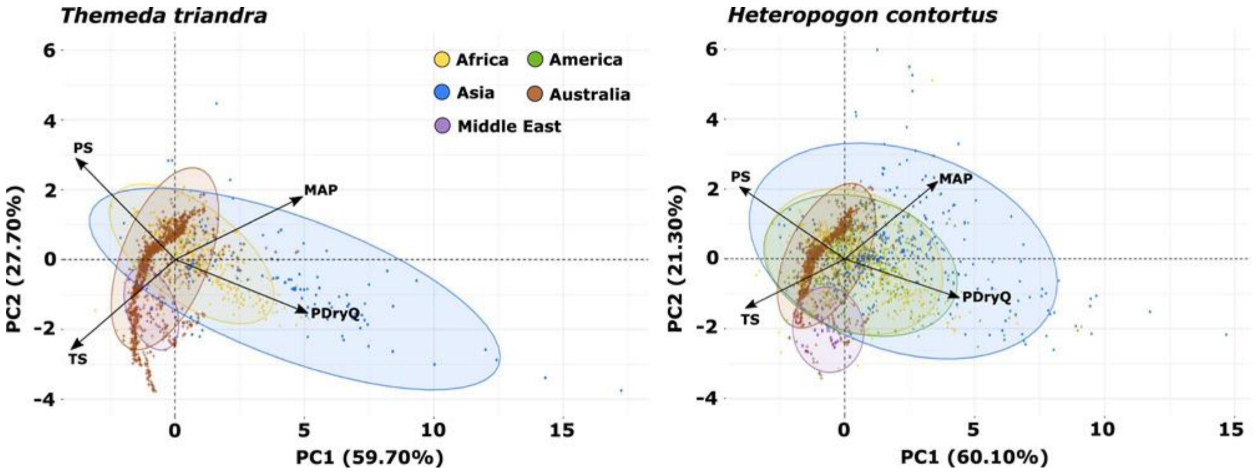

Figure 4.3. Principal component analyses of climatic niche space using the four bioclimatic variables between *Heteropogon contortus* and *Themeda triandra* populations from Africa, America, Asia, Australia, and the Middle east. MAP = mean annual precipitation, PDryQ = precipitation of driest quarter, PS = precipitation seasonality, and TS = temperature seasonality.

4.3.5 Evolution of Climatic Niches and Functional Traits of the Grassland/Savanna and Wetland Species

Both bioclimatic niche and functional trait evolution had low phylogenetic signals as estimated by the K and indices (Table 4.6). The maximum likelihood estimation of bioclimatic variables on the phylogeny predicted intermediate levels of PS (PS ~ 90; Fig. 4.4C) and annual precipitation, but a low level of precipitation during the driest quarter (~60 mm; Fig. 4.4D) at the ancestral node of the wetland clade comprising *T. arundinacea*, *T. caudata*, *Themeda intermedia*, and *T. villosa* (Figs. 4.4C–D). Shifts into wetter conditions occur twice, one in the *T. arundinacea*, *T. caudata*, *T. intermedia*, and *T. villosa* clade, and the other in *Themeda novoguineensis* (Figs. 4.4C–D). A possible reversal from mesic habitats to a drier savanna environment was also observed in the clade of *Themeda avenacea* and *Themeda trichiata*.

Table 4.6. Comparative phylogenetic analyses of functional traits showing estimates of phylogenetic signal based on the maximum likelihood method with 1000 simulations

Traits	**Phylogenetic signal**		**Best Model**	**AICc**	**AIcc weight**	$\boldsymbol{\theta_1}$ **(grassland/ savanna)**	$\boldsymbol{\theta_2}$ **(wetland)**	$\boldsymbol{\alpha_1}$ **(grassland/ savanna)**	$\boldsymbol{\alpha_2}$ **(wetland)**	$\boldsymbol{\sigma_1^2}$ **(grassland/ savanna)**	$\boldsymbol{\sigma_2^2}$ **(wetland)**
	K	$\boldsymbol{\lambda}$									
Maximum plant height	0.18*	0	BM	22.94	< 0.01	-	-	-	-	0.061	0.061
			BMS	13.46	<0.01	-	-	0.975	0.975	0.204	0.204
			OU	19.99	<0.01	0.325	2.219	-	-	0.029	0.155
			OUM	8.72	0.02	0.072	2.111	11.967	11.967	1.443	1.443
			OUMA	**1.55**	**0.96**	0.102	2.094	0.754	0.861	0.105	0.105
			OUMV	10.25	0.01	0.081	2.112	9.244	9.244	1.318	0.399
Maximum leaf length	0.10*	0	BM	20.30	<0.01	-	-	-	-	0.070	0.070
			BMS	10.14	0.02	-	-	0.815	0.815	0.192	0.192
			OU	14.92	<0.01	0.333	1.634	-	-	0.030	0.164
			OUM	6.95	0.12	0.079	1.536	7.277	7.277	1.069	1.069
			OUMA	**3.17**	**0.79**	0.121	1.517	0.673	0.727	0.097	0.097
			OUMV	8.38	0.06	0.093	1.536	3.538	3.538	0.569	0.410
Leaf area	0.14*	0	BM	28.95	<0.01	-	-	-	-	0.263	0.263
			BMS	14.58	<0.01	-	-	1.578	1.578	1.059	1.059
			OU	26.56	<0.01	0.683	1.591	-	-	0.142	0.634
			OUM	**5.10**	**0.50**	0.103	1.344	27.121	27.121	9.634	9.634
			OUMA	9.02	0.07	0.153	1.353	1.332	1.320	0.534	0.534
			OUMV	5.46	0.42	0.112	1.353	21.510	21.510	9.157	2.145
Leaf width to length ratio	0.10*	0	BM	46.50	<0.01	-	-	-	-	0.135	0.135
			BMS	16.81	<0.01	-	-	20.222	20.222	3.491	3.491
			OU	32.18	<0.01	-1.670	0.405	-	-	0.034	0.397
			OUM	18.42	<0.01	0.159	-1.73	10.080	10.080	1.690	1.690
			OUMA	**3.13**	**0.99**	0.158	-1.70	1.186	1.306	0.154	0.154
			OUMV	16.75	<0.01	0.065	-1.70	5.794	5.794	0.992	1.250
Awn length	0.06*	0	BM	33.54	<0.01	-	-	-	-	0.139	0.139
			BMS	8.38	0.28	-	-	38.006	38.006	7.868	7.686
			OU	23.38	<0.01	0.914	0.425	-	-	0.039	0.361
			OUM	10.99	0.08	0.720	0.074	16.709	16.709	5.695	5.695
			OUMA	**6.80**	**0.62**	0.760	0.133	0.841	0.892	0.171	0.171
			OUMV	13.71	0,02	0.727	0.089	6.802	6.802	1.426	1.557

Parameter estimations (θ, α, and σ) from the best evolutionary model determined by the lowest value of Akaike's Information Criterion with a correction for a small design (AICc) and AICc weight value among six candidate models (BM, BMS, OU, OUM, OUMA, and OUMV). The best models are marked by bold letters; asterisks above the values of phylogenetic signal indicate that they are significantly different from zero. AICc, Akaike's Information Criterion with a correction.

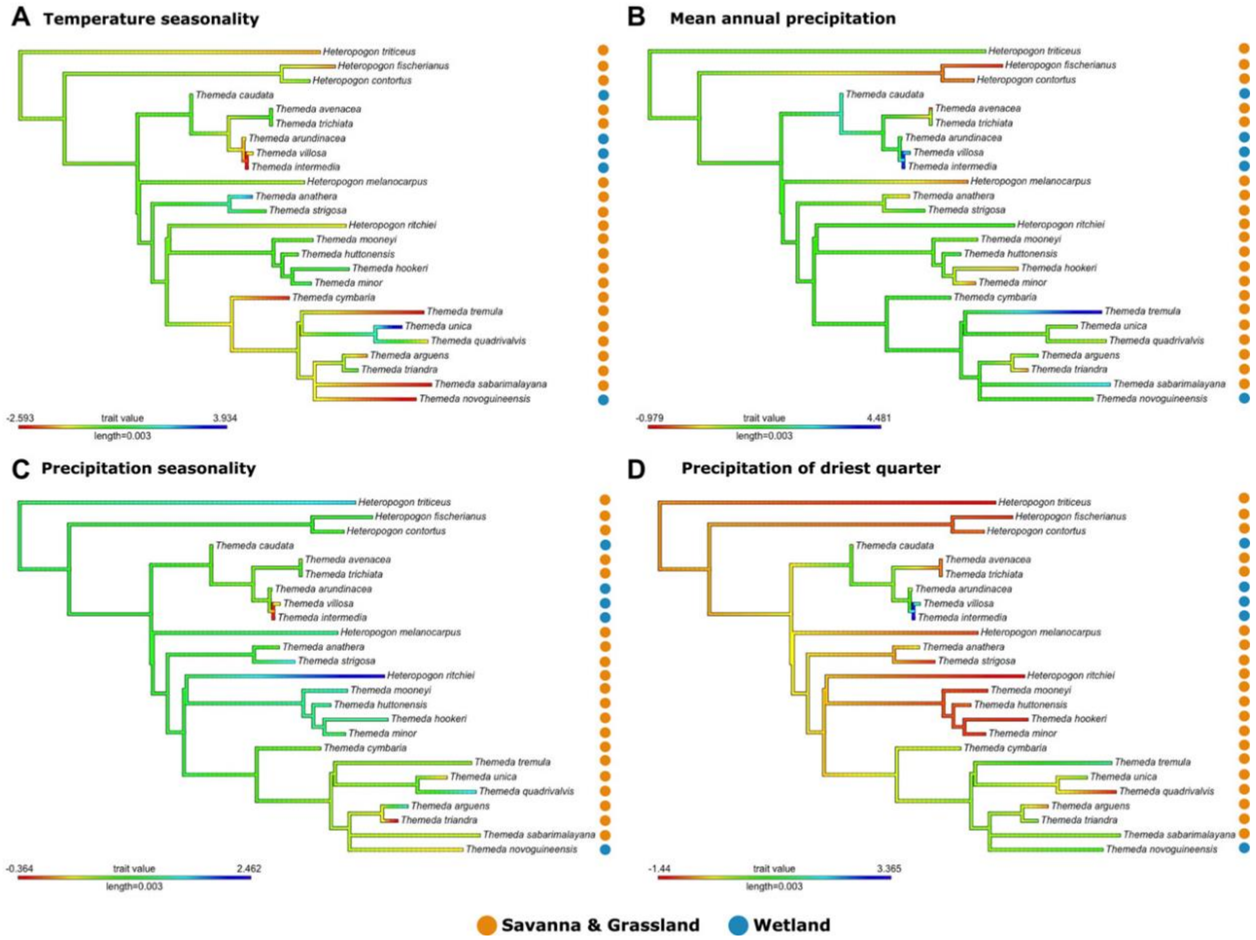

Figure 4.4. Phylogenetic visualization of ancestral state reconstructions of four bioclimatic niche evolution, temperature seasonality (**A**), mean annual precipitation (**B**), precipitation seasonality (**C**), and precipitation of the driest quarter (**D**).

Plant height, leaf length, leaf width, leaf area, and awn length showed low phylogenetic signals (0.06–0.18; Table 4.6). The analyses suggested OUMA best-fit models are selected for culm height, leaf length, leaf area, leaf width to length ratio, and awn length. The OUMA model suggested that the wetland functional traits diverged toward significantly higher trait values than the grassland/savanna ones as indicated by higher θ values. Nonzero α values indicated that selective pressure was put on trait adaptation in the grassland/savanna and wetland groups (Fig. 4.5A; Table 4.6).

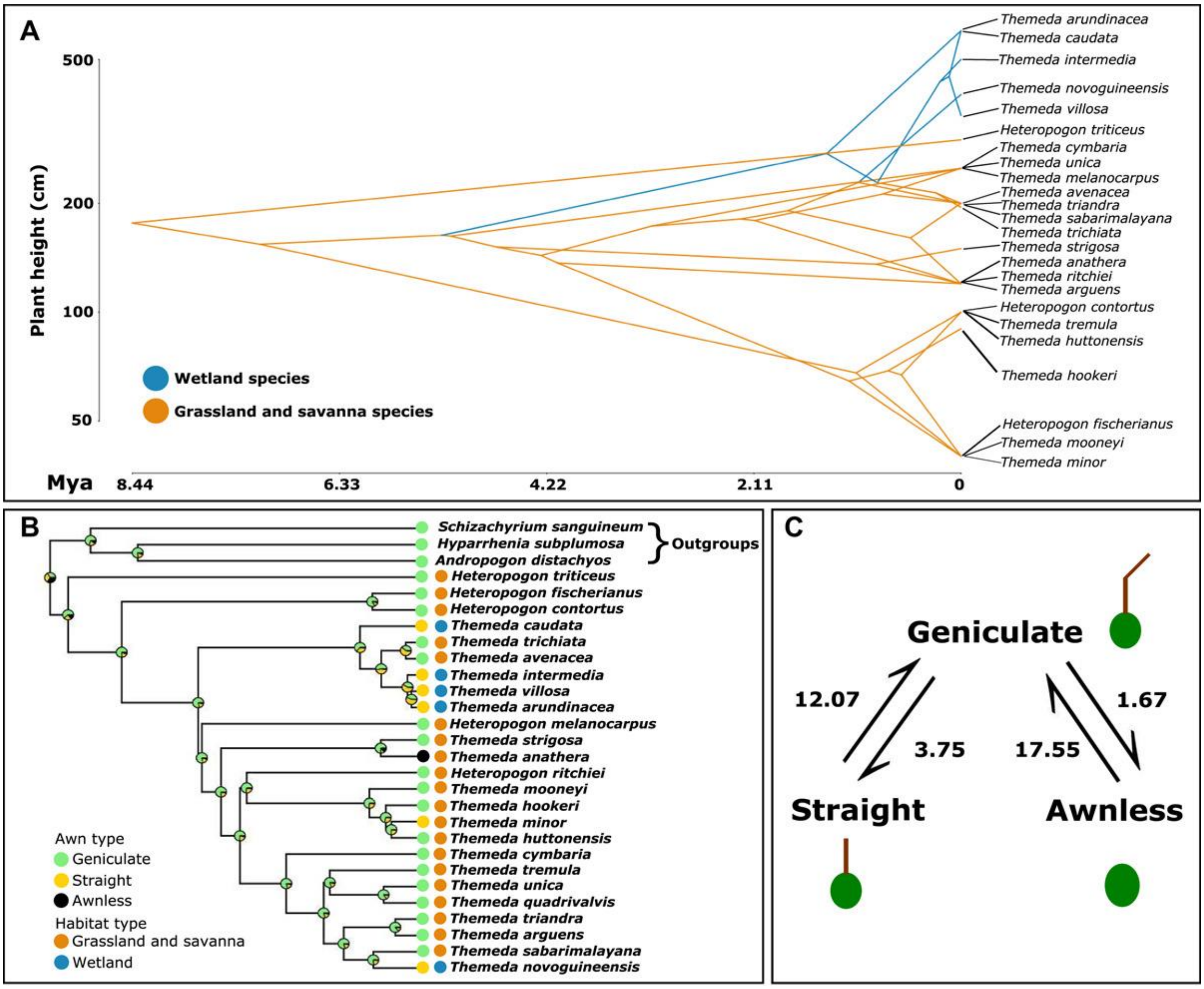

Figure 4.5. Phylogenetic comparative analysis of two morphological traits, maximum plant height (**A**) evolved through the Ornstein–Uhlenbeck (OU) model towards different trait optima, ancestral state reconstruction of awn type (**B**), and transition diagram between states (**C**).

The most likely ancestral state of the *Heteropogon-Themeda* clade was the geniculate awn with a probability of 0.62 (Fig. 4.5B; Table 4.7). Character mapping made it clear that straight awns are mostly present in wetland species, while the awns of the grassland/savanna species were mostly geniculate (Fig. 4.5B). The best model of awn evolution showed unequal and reversible states between geniculate and straight types, and between geniculate and awnless ones, but not between straight and awnless (Fig. 4.5C; Appendix XIII). Transition rates between states were obtained from median values and presented in the state transition diagram (Fig. 4.5C). The rates of changes from the derived states back to the geniculate state were much higher than those of changes from geniculate towards the derived states, 3.75 versus 12.07 (geniculate ⇌ straight) and 1.67 versus 17.55 (geniculate ⇌ awnless) (Fig. 4.5C; Table 4.7). Furthermore, transitions from geniculate to straight were faster than the transition to awnless (3.75 vs. 1.67; Fig. 4.5C; Table 4.7). The reversible rates between straight and awnless states were equal to zero.

Table 4.7. Awn-type evolution analysis showing transition rates with a 95% confidence interval (CI) and mean between three states (geniculate [0], straight [1], and awnless [2]), probabilities at the ancestral node of the *Heteropogon-Themeda* clade, and the total time spent in each state

	Geniculate [95% CI (mean)]	**Straight [95% CI (mean)]**	**Awnless [95% CI (mean)]**	**Probability at the ancestral node**	**Mean total time spent in each state**
Geniculate	-	3.72–3.77 (3.75)	1.66–1.68 (1.67)	0.62	0.79
Straight	12.01–12.13 (12.07)	-	0 (0)	0.23	0.17
Awnless	17.47–17.63 (17.55)	0 (0)	-	0.15	0.04

Note that there are 48.63 changes between states on average.

4.4 DISCUSSION

We present evidence for repeated biome shifts between savannas and wetlands related to functional traits that have adaptive significance. Within the *Heteropogon-Themeda* clade, climatic niche shifts between grasslands/savannas and wetlands are labile evolutionary processes that have occurred multiple times in a relatively short period (~10 million years). The evolutionary lability that we observe might be related to three different processes. First, grassland/savanna-wetland mosaics represent habitat proximity and facilitate species movements from grasslands/savannas to wetlands and vice versa (Donoghue & Edwards, 2014). Second, wetlands could have left some functional niche roles vacant due to being a relatively low biodiversity habitat (Hector, 2011; Deane et al., 2016). Wetlands could also have imposed functional constraints, as reflected in the small number of grass lineages found within them (Du et al., 2016) and costly specialized functional adaptations to flooding stress (Moor et al., 2017; VanWallendael et al., 2019). Lastly, natural grass invasiveness (e.g., tall stature) permits grasses to compete and replace other species (Linder et al., 2018; Canavan et al., 2019).

Although biome shifts were documented to drive evolution to form distinct habitat groups of the *Heteropogon-Themeda* clade, discordance between habitat occupancy and distribution patterns leaves some questions unanswered. Currently, wetland species are confined to Southeast Asia and parts of India (POWO, 2019), and a high proportion of tropical wetlands exist in Southeast Asia (Greb et al., 2006; Finlayson et al., 2018; Toochi et al., 2019). Within the *Heteropogon-Themeda* lineage, the observation of fewer species in wetlands than in grasslands/savannas (7 vs. 24 species) may reflect the limitations of the wetland species in dispersal and/or establishment. The dispersal limitations could be due to (1) habitat unavailability, (2) insufficient time to diversify, and (3) failure to diversify (Sexton et al., 2017; Sheath et al., 2020). Habitat unavailability is an unlikely cause since savanna-wetland mosaics are prevalent (Bertassello et al., 2021), but African wetlands have not been colonized by *Heteropogon-Themeda* wetland species despite some wetland species sharing bioclimatic preferences with other species (e.g., *Themeda arundinacea*; Table 4.5). The patchy nature of wetlands across the tropics could also slow the rate of dispersal. Insufficient time might not be the case as the speciation events of the clade occurred in a relatively short timescale. Failure to diversify is likely, but largely understudied. One possibility is that the wetland species might not possess enough diverse subpopulations to migrate and adapt to new local conditions (Sexton et al., 2017).

Within the *Heteropogon-Themeda* clade, we documented clearly distinct trait syndromes related to growth and dispersal between the grassland/savanna and wetland species. Greater culm height, leaf length, and leaf area in the wetland species indicated that they use different growth strategies from the grassland/savanna species. The tall stature of wetland species could simply be a result of higher water availability that promotes plant growth (Moles et al., 2009), and facilitates light capture in a competitive environment (Craine & Dybzinski, 2013). In contrast, the overall shorter stature of savanna species is likely related to water availability and seasonal dryness (Fig. 4.1; Colmer & Voesenak, 2009; Olson et al., 2018), although within savannas, positive relationships between plant height and flammability have also been observed (Simpson et al., 2016), just as positive correlations have also been found between plant height and range size in the Andropogoneae (Mashau et al., 2021). Within the wetland species, greater leaf area is thought to have parallel adaptation with plant height to accommodate plant production, where the smaller leaves of grassland/savanna species could help mitigate drought effects by reducing transpiration (Farooq et al., 2012). Under inundating conditions, wetland species should benefit from non-hygroscopic straight awns through vertical diaspore burial rather than the twisting activities produced by geniculate awns (Peart, 1981). Alternatively, there could be a reduction in awn function that results in a dispersal mode relying on hydrochory (Nilsson et al., 2010). Active twisting functions in hygroscopic awns of the grassland/savanna species should bury diaspores well in humid accessible soil or cracking surface, enabling avoidance of fire (Peart, 1979, 1981). Peart & Clifford (1987) showed that moisture and soil types show the composite effects in awn functions. However, the exact selective pressures between these two awn types and their associations with dispersal and burial efficiency remain unknown. Apart from the moisture, Garnier & Dajoz (2001) found that fire characteristics positively correlate with awn length, where significantly different awn lengths in the grassland/savanna and wetland species could indicate the different fire regimes in these systems. Fine-grained fire, community composition, and awn length data would be required to test the effect of fire on dispersal traits.

Trait adaptability aligns well with the concept of pre-existing traits, or preadaptation facilitating biome shifts (Donoghue & Edwards, 2014). Tall stature is a conserved trait of the Andropogoneae (including the *Heteropogon-Themeda* clade) that has increased since the emergence of the ancestor of Andropogoneae (Liu et al., 2012). The ancestor of the *Heteropogon-Themeda* clade had a relatively high stature of approximately two meters, taller than most other C_4 grasses (Fig. 4.5A). The grassland/savanna and wetland species evolved towards different optimal heights to survive in different environmental conditions and competitive environments. Selection acting on leaf length and area by precipitation was estimated in this study (different values; Table 4.6) and supported by Gallaher et al. (2019). Evolution towards higher trait optima in wetlands is more constrained (higher α values) than in grassland/savanna environments. Taller height and greater size-related leaf traits among the wetland species imply adaptive phenotypes as they invest and maintain growth in the presence of inter- and intraspecific competition under high availability of water (van Kleunen & Fischer, 2005). In contrast, reductions in plant height or leaf length in savanna species are considered passive adaptations as the plant does not allocate sufficient resource to growth in the limited resource (Falster & Westoby, 2003). In addition, awn characteristics are not conserved within the lineage as they commonly vary within grass lineages (Humphreys et al., 2010; Teisher et al., 2017). The lability may be linked to genetic control of awn development based on multiple genes regulating the expression of multiple characteristics (e.g., length, type, awn presence; Ntakirutimana & Xie, 2019; Huang et al., 2021).

Bioclimatic factors, habitats, and functional traits partially explained broad-level distributions at the species level. Overall climatic variables of *Heteropogon contortus* and *Themeda triandra* have significantly different climatic niches (Fig. 4.2; Table 4.4). Wider windows of temperature and PS of *H. contortus* (Figs. 4.2A, 4.2C) could explain success in the ecological establishment of *H. contortus* on islands (Tothill & Hacker, 1976; Oviedo Prieto et al., 2012). In general, wide gradient and fluctuation of seasonality and aridity are observed within a single island and between islands, which leads to vulnerability to climate change (Veron et al., 2019). However, *H. contortus* can grow along a precipitation gradient of Hawaii and drought-tolerant populations remain after the invasion of alien species, showing high adaptability to precipitation of this species (Goergen & Daehler, 2001). *H. contortus* usually colonizes dry habitats and exposed rock outcrops where *T. triandra* is absent (Wang et al., 2016; Xavier & D'Antonio, 2017, pers. obs.). This contrast aligns well with a low range of precipitation of the driest quarter that most *H. contortus* can tolerate (Fig. 4.2D). Shorter plant height, leaf length, and smaller leaf ratio of *H. contortus* hinted at drought avoidance in arid conditions and tolerate intense solar radiance in low shade (Wang et al., 2016). In contrast, Snyman et al. (2013) suggested that *T. triandra* grows in the areas where annual rainfall reaches higher than 750 mm, and this results in taller stature and greater leaf size of *T. triandra* than those of *H. contortus,* as also found in this study (Fig. 4.2F). *Themeda triandra* fails to persist through the long dry season as water shortage leads to loss of leaves more quickly than *H. contortus* under equivalent conditions (Mott et al., 1992).

At a continental scale, precipitation and seasonality regimes cannot explain the geographic separation between *H. contortus* and *T. triandra*. The climatic similarity between African *T. triandra* and South American *H. contortus* showed that climatic conditions might not limit the spread of *T. triandra* to South America (Fig. 4.3; Appendix X), where *T. triandra* may be the most likely to colonize. Alternatively, biotic interactions may regulate population dynamics at a local scale (Wisz et al., 2013). Use of climatic variables to explain smaller-scale distribution patterns at the species level could pose some technical limitations (Jardine et al., 2020). Alternatively, underlying factors controlling these unequal distributions of *H. contortus* and *T. triandra* (e.g., fire, edaphic properties, competition) and environment–trait correlations have not been revealed in this study. Fine-grained plot data from local community assemblages are required to address these questions.

The grassland/savanna species provide an example of a common phenomenon that widespread pantropical species, *H. contortus* and *T. triandra*, encompass bioclimatic envelopes of their relatives with more narrow ranges (Table 4.5). For example, *H. contortus* and *T. triandra* co-exist with *Themeda anathera* in subtropical montane savanna in the absence of other relatives. An underlying cause may be that *H. contortus* and *T. triandra* consist of ecologically distinct populations, where some populations can tolerate environmental stress at a time through local adaptations (e.g., multiple ploidy levels; Tothill & Hacker, 1976; Ahrens et al., 2020; or phenotypic/genotypic plasticity; Dell'Acqua et al., 2014). In addition, species with more narrow ranges or restricted distribution hinted at *H. triticeus* and *Themeda arguens* being Southeast Asian natives, and Asian savannas are known to have unique climatic control (Ratnam et al., 2016). Likewise, completely dissimilar climatic preferences of *Heteropogon ritchiei* and *T. tremula* (Indian peninsula endemics) also reflect habitat diversity across savannas.

4.5 CONCLUSION

The *Heteropogon-Themeda* clade shows clear climatic niche shifts between grasslands/savannas and wetlands, and adaptive traits associated with these habitats. In our bioclimatic analyses, precipitation is the main correlate separating habitat types and where between habitats, there are systematic differences in plant height, leaf length, leaf area, leaf width to length ratio, awn length, and awn types in grassland/savanna and wetland species. The clear delimitation of habitat subgroups indicates that C_4 grassy biomes are diverse in their environments and functional traits. Phylogenetic investigations suggest that the *Heteropogon-Themeda* clade originated in savanna environments, with adaptive traits of the grassland/savanna and wetland species diverging into wetland-associated climatic niches under distinct selective pressures. Biogeographic and functional ecology research in other grass clades with expanded environment, trait, and molecular data will provide broader insight into the assembly of tropical grassy ecosystems.

Both *Themeda* and *Heteropogon* species can be keystone species in the environments in which they are found (Snyman et al., 2013). As impacts of climate change and human activities increase, it is worth paying attention to wetlands and their endemic and overlooked grass species that occupy specific and climatically sensitive habitats. Likewise, for savannas, degradation processes impact taxonomic and functional diversity.

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CHAPTER 5

INTEGRATIVE TAXONOMIC REVISION OF *HETEROPOGON* AND *THEMEDA* (POACEAE) INFORMED BY EVOLUTION, CLIMATIC NICHE HISTORY, AND MORPHOLOGY

5.1 INTRODUCTION

Incongruence and instability in both generic and species delimitations has been an issue debated by diversity scientists for centuries, reflecting the complexity of organisms and their evolutionary histories, inconsistent use of biological data, and inconsistent criteria used to define taxa (Wells et al., 2022). Traditionally, defining genera relied on morphological similarity by either comparing plants of interest with a generic type or considering whether those plants are more similar to each other than the ones outside the group (Robinson, 1906). More recently, the concept of monophyly, where all species in the genus are descended from common ancestor, has gained widespread acceptance (Schrire & Lewis, 1996; West, 1987). Below the level of genus, species concepts are used as a central paradigm to unify criteria for species delimitation (Zachos, 2016). Species-level classifications are somewhat less constant than their generic-level counterparts since reticulate evolutionary mechanisms such as hybridization seem to be more common at the species level and below (Fišer et al., 2018, De Queiroz, 2007). In order to set species boundaries, recent workers aim to integrate evolutionary, ecological, and phenetic concepts using phylogenetic divergence, climatic, and morphological properties (De Queiroz, 2005). Applying multidisciplinary methodology as systematic standard bring the benefits of data accessibility, more objective interpretations, statistically explicit species differentiation, and are becoming more common (Wells et al., 2022).

Andropogoneae, one of the most diverse tribes in Poaceae, contain more than 1,200 species (Kellogg, 2015), and the tribe exemplifies the evolving nature of genus- and species-level classifications in Poaceae (Gallaher et al., 2022; Welker et al., 2020). Most genera of Andropogoneae have been confirmed with concordant evidence from synapomorphies and phylogenetic relationships (Arthan et al., 2016; Arthan et al., 2017; Welker et al., 2020). For example, *Eremochloa* and *Glyphochloa* are treated as two different genera as they form separate clades (Gosavi et al., 2015; Welker et al., 2020) and all species members shared glume characteristics, presence of margin appendages on glumes and reduced pedicelled spikelets in *Eremochloa* (Buitenhuis & Veldkamp, 2001) and highly aristate and ornamented glumes in *Glyphochloa* (Clayton & Renvoize, 1986). Within these genera, species delimitation is clearly defined due to stable morphological differences with distinct arrangement patterns of margin barbs on the glumes and level of pedicelled spikelet reduction. However, taxonomic problems emerges when some genera have no clear-cut shared morphology based on traditional classifications. Plus, the concept of monophyly in the modern-day sense does not even apply to those genera. According to McAllister et al. (2019), a plastome phylogeny indicated that the generic limits of *Andropogon* L. and *Schizachyrium* Nees are polyphyletic (based on phylogenetic position of generic type), and no shared characters have been specified for species within the clade. Such circumstances could lead to shifts in generic concepts (e.g., resurrection of former taxonomic ranks) and reclassification of species under a new genus-level delimitation. Likewise, some cases of species delimitation within Andropogoneae are more complex and less stable due to complex evolutionary history (e.g., polyploidization and introgression), cryptic morphology, and indistinguishable ecotypes (Hodkinson, 2018). Morphology is sometimes not useful to tell species apart (Mayo, 2022). Combining the application of phylogenetic relationships help sets morphological boundaries in species delimitation (e.g., *Eriochrysis*; Welker et al., 2012).

Dominant savanna genera *Heteropogon* Pers. and *Themeda* Forssk., recent subjects of evolutionary and ecological studies (Arthan et al., 2022; Dunning et al., 2017, 2022; Snyman, 2013, Wang et al., 2016) are Andropogoneae genera whose generic and species delimitation are in flux. Forsskåhl (1775) proposed the genus name *Themeda* with a single species *Themeda triandra,* while *Heteropogon* was first coined as a genus by Persoon (1807) with *H. glaber* as the type species. The morphological descriptions of the two original taxa were used as criteria for generic characteristics. *Themeda* was described as having racemes subtended by a spatheole, four involucral homogamous spikelets, no spikelet pairs, and a terminal triad (Veldkamp, 2016). The morphological characteristics of *Heteropogon* are a solitary raceme, several homogamous spikelets, several spikelet pairs, and a terminal triad (Deshpande, 1988). The arrangement of involucral homogamous spikelets, awn type, glume indumentum, inflorescence architecture, the number of spikelet pairs, and quantitative characters (e.g., length and width) were applied in species delimitation in both genera (Clayton & Renvoize, 1986; Deshpande, 1988; Veldkamp, 2016). For instance, *Themeda arguens* and *Themeda triandra* are distinguished by reduced homogamous spikelets in the former species and this morphological difference is constant within populations of each species. With the accumulation of DNA data, a phylogenetic species concept help disentangle species problems and guide morphological redefinition. Morphologically similar species of *Themeda* were nested in the *Themeda triandra* clade and then treated as synonyms of *Themeda triandra* (Arthan et al., 2021, Dunning et al., 2022). In this case, morphological criteria are expanded to cover a wider range of quantitative characters. A phylogenetic framework also yielded new information that prompted taxonomic changes. Recently, Arthan et al. (2021) showed that *Heteropogon* is polyphyletic with *H. melanocarpus* and *H. ritchiei* intermixed in the *Themeda* clade. Some phylogenetic positions were newly informed, for example, a clade of *Themeda avenacea* and *Themeda caudata,* the species limits of which should be revised. Arthan et al. (2022) investigated the associations between evolutionary and climatic niche histories, which could be relevant to the definition of species limits.

The classification of *Heteropogon* and *Themeda* is in need of an update informed by new knowledge. This study aims to 1) provide integrated evidence from ecological, morphological, phylogenetic data for new generic and species limits of *Heteropogon* and *Themeda* and 2) update the systematics of *Heteropogon* and *Themeda*.

5.2 MATERIALS AND METHODS

5.2.1 Species Delimitation

A. Morphological Examination

Specimens of *Heteropogon* and *Themeda* were provided by Herbarium of the Arnold Arboretum, Harvard University (A), the Natural History Museum, London (BM), Royal Botanic Gardens, Edinburgh (E), Royal Botanic Gardens, Kew (K), Naturalis Biodiversity Center, Leiden (L), and Chinese National Herbarium, Institute of Botany, Chinese Academy of Sciences, Beijing (PE), and online digitized materials of the Muséum National d’Histoire Naturelle, Paris (P), Missouri Botanic Garden (MO), Smithsonian Institution (US), China Virtual Herbarium (CVH; https://www.cvh.ac.cn), and India Virtual Herbarium (IVH; https://ivh.bsi.gov.in). All herbarium acronyms are based on Thiers (2016). *Heteropogon* and *Themeda* specimens were chosen to cover their distribution ranges, based on the database of Plants of the World Online (POWO, 2022). At least 30 specimens per species, where this was available, for quantitative measurements to assess morphological variations. Morphological descriptions of *T. odishae* Chorghe, K.Prasad, Prasanna & Y. V. Rao, *T. palakkadensis* Chorghe, K. Prasad & Lakshmin, and *T. unica* S.L.Chen & T.D.Zhuang are based on the literature because herbarium material was unavailable (Chorge et al., 2016, 2019). Qualitative and quantitative morphology was examined under a Leica S9E stereoscope and measured by ruler and digital caliper 150 mm APO10929. Raceme, spikelets, caryopses, and awns were imaged using a Leica S9i dissecting microscope.

Morphological terminology follows Vegetti (1999). Grass inflorescence terms have been used variably in the literature. We use the term inflorescence for the grass reproductive structure while other literature might adopt the term ‘synflorescence’. The term ‘inflorescence’ in this study includes the main axis and their axillary branches (aka paraclades). In Andropogoneae, the paraclades form complex branching systems where each paraclade produces its own axillary branches and higher branching orders (Fig. 5.1). The term raceme refers to a group of spikelets borne on the main axis and the axillary branches; spikelets are in pairs in most genera of the Andropogoneae. In *Heteropogon* and *Themeda,* the term ‘triad’ is used for the terminal structure in the racemes of *Heteropogon* and *Themeda,* comprising one sessile spikelet and two pedicelled spikelets (Fig. 5.2).

B. Mapping Diagnostic Characters onto the Phylogeny

We use the phylogeny of Arthan et al. (2021) as a framework for character evolution. Inflorescence architecture was categorized as three states: 1) first-order branching, 2) second-order branching, and 3) third-order branching. The number of homogamous spikelets is coded as numerous (more than 8), several (5 to 8), or four. Lastly, the number of spikelet pairs was divided into three states: 1) numerous (more than 6), 2) several (four to six) and 3) less than four. Character mapping and ancestral state reconstruction were caried out using the ‘phytools’ package (Revell, 2012) in R. Three models of discrete character transitions, Equal Rate (ER), All Rates Different (ARD), and Symmetry (SYM), were tested by using Akaike information criterion with a correction for small sample sizes (AICc). The best model was used for stochastic mapping with 1,000 simulations. All 1,000 simulated trees were summarized to yield one consensus tree.

C. Multivariate Analyses of Qualitative and Quantitative Characters

We selected qualitative and quantitative characters from morphological examination. Fourteen qualitative characters and five quantitative characters were measured. At least 30 specimens per species were examined except for 17 rare species where only a few specimens were available. Scored qualitative characters and quantitative values were combined and standardized before analyses. The combined dataset was analyzed by Factor Analysis of Mixed Data (FAMD) to investigate how species are grouped by morphological data. The analysis was conducted in R using the function ‘famd’ from the package ‘FactoMineR’ and ‘factoextra’ packages (Lê et al., 2008; Kassambara & Mundt, 2020).

D. Ecological Characterization

Habitat categorization was compiled from the literature and floras. Climatic niche characteristics among species were determined by the results of niche overlap analyses and niche equivalency/similarity by Arthan et al. (2022). To briefly explain the method from Arthan et al. (2022), four bioclimatic variables, temperature seasonality (BIO1), mean annual precipitation (BIO12), precipitation seasonality (BIO15), and precipitation of driest quarter (BIO17), were used for ecological niche analyses. Schoener’s D and Warren’s I niche overlap values were calculated to evaluate the extent of climatic niche overlap between species. Niche equivalency/similarity tests were performed to predict if niche overlaps between species are significantly different and not a result from climatic differences cause by distinct geographic distribution. To support climatic separation, climatic spaces of wetland species were visualized using the results from Arthan et al. (2022). Niche analyses cannot be achieved for all species due to insufficient occurrence records, especially for rare or endemic species that have fewer than 5 records. Interpretations of habitat suitability from ecological niche modeling by Fierro (2014) were also used for species delimitation.

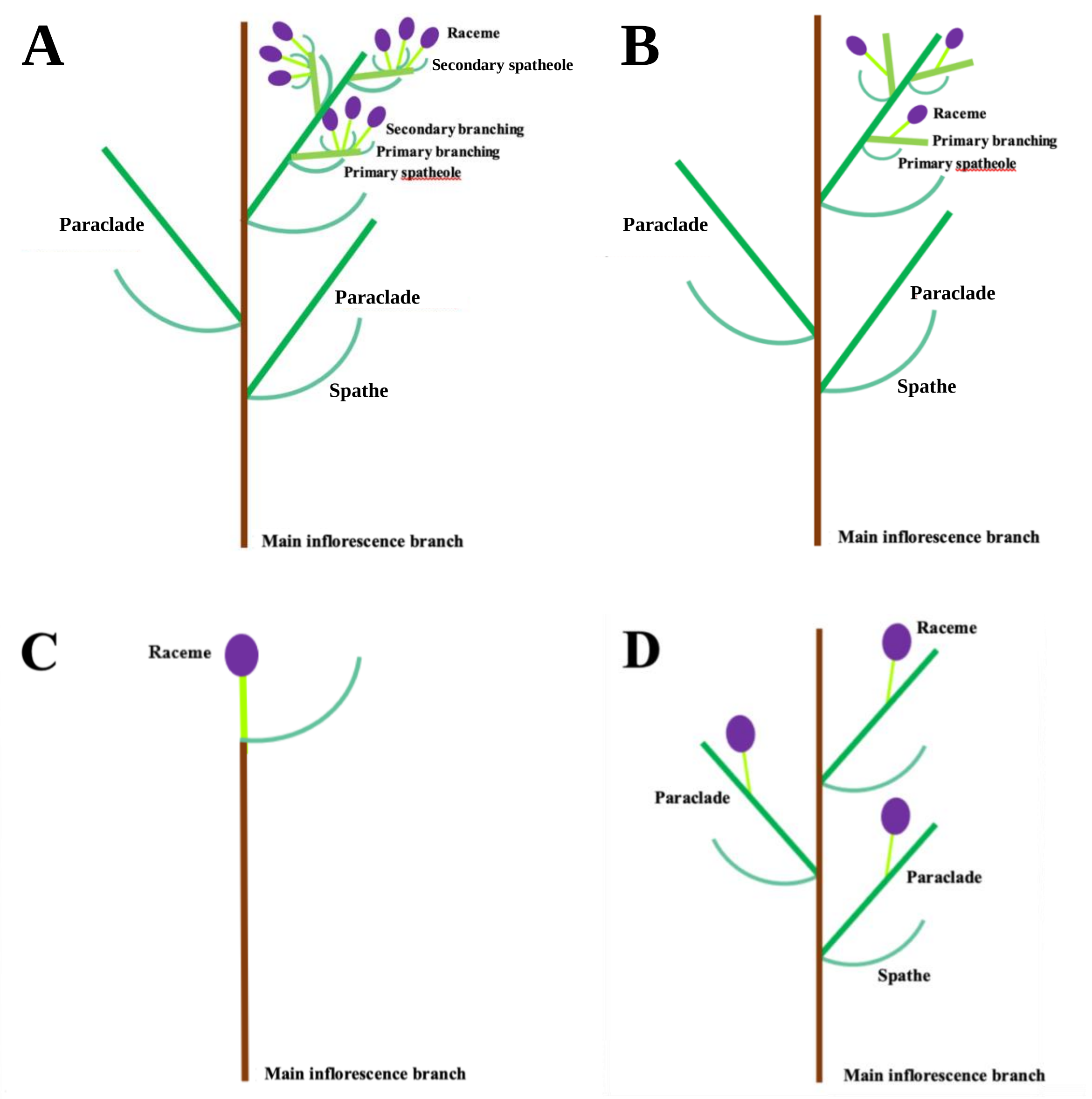
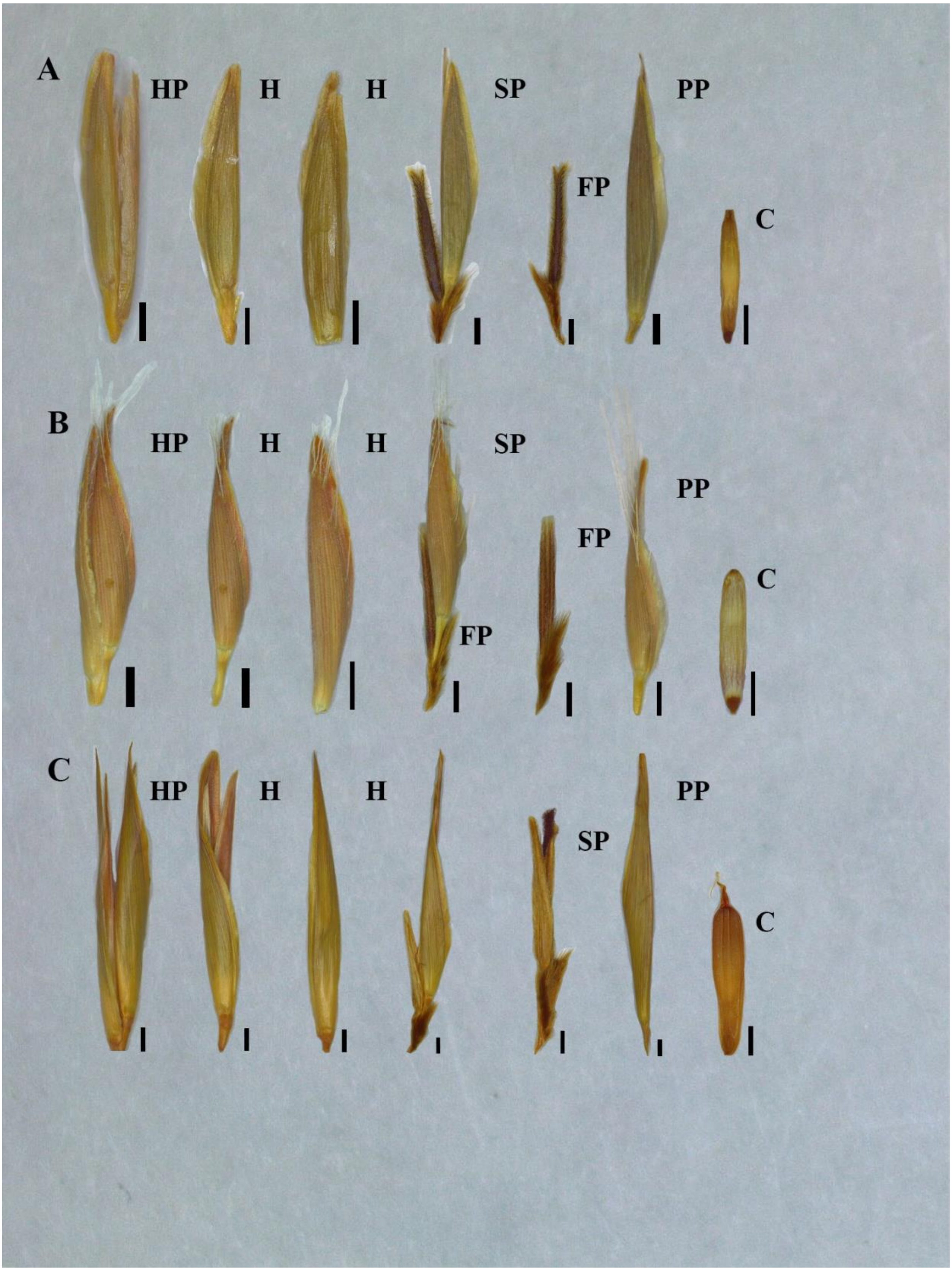


Figure 5.1. Diagram of some inflorescence and spikelet structures in the *Heteropogon*-*Themeda* group. Paniculate inflorescence with clustered spikelets (e.g., *Themeda quadrivalvis*, *Themeda triandra*, and *Themeda tremula*) **(A)** Paniculate inflorescence with a single spikelet (e.g., *Heteropogon contortus*, *Themeda arundinacea*, *Themeda caudata*, and *Themeda villosa*) **(B)** Solitary inflorescence with single spikelet (only in *Themeda saxicola*) **(C)** A inflorescence with a single raceme (e.g., *Heteropogon contortus*) **(D)**.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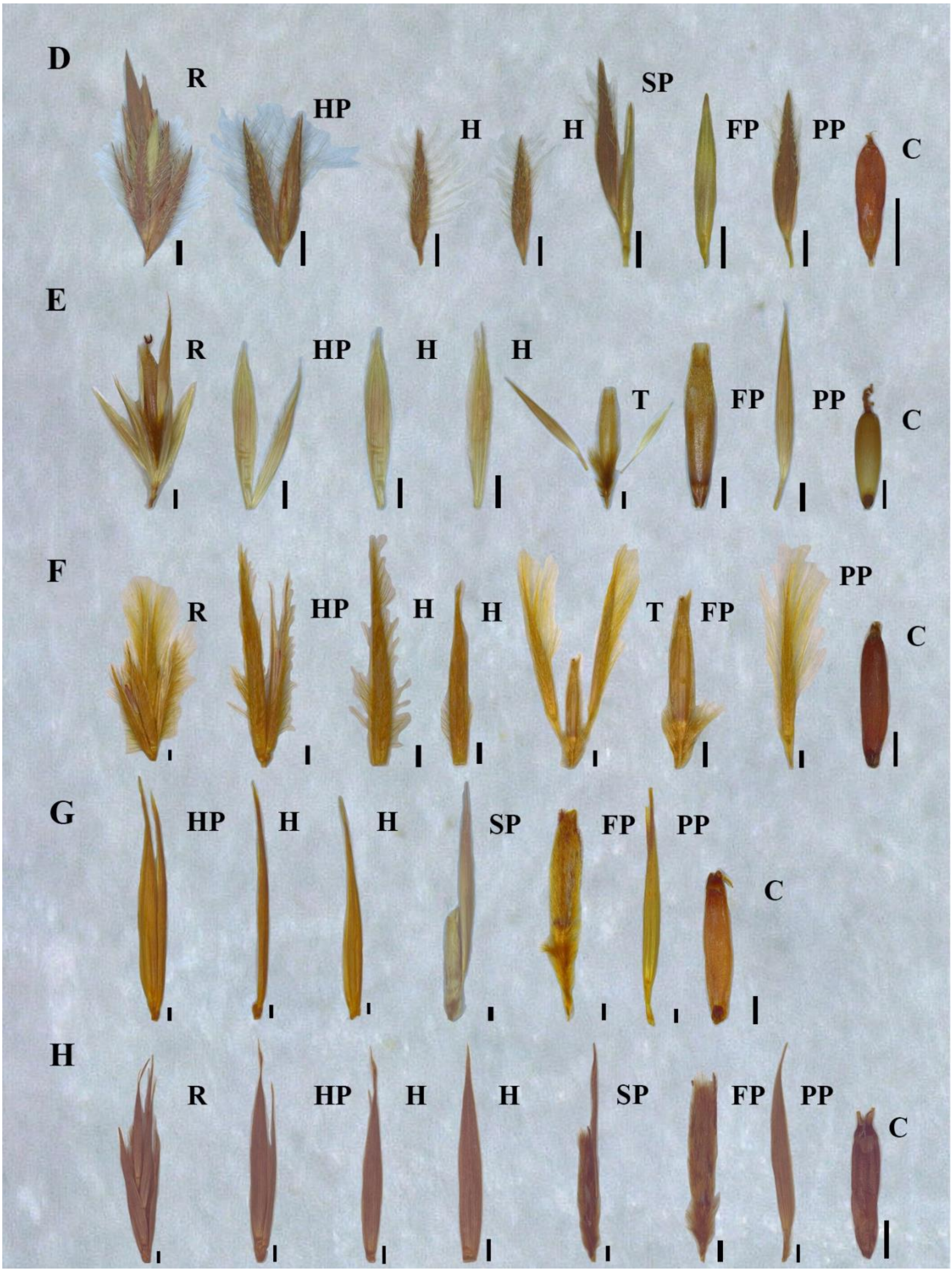
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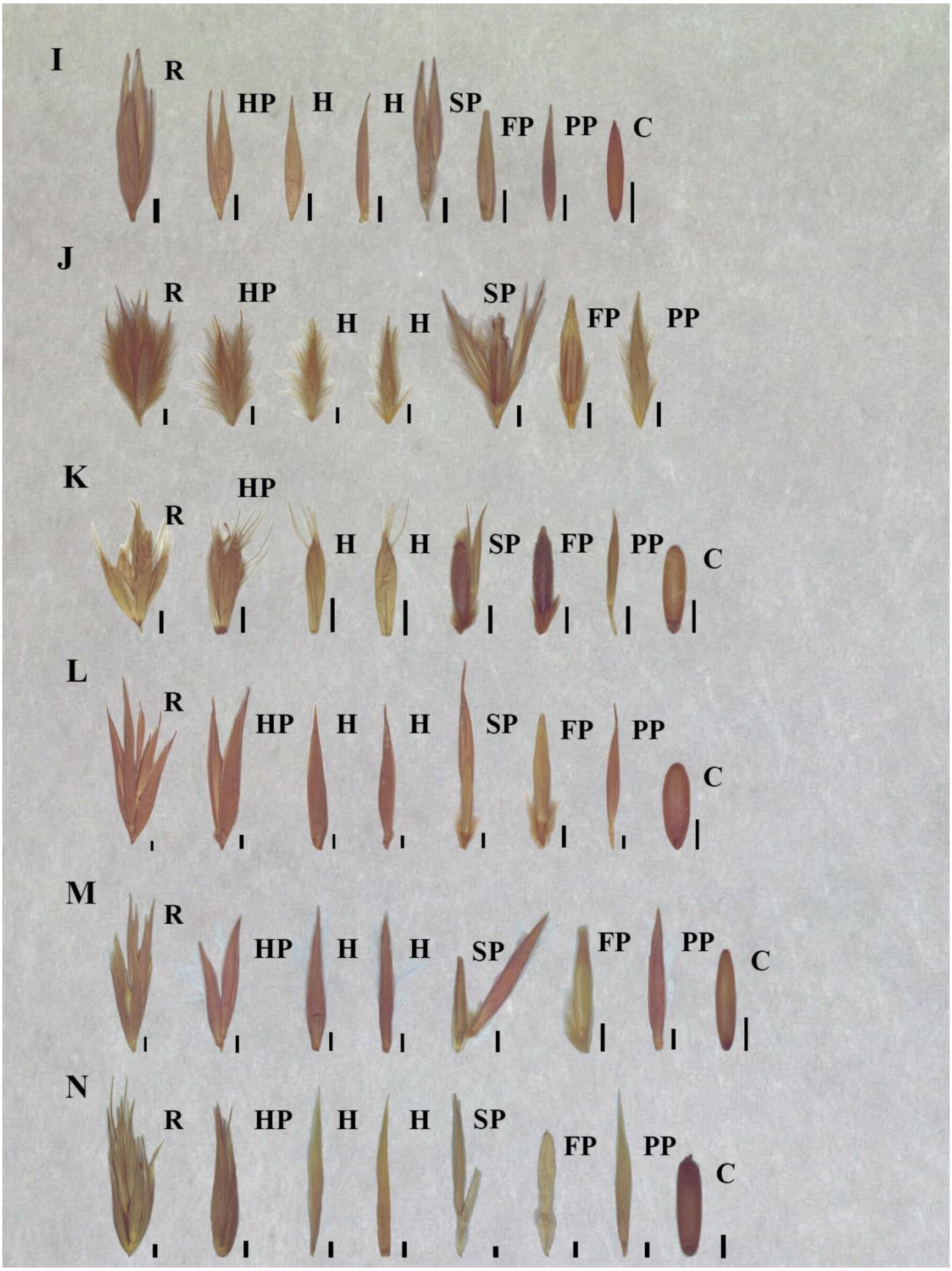
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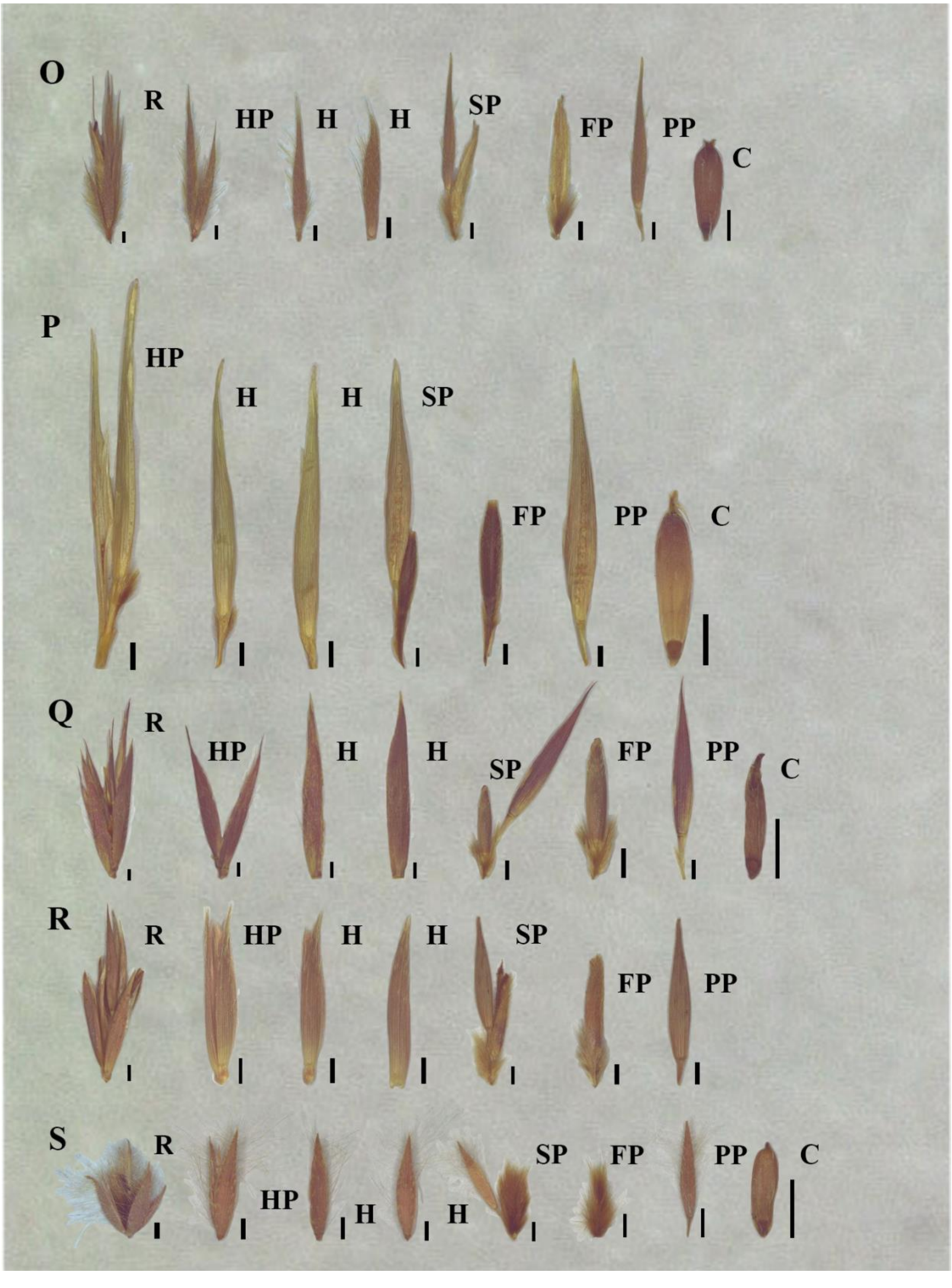
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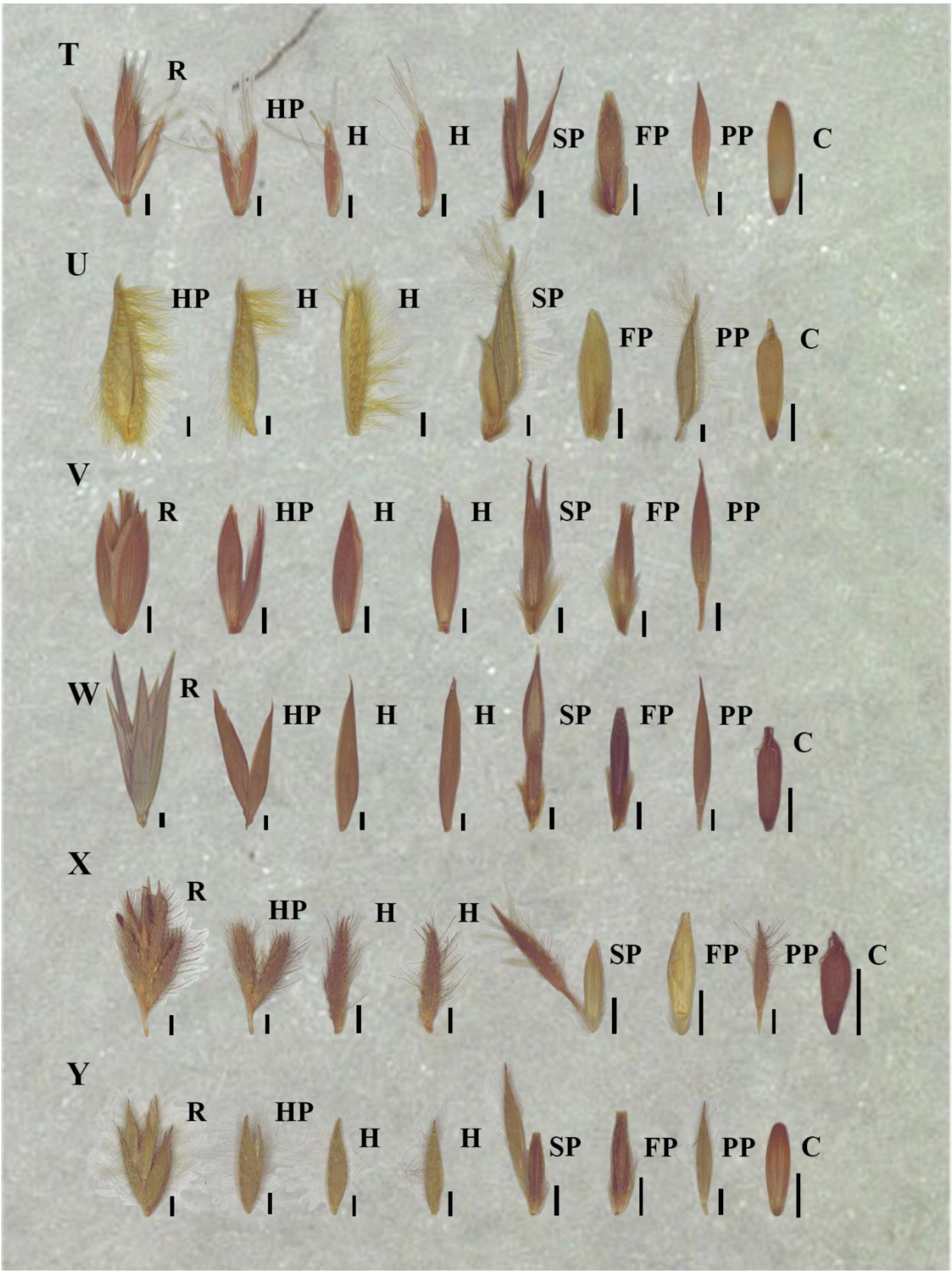
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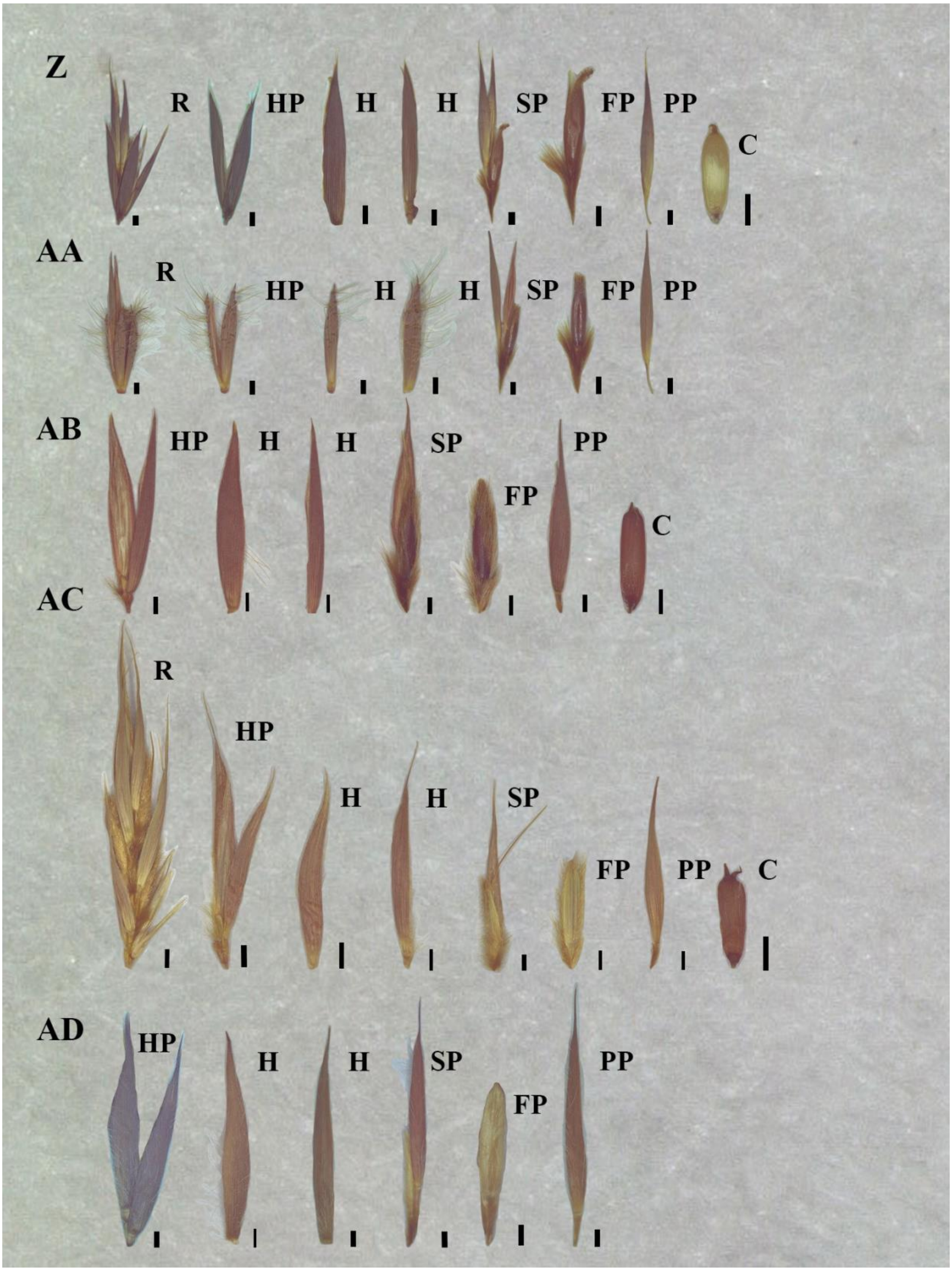

Figure 5.2. Key reproductive structures of *Heteropogon* and *Themeda* species. *Heteropogon contortus*–glabrous form **(A)**, *Heteropogon contortus*–hairy form **(B)**, *Heteropogon triticeus* **(C)**,

Themeda anathera **(D)**, *Themeda arguens* **(E)**, *Themeda arundinacea* **(F)**, *Themeda avenacea* **(G)**, *Themeda caudata* **(H)**, *Themeda cymbaria* **(I)**, *Themeda gigantea* **(J)**, *Themda helferi* **(K)**, *Themeda hookeri* **(L)**, *Themeda huttonensis* **(M)**, *Themeda idjenensis* **(N)**, *Themeda intermedia* **(O)**, *Themeda melanocarpa* **(P)**, *Themeda mooneyi* **(Q)**, *Themeda novoguineensis* **(R)**, *Themeda pseudotremula* **(S)**, *Themeda quadrivalvis* **(T)**, *Themeda ritchiei* **(U)**, *Themeda sabarimalayana* **(V)**, *Themeda saxicola* **(W)**, *Themeda strigosa* **(X)**, *Themeda tremula* **(Y)**, *Themeda triandra*–glabrous form **(Z)**, *Themeda triandra*–hairy form **(AA)**, *Themeda trichiata* **(AB)**, *Themeda villosa* **(AC)**, *Themeda yunnanensis* **(AD)**.

Scale bar measures 1 mm. Abbreviations: raceme = R; Homogamous spikelet pair = HP; homogamous spikelets = H; spikelet pair = SP; fertile spikelet = FP; pedicelled
spikelet = PP; triad = T; caryopses = C.

5.2.2 Taxonomic Treatment

A. Taxonomic Investigation

Published names of *Heteropogon* and *Themeda* species were reviewed, compiled, and checked by consulting the protologues, taxonomic literature (Anil et al., 2018; Chorge & Kulloli, 2022; Drisya & Pradeep, 2020; Karthigeyan & Murugan, 2018; Kellogg et al., 2020; Siddabathula et al., 2020; Thomas, 2019; Veldkamp, 2016) and databases (e.g., IPNI, 2012; Tropicos, 2018; The Plant List, 2010). Type specimens were examined manually and virtually from the herbaria and online databases listed above. Typifications were performed where necessary. All herbaria codes mentioned in this study are based on Index Herbariorum (Thiers, 2022). Etymological terms are based on Clifford & Bostock (2007).

B. Evaluation of Conservation Status

The Rapid Least Concern interface was used to assess IUCN threat categories of *Heteropogon* and *Themeda* species (Bachman et al., 2020). Occurrence data were compiled from herbarium specimens, Global Biodiversity Information Facility (GBIF), and Botanical Information and Ecology Network (BIEN). As overestimation of AOO and EOO values can occur (Bachman et al., 2020), these data were cleaned to avoid non-native distribution using criteria from POWO (2022), mislabeled taxa, and taxa with incorrect coordinates (e.g., in the sea). Area of Occupancy (AOO) and Extent of Occurrence (EOO) were calculated from the cleaned occurrence data. Thresholds for the least concern category were set by default as suggested by Bachman et al. (2020). Guidelines for the IUCN Red List Categories and Criteria (IUCN, 2022) were applied to evaluate threat categories. In this study, extent of occurrence and area of occupancy of criteria B were applied as only occurrence data were available to assess threatened categories. In addition, a few endemic species do not have sufficient data (N < 3) to evaluate the Red List status.

5.3 RESULTS

5.3.1 Morphological Boundaries by Multivariate Analyses

According to the Factor Analysis of Mixed Data (FAMD), the first five components accounted for 61.41% of the variation of combined qualitative and quantitative data separating the species (Table 5.1). The FAMD plot from the first two principal components (total 37.90% of the variance) clearly showed species clusters (Fig. 5.3; Table 5.2). Most putative *Themeda* species were clearly separated from all other *Heteropogon* species except for *Themeda melanocarpus* (*Heteropogon melanocarpus*) and *Themeda ritchiei* (*Heteropogon ritchiei*) which were placed near *Heteropogon* species in FAMD plot mainly due to the size of their homogamous spikelets (Fig. 5.3).

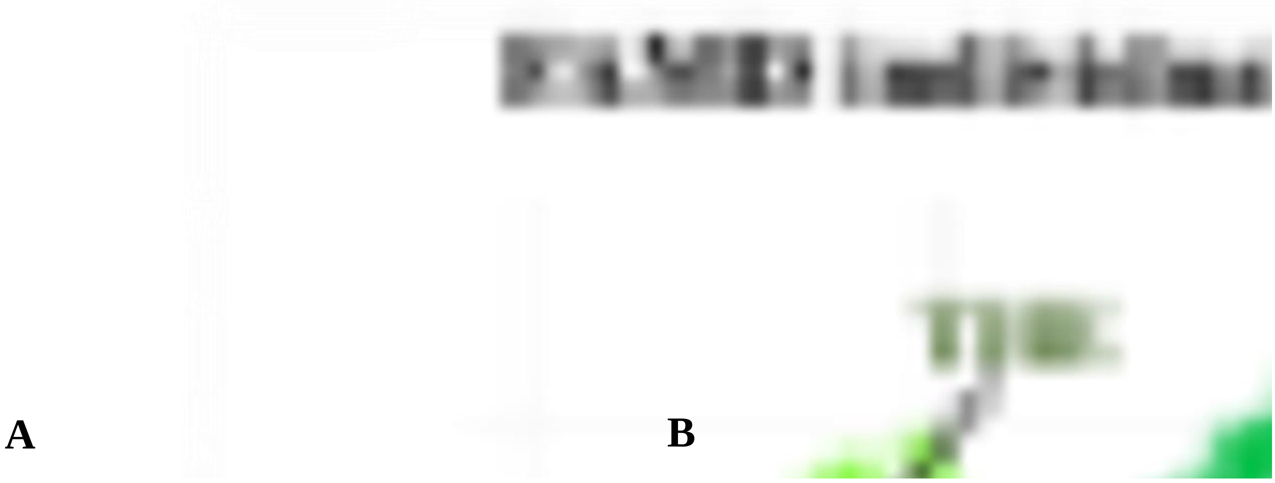

Figure 5.3 FAMD individual **(A)** and variable contribution **(B)** plots from the first two dimensions analyzed from 14 qualitative and 6 quantitative characters of 35 *Heteropogon* and *Themeda* species.

Abbreviations*:* HC = *Heteropogon contortus,* HP = *Heteropogon polystachyos,* HT = *Heteropogon triticeus,* TAN = *Themeda anathera,* TA = *Themeda arguens,* TAR = *Themeda arundinacea,* TAV = *Themeda avenancea,* TC = *Themeda caudata,* TCYM = *Themeda cymbaria,* TG = *Themeda gigantea,* THE = *Themeda helferi,* THO = *Themeda hookeri,* THU = *Themeda huttonensis,* TID = *Themeda idjenensis,* TIN = *Themeda intermedia,* TM = *Themeda melanocarpa,* TMI = *Themeda minor,* TMO = *Themeda mooneyi,* TNO = *Themeda novoguineensis,* TOD = *Themeda odishae,* TPA = *Themeda* *palakkadensis,* TPS = *Themeda pseudotremula,* TQ = *Themeda quadrivalvis,* TR = *Themeda ritchiei,* TSAB = *Themeda sabarimalayana,* TSAX = *Themeda saxicola,* TSTR = *Themeda strigosa,* TTR = *Themeda tremula,* TTRI = *Themeda triandra,* TCH = *Themeda trichiata,* TU = *Themeda unica,* TVI = *Themeda villosa, and* TYUN =*Themeda yunnannensis.*

Table 5.1. Results from Factor Analysis of Mixed Data (FAMD) using 14 qualitative and 6 quantitative characters of 35 *Heteropogon* and *Themeda* species.

Component	**Eigenvalue**	**Percentage of variance**	**Cumulative percentage of variance**
Component 1	7.09	23.63	23.63
Component 2	4.29	14.29	37.92
Component 3	2.80	9.33	47.25
Component 4	2.27	7.55	54.80
Component 5	1.98	6.61	61.41

Among quantitative variables, awn length separates *Heteropogon* and *Themeda* species from each other, except for *Themeda avenacea* (F.Muell.) Lugger (Fig. 5.3). Species are clustered by branching orders; a group of three branching orders (e.g., *Themeda triandra* and *Themeda tremula* (Nees ex Steud.) Hack.) is distinct from a group of one branching order (e.g., *Heteropogon contortus* and *Heteropogon triticeus* (R.Br.) Stapf ex Craib) in different quadrants. For qualitative characters, awn hair types and raceme arrangements significantly contribute to both dimensions. In the first dimension, the number of homogamous spikelets is the most important qualitative character in species groupings. The arrangement of homogamous spikelets gave slightly lower percent contribution than the number of homogamous spikelets in the same dimension. In the second dimension, awn type has the second-highest percent contribution after awn hairs. Other qualitative characters such as the presence of stilt roots, habit, raceme disarticulation, and presence of tuberculate hairs yielded lower percent contribution.

Table 5.2. Significant percent contribution of qualitative and quantitative characters analyzed by Factor Analysis of Mixed Data (FAMD) in the first two dimensions.

Characters	Percent contribution (dimension 1)	Precent contribution (dimension 2)
Number of branching orders	11.87	Not significant
Raceme length	11.15	Not significant
Caryopsis ratio	11.02	Not significant
Number of homogamous spikelets	9.48	Not significant
Number of spikelet pairs	9.31	Not significant
Awn hair types	9.05	15.80
Awn length	6.29	9.40
Raceme arrangement	5.92	7.40
Homogamous spikelet arrangement	5.76	Not significant
Awn type	Not significant	15.42
Stilt root	Not significant	9.64
Habit	Not significant	8.37
Disarticulation	Not significant	7.35
Presence of tuberculate hairs	Not significant	6.31

5.3.2 Morphological Trends on Phylogenetic Tree

The *Heteropogon-Themeda* phylogeny revealed changes in inflorescence architecture and spikelet arrangements (Fig. 5.4; Table 5.3). Homogamous spikelet are numerous at the base of the phylogeny in early diverging species *Heteropogon contortus* and *Heteropogon triticeus* and reduced to a fixed number of four homogamous spikelets in *Themeda* (Fig. 5.4C). Differences in the number of homogamous spikelets separate the genus *Heteropogon* from *Themeda*. Likewise, *Heteropogon* species produce numerous spikelet pairs, usually more than four (Fig. 5.4D). In contrast, the number of spikelet pairs is lower in *Themeda*, and the spikelet pairs are absent in the late diverging clades (e.g., *Themeda arguens* (L.) Hack. and *Themeda triandra*). The complexity of inflorescence architecture is observed in the branching patterns. In *Heteropogon* species, racemes branch off after the first paraclade. Branching orders increased in *Themeda* species with single racemes produced after primary branching (e.g., *Themeda anathera* (Nees ex Steud.) Hack., *Themeda caudata* (Nees ex Hook.

& Arn.) A. Camus, and *Themeda villosa* (Lam.) A. Camus) and clustered racemes on primary branching (e.g., *Themeda cymbaria* Hack.) and secondary branching (e.g., *Themeda tremula* and *Themeda triandra*). Glume ornamentation (e.g., hairiness), awn characteristics, and caryopses provide finer-scaled criteria to delimit species (Fig. 5.2 and Fig. 5.3). For example, wetland species, comprising *T. arundinacea*, *T. caudata*, *T. gigantea*, *T. idjenensis*, *T. intermedia*, *T. novoguineensis*, and *T. villosa*, shared inflorescence architecture and spikelet arrangements, but some species are awnless (e.g., *Themeda gigantea*) while the other species have long and robust awns (e.g., *T. arundinacea*).

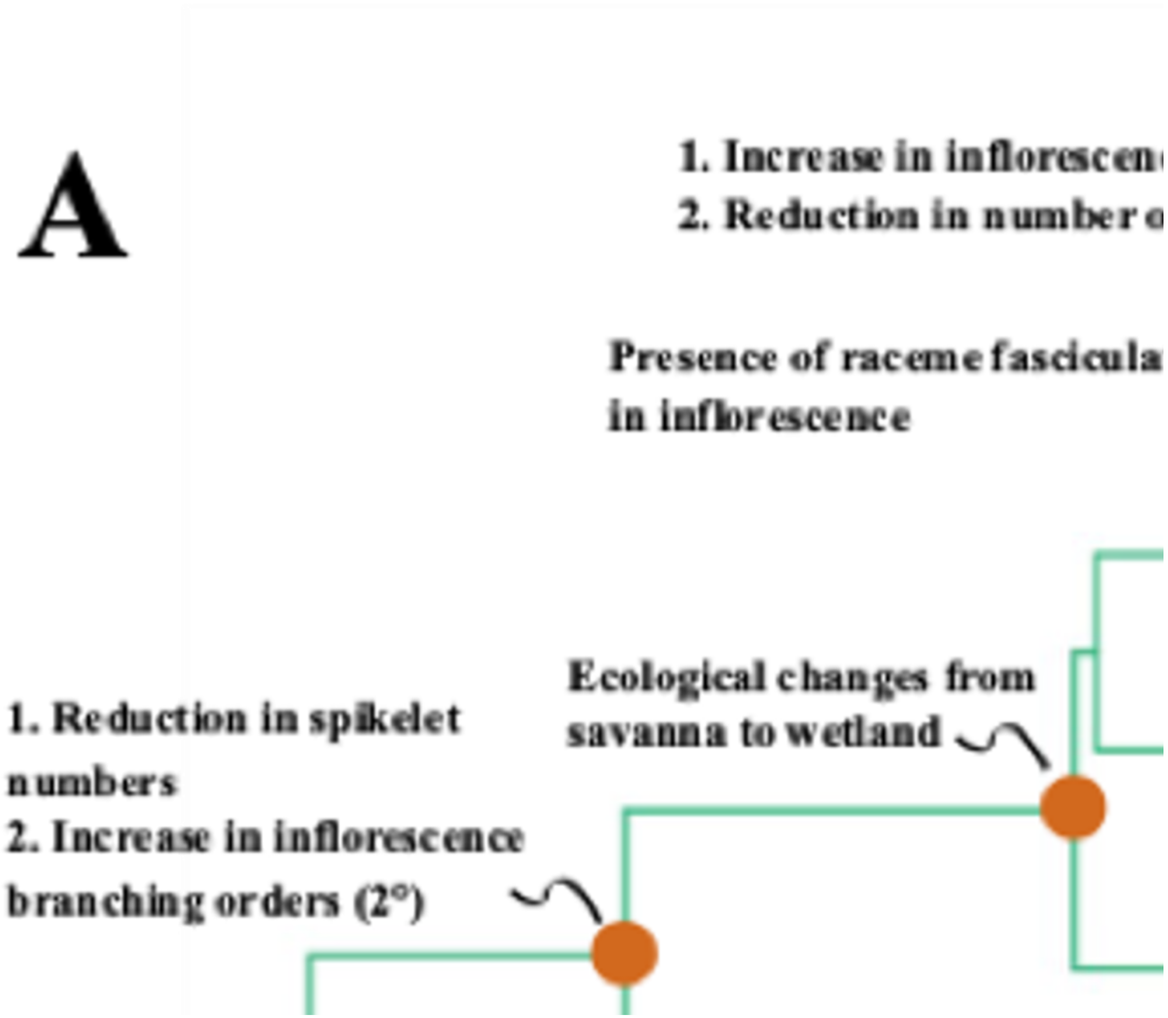

Figure 5.4. Mapping of major events of changes in inflorescence architecture and spikelet compositions of *Heteropogon-Themeda* clade, using the phylogeny adapted from Arthan et al. (2021) **(A)** and character evolution of branching orders **(B)**, the number of homogamous spikelets **(C)**, and the number of spikelet pairs **(D)**.

Table 5.3. Character evolution of inflorescence branching orders, the number of homogamous spikelets, and the number of spikelet pairs in the *Heteropogon-Themeda* lineage, showing best models and transition rates of three characters.

Character	**Best model**	**Rate of character changes**			
			1	2	3
Branching orders	ARD	1	0	0.055[†], 0[‡], 0.102[§]	0[†], 0[‡], 0.034[§]
The number of homogamous spikelets	ARD	2	0[†], 0.047[‡], 0[§]	0	0.028[†], 0[‡], 0[§]
The number of spikelet pairs	ARD	3	0[†], 0[‡], 0.126[§]	0[†], 0.054[‡], 0[§]	0

† Change rate of branching orders

‡ Change rate of the number of homogamous spikelets

§ Change rate of the number of spikelet pairs

Note: 1, 2, and 3 indicates each state for each character. ‘1’ represents one branching order, numerous homogamous spikelets, and numerous spikelet pairs. ‘2’ represents two branching orders, a few (4–6) homogamous spikelets, and a few (4–6) spikelet pairs. ‘3’ represents three or more branching orders, four homogamous spikelets, and absence of spikelet hairs.

5.3.3 Ecological Characteristics

In *Heteropogon,* ecological data suggests that *H. contortus* occupies a drier climatic niche than *H. triticeus*, which its distribution covers wetter savannas in Southeast Asia (Table 5.4). Niche analyses by Arthan et al. (2022) yielded significant climatic differences between these two species.

In *Themeda*, most species do not share climatic niche space and habitats (Arthan et al., 2022). Habitats and climatic niches of endemic species are separate from widespread species and other endemic species. The endemic species *Themeda anathera* in Chir Pine savannas in Himalayan regions has niche overlap estimates with other species which are mostly very low and climatic niches between *T. anathera* and other species were not significantly similar (Arthan et al., 2022). Likewise, other Indian endemic or narrowly-ranging species, *Heteropogon ritchiei*, *Themeda cymbaria*, *Themeda hookeri* (Griseb.) A.Camus, *Themeda mooneyi* Bor, and *Themeda tremula*, did not share climatic niche with most species. Wetland species share geographic distribution in Southeast Asia and Melanesia, but their climatic niche spaces do not entirely overlap (Fig. 5.5). *Themeda villosa* occupied the least wet parts of wetland climatic space. In contrast, the climatic niche space of *Themeda intermedia* (Hack.) Bor was situated in the wetter part of the space. The plot (Fig. 5.5) shows that two morphologically similar species *Themeda gigantea* (Cav.) Hack. Ex Duthie and *Themeda intermedia* co-occurring in the Philippines did not share climatic spaces. In addition, findings from habitat suitability analyses by Fierro (2014) indicated that the contribution of climatic variables to species distribution are different among species.

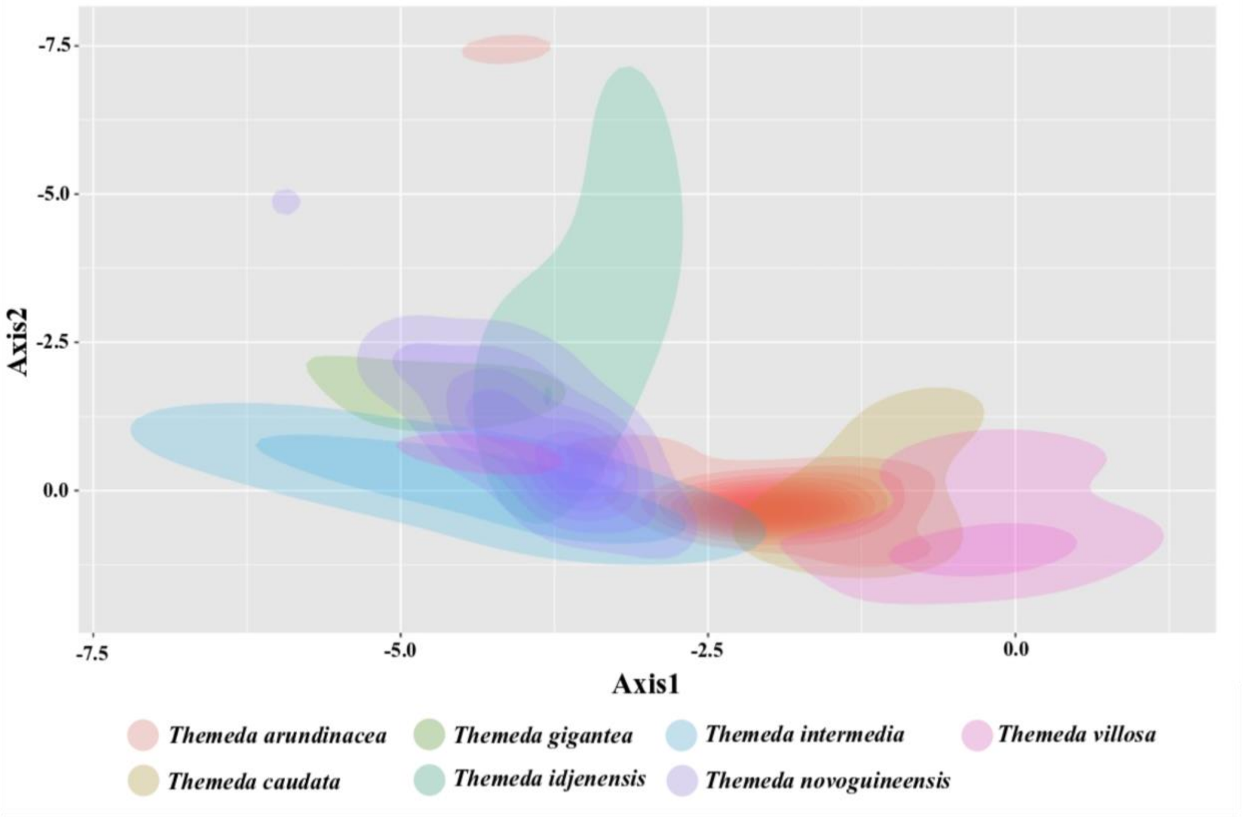

Figure 5.5. Climatic spaces of the wetland species analyzed by Principal Component Analysis using four climatic variables based on Arthan et al. (2022).

5.3.4 Conservation Status

AOO and EOO values range from 200 km^2 in *T. trichiata* to 821400 km^2 in *T. triandra*, and 381 km^2 in *T. huttonensis* to 242,835,098 km^2 in *H. contortus*, respectively. IUCN assessment cannot be performed for nine species that have coordinate data for fewer than 3 records (Table 5.5). Only 8 out of 37 species are categorized as Least Concern, using criteria B2 (IUCN, 2022). Other species were assessed to be ‘near-threatened’, ‘vulnerable’, and ‘endangered’ (Table 5.5).

Table 5.4. Comparison table of biogeographical, ecological, morphological, and phylogenetic characteristics of accepted *Heteropogon* and *Themeda* species

Species	**Distribution**	**Habitat**	**Key species morphology**	**Phylogenetic position**
Heteropogon contortus	Pantropical, subtropical, and temperate regions	Savannas around the world and arid habitats in Middle East and China	Numerous homogamous spikelets and spikelet pairs, awns interwined, plant andromonoecious	Early-diverged species of *Heteropogon-Themeda* lineageand sister to *H. triticeus*
Heteropogon polystachyos	Endemic to India	Unknown	Terminally borne racemes	Unknown phylogenetic position
Heteropogon triticeus	India and Southeast Asia	Southeast Asian savannas such as Pine savannas and deciduous savannas	Numerous homogamous spikelets and spikelet pairs,awns not interwined, fertile spikelet bisexual	Early-diverging species of *Heteropogon-Themeda* lineage and sister to *H*. contortus
Themeda anathera	Endemic to Himalayan regions	Chir pine savannas at high altitude	Several spikelet pairs and awnless	Early-diverging *Themeda* species
Themeda arguens	India, Southeast Asia, and Australia	Southeast Asian savannas	Homogamous spikelet reduced to a single glume	Late-diverging group and closely related to *T. triandra*
Themeda arundinacea	India and Southeast Asia	Wetland	Tawny tuberculate hairs on homogamous spikelet	Wetland group and closely related to *T. villosa* and *T. intermedia*
Themeda avenacea	Endemic to Australia	Australian savannas (e.g., Melaleuca savannas) and	Fluffy butt sheath	Closely related to wetland species

Table 5.4. Comparison table of biogeographical, ecological, morphological, and phylogenetic characteristics of accepted *Heteropogon* and *Themeda* species (continued).

Species	**Distribution**	**Habitat**	**Key species morphology**	**Phylogenetic position**
Themeda caudata	India and Southeast Asia	Wetland	Homogamous spikelets with tuberculate hairs; awn well-developed	Wetland group
Themeda cymbaria	India and Sri Lanka	Seasonally inundated grassland in Sri Lanka	Higher inflorescence branching orders and raceme still contain spikelet pairs	Late-diverging species with isolated phylogenetic position before *T. triandra* and its relatives
Themeda gigantea	The Philippines, Indonesia (Java and Lesser Sunda Islands), and Pacific islands	Wetland	Awnless and tawny tuberculated hairs in homogamous spikelets	Unknown phylogenetic position
Themeda hookeri	India, South-Central China, and Thailand	Hot, dry habitats such as subtropical karst in China and desert shrubland; associated with *H. contortus*	Second-order inflorescence branching, raceme with 2 spikelet pairs	Phylogenetic position sister to *Themeda mooneyi* and *Themeda huttonensis*
Themeda huttonensis	Endemic to India	Near watercourse and stream banks at high altitude (~1,500 m)	Second-order inflorescence branching, raceme with 2 spikelet pairs	Phylogenetic position is sister to *Themeda mooneyi* and *Themeda hookeri*
Themeda idjenensis	Endemic to Java, Indonesia	Wetland	Second-order inflorescence branching, raceme with a single spikelet pair, and aristate glume	Unknown phylogenetic positions

Table 5.4. Comparison table of biogeographical, ecological, morphological, and phylogenetic characteristics of accepted *Heteropogon* and *Themeda* species (continued).

Species	**Distribution**	**Habitat**	**Key species morphology**	**Phylogenetic position**
Themeda intermedia	The Philippines, Indonesia (Java and Lesser Sunda Islands), and Pacific islands	Wetland	Awnless and tawny tuberculated hairs in homogamous spikelets	Wetland group
Themeda minor	Endemic to China	Semi-arid region in China dominated by *Robinia pseudoacacia*	Second-order inflorescence branching, raceme with a few spikelet pairs	Phylogenetic position sister to *T. hookeri* and *T. huttonensis*
Themeda mooneyi	Endemic to India	Moist savannas such as semi-evergreen forest and mixed deciduous savannas	Second-order inflorescence branching, homogamous spikelet with hairs, and raceme with a single spikelet pair	Phylogenetic position belong to a subclade comprising *T. hookeri*, *T. huttonensis*, and *T. minor*
Themeda melanocarpa	India, tropical Africa, subtropical North America, and tropical South America	Seasonally inundated grasslands or swamp areas	Glandular line on midrib and asymmetric glume	Phylogenetic position sister to *Themeda ritchiei*
Themeda novoguineensis	Endenic to Papua New Guinea	Wetland	Higher-order inflorescence branching and raceme without spikelet pairs	Late-diverging species and sister to *T. triandra*
Themeda odishae	Endemic to India	Rock outcrops at high altitude (1,300–1,400 m)	Second-order inflorescence branching, 3 racemes, raceme with a single spikelet pair, hairy lower glume	Unknown phylogenetic position

Table 5.4. Comparison table of biogeographical, ecological, morphological, and phylogenetic characteristics of accepted *Heteropogon* and *Themeda* species (continued).

Species	**Distribution**	**Habitat**	**Key species morphology**	**Phylogenetic position**
Themeda palakkadensis	Endemic to India	Rock outcrops at high altitude (1,600–1,900 m)	Higher-order inflorescence branching, raceme without spikelet pairs, densely pilose fertile spikelet	Unknown phylogenetic position
Themeda pseudotremula	Endemic to India	Moist savannas such as moist deciduous savannas	Densely pilose fertile spikelet	Unknown phylogenetic position
Themeda ritchiei	Endemic to India	Both dry and wet deciduous or open marchy areas	Dense tawny tuberculate hairs on homogamous spikelets and asymmetric glume	Phylogenetic position sister to *Themeda melanocarpa*
Themeda sabarimalayana	Endemic to India	NA	Higher-order inflorescence branching and raceme without spikelet pairs	Late-diverging species and sister to *T. triandra*
Themeda saxicola	Endemic to India	Granite rock outcrops with long dry seasons and extreme temperature	Strictly terminally-borne inflorescence and raceme with a few spikelet pairs	Unknown phylogenetic positions
Themeda strigosa	Endemic to India	NA	Second-order inflorescence branching and raceme with 2-3 spikelet pairs	Sister to *Themeda anathera*

Table 5.4. Comparison table of biogeographical, ecological, morphological, and phylogenetic characteristics of accepted *Heteropogon* and *Themeda* species (continued).

Species	**Distribution**	**Habitat**	**Key species morphology**	**Phylogenetic position**
Themeda tremula	Endemic to India	Seasonally inundated grasslands in lowland and upland area	Higher-order inflorescence branching and raceme with a single spikelet pair	Late-diverging species and sister to *T. triandra* relatives
Themeda triandra	Pantropical, subtropical, and temperate regions	Wet Southeast Asian savannas to drier savannas in Africa and Australia	Higher-order inflorescence branching and raceme without spikelet pairs	Late diverging species
Themeda trichiata	Endemic to China	Dry mountain slopes	Homogamous spikelets inserting at the same level and dense hairs on leaves and culm	Sister to *T. avenacea* and wetland species
Themeda unica	Endemic to China	Hill slopes	Higher-order inflorescence branching, raceme without spikelet pairs, awnless or less developed awns	Late-diverging species and sister to *Themeda tremula*
Themeda villosa	India and Southeast Asia	Wetland	Homogamous spikelet glabrous, awn less developed	Species in wetland group
Themeda yunnanensis	Endemic to China	Dry open grasslands at high altitude	Homogamous spikelets with white tuberculate hairs and shallow median groove on fertile spikelet	Unknown phylogenetic position

Table 5.5. Conservation status of *Heteropogon* and *Themeda* species evaluated by AOO and EOO based on criteria category B in IUCN (2022).

Species/Taxa	**EOO (km^2)**	**AOO (km^2)**	**TDWG Count**	**Least concern**	**IUCN category**
Heteropogon contortus	242835098	202100	140	Yes	LC
Heteropogon polystachyos	NA	NA	NA	NA	DD
Heteropogon triticeus	10053035	20500	14	Yes	LC
Themeda anathera	279019	4300	5	No	NT
Themeda arguens	13009898	25500	20	Yes	LC
Themeda arundinacea	8534482	4700	19	No	NT
Themeda avenacea	7211758	45400	6	Yes	LC
Themeda caudata	9439602	6800	19	Yes	LC
Themeda cymbaria	138435	2300	2	No	NT
Themeda gigantea* var. *gigantea	3901670	1300	7	No	VU
Themeda gigantea* var. *intermedia	12348326	3500	17	No	NT
Themeda hookeri	1511705	2800	6	No	NT
Themeda huttonensis	381	300	1	No	EN (B1, B2)
Themeda idjenensis	10992	500	2	No	VU (B1, B2)
Themeda melanocarpa	103403719	42200	57	Yes	LC
Themeda minor	NA	NA	NA	NA	DD
Themeda mooneyi	750	300	1	No	EN (B1, B2)
Themeda novoguineensis	44640	1200	1	No	VU (B1)
Themeda odishae	NA	NA	NA	NA	DD
Themeda palakkadensis	0	200	1	No	CR
Themeda pseudotremula	NA	NA	NA	NA	DD
Themeda ritchiei	791847	600	2	No	VU (B2)
Themeda sabarimalayana	NA	NA	NA	NA	DD
Themeda saxicola*	42	8		No	CR (B1, B2biii)
Themeda strigosa	NA	NA	NA	NA	DD
Themeda tremula	315397	3200	4	No	NT

Species/Taxa	EOO (km^2)	AOO (km^2)	TDWG Count	Least concern	IUCN category
Themeda triandra* var. *triandra	130221035	821400	84	Yes	LC
Themeda triandra* var. *quadrivalvis	3353532	3200	9	No	NT
Themeda trichiata	0	200	3	No	EN (B1, B2)
Themeda villosa	16638493	18600	27	Yes	LC
Themeda yunnanensis	NA	NA	NA	NA	DD

Note that conservation status of species marked with NA cannot be determined as there were not sufficient occurrence records set by the analyses (n < 3).

*Conservation of *Themeda saxicola* is based on Chorge & Kulloli (2022).

5.4 DISCUSSION

5.4.1 Diagnostic Morphological Characters

Patterns of variability in the number of homogamous spikelets, the number of spikelet pairs, presence of triads, and inflorescence architecture are associated with underlying evolutionary history. The genera *Heteropogon* and *Themeda* are recognized morphologically by unique inflorescence structure with basal homogamous spikelets, and triad. Such structure is not common in Andropogoneae genera. These characters could be either homoplasious or synapomorphic in the tribe Andropogoneae.

A. Homogamous Spikelet and Spikelet Pairs

The homogamous spikelet is shown to independently evolve as early as lineages outside core Andropogoneae (e.g. *Apocopis* Nees and *Germainia* Balansa & Poitr.; Arthan et al., 2017) but is more prevalent in genera closely related to *Heteropogon* and *Themeda* (e.g., *Cymbopogon* Spreng., *Hyparrhenia* Andersson ex E.Fourn., and *Iseilema* Andersson; Arthan et al., 2021). The number of homogamous spikelets varies between genera (POWO, 2022). Connor (1981) pointed out an evolutionary hypothesis that the production of homogamous spikelets increases the number of stamens and the male: female ratio and then male fertility which suggest high value of pollen. Presence-absence conditions of homogamous spikelets offer taxonomic value. Similarly, the number of spikelet pairs are decreased from numerous in *Heteropogon* to completely absent in the terminal lineage of the group (e.g., *Themeda arguens* and *Themeda triandra*), but whether reduction in fertile spikelets is associated with male fertility needs more evidence. The triad is more prevalently observed in the subtribe Anthistiriinae than any other lineages of Andropogoneae (Arthan et al., 2021) and is only present in a few genera outside the subtribe (e.g., *Chrysopogon* Trin.). However, that such characters are related to specific selective pressure or genetic control remains unclear.

B. Inflorescence Architecture

Variation in inflorescence architecture is valuable for interspecific classifications as they are highly variable in the *Heteropogon-Themeda* clade. Trends in inflorescence architecture of Andropogoneae have usually evolved towards more complexity of branching patterns (Perreta et al., 2009). In the early-diverging genus *Heteropogon*, the development of inflorescence architecture terminates at primary branching from the main inflorescence stem (Fig. 5.3A). On the other hand, *Themeda* inflorescence branching reaches secondary (e.g., Fig 5.3B; *Themeda arundinacea* and *Themeda anathera*) or tertiary (Fig. 5.3B; as a cluster of racemes as seen in *Themeda triandra*) steps. Furthermore, species that have tertiary branching can be differentiated by the number of clusters borne from the secondary branching. These branching patterns are regulated by genes and other regulatory factors (Kellogg, 2022).

C. Glume Indumentum and Awn

At finer-scale classifications, glume hairiness and its density, and awn characteristics are useful functional traits to delimit species. Although hairiness in plants and awn length are labile characters (Garnier & Dajoz, 2001; Hou & Simpson, 1992), we found that there are sufficient fixed patterns to distinguish species (Fig. 5.4). In the wetland group, a combination of hairiness, awn type, and awn length yielded 6 species (Figs. 5.4, 5.3A). Likewise, hairs, awns, and caryopses also support the separation of Indian endemic species (e.g., *T. hookeri*, *T. huttonensis*, and *T. mooneyi*; Fig. 5.4). Several experiments demonstrated that macrohairs respond to humidity and navigate diaspores to embed in suitable sites (Peart & Clifford, 1987). Awn types and lengths are postulated to move in response to moisture and fire frequency and intensity (Garnier & Dajoz, 2001; Ntakirutimana & Xie, 2020). These associations between traits and climate between species make a contribution to species demilitation.

5.4.2 Ecological Data

Ecological data, and especially climate data, have been used to help delimit species as powerful determinants of species distribution (Guisan & Thuiller, 2005) and predictors of functional traits (Kühn et al., 2021). Here, ecological niche modeling highlighted diverse ecological characteristics determining habitat suitability of *Heteropogon* and *Themeda* species. Niche overlap analyses also testify that their climatic niche spaces are significantly different, especially endemic species that might share geographic ranges.

Climatic data has set broad boundaries within the *Heteropogon-Themeda* clade. Ecological transitions from savanna to wetland (Fig. 5.4) show a clear-cut division between the wetland species and the rest (Arthan et al. 2022). Wetland species comprise of *T. arundinacea*, *T. caudata*, *T. gigantea*, *T. idjenensis*, *T. intermedia*, *T. novoguineensis*, and *T. villosa*. These species inhabit wetlands in the adjacent geographic area in Southeast Asia; however, most of their climatic occupations do not totally overlap (Fig. 5.5; Arthan et al., 2022). In the case of *T. novoguineensis*, climatic data justified its species status as its distribution is restricted to wetter habitats in Papua New Guinea, despite morphology similar to *T. triandra*. Climatic data provide a guide to using vegetative parts to recognize wetland species as they produce stilt roots and straight awns while other species lack these features. Climatic data, together with phylogenetic relationships, affirm that morphologically similar species in the clade do not share a direct common ancestor.

5.4.3 Generic and species Delimitation

Here, concept of monophyly was an initial step for generic delimitation. Chloroplast and nuclear trees revealed that *Heteropogon* and *Themeda* form monophyletic groups. Although the evidence of chloroplast capture is shown by discordant positions of *Heteropogon triticeus* in the plastome tree, most of the genetic makeup is contributed by *H. triticeus* as suggested by the nuclear gene tree. Therefore, *H. triticeus* is considered belonging to the genus *Heteropogon*, supported by shared morphology or synapomorphies as shown in Figure XX. *Heteropogon* and *Themeda* are distinguished by the number of spikelets and branching patterns, which are subsets of characters determining inflorescence architecture. These characters are controlled by genes and fixed in the genus (Kellogg, 2015; Kellogg et al., 2013); thus, they are evolutionarily significant and taxonomically identifiable. Likewise, species was delimited by phylogenetic placements under monophyletic groups and differences in morphology and ecological functions. we maintain the generic status of *Heteropogon* and *Themeda* and accept 3 *Heteropogon* species, 26 *Themeda* species and 2 *Themeda* varieties.

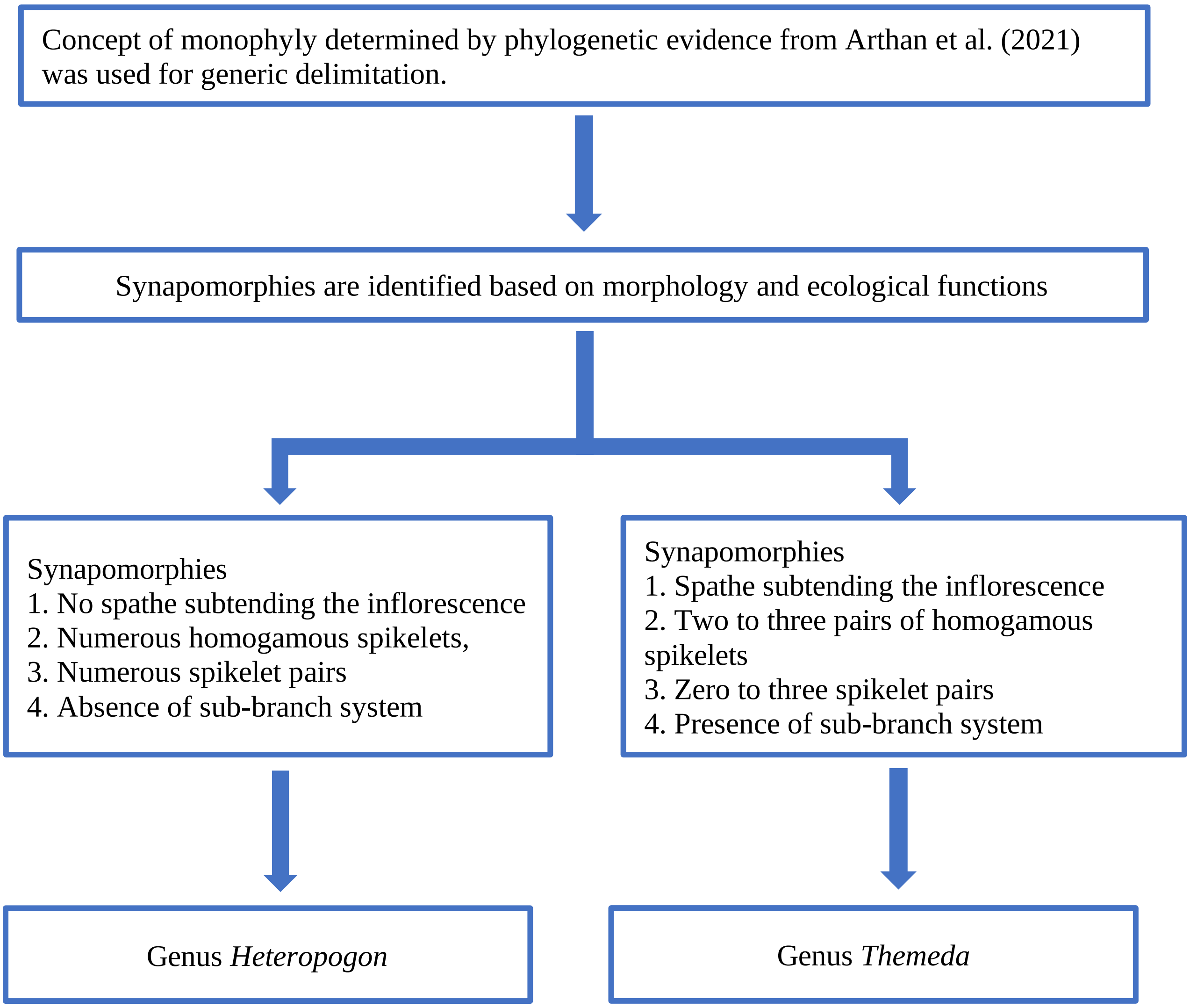

Figure 5.6. Decision flowchart for generic and specific delimitation of *Heteropogon* and *Themeda*.

Phylogenomic evidence from both chloroplast genome and nuclear genes clearly indicate that the number of species of ‘true’ *Heteropogon* is reduced from five species to three species, *H. contortus*, *H. polystachyos* (Roxb.) Schult., and *H. triticeus*. The expression of several homogamous spikelet and fertile spikelet pairs and the absence of triads are considered synapomorphies of the *Heteropogon* group.

In this study, *H. melanocarpus* and *H. ritchiei* have been transferred to the genus *Themeda*. The number of homogamous spikelets and spikelet pairs is reduced from numerous to a few pairs, and the triad is present in both species. Although clusters of *T. melanocarpus* and *T. ritchiei* individuals are located near other *Heteropogon* species, this might be that the number of homogamous spikelets and spikelet pairs, and the size of awns and spikelets, are elusive for morphological interpretation due to convergent evolution or exact underlying causes have not yet been identified (e.g., developmental processes). However, when considering phylogenetic positions and morphological trends in the whole group, these two species should be placed in genus *Themeda*.

Five wetland species are accepted: *T. arundinacea* (Roxb.) A.Camus, *T. caudata*, *T. gigantea*, *T. novoguineensis* (Reeder) Jansen, and *T. villosa* (Fig. 5.4). Multivariate analysis of climatic data illustrates that these species do not a share similar bioclimatic space. Here, we recognize *T. intermedia* as a variety of *T. gigantea* as they are only different in size of spikelets and their climatic spaces mostly overlap.

Morphologically similar species, especially Indian endemic species, are considered separate. *T. hookeri*, *T. huttonensis* Bor, and *T. mooneyi* are grouped in the same clade where the topology of the phylogeny clearly separates the three species (Fig. 5.4). A set of morphology to separate these three species comprises of the number of spikelet pairs, branching patterns, glume hairiness, glume morphology, and awn morphology. Size of glumes is used as supporting evidence to separate them (Table 5.1). Climatic spaces of *T. hookeri* and *T. huttonensis* cannot be defined due to limited coordinate records, thus, their climatic envelopes cannot be compared.

The number of spikelet pairs is reduced to one in *T. cymbaria* and *T. tremula* before becoming completely absent in the next clade (Fig. 5.4). Their distinct phylogenetic positions are clearly illustrated in both nuclear and plastome trees. The distribution ranges of both species overlap India and Sri Lanka but their climatic niches are dissimilar. Morphologically, *T. tremula* has dense tuberculate hairs on the homogamous spikelets whereas those of *T. cymbaria* are non-tuberculate. Longer and thicker awns are found in *T. tremula*. *T. cymbaria* bears fewer and smaller racemes in a cluster than *T. tremula*.

A complex group of *T. triandra* and related species is recognized here as three species, *Themeda helferi* Hack., *Themeda laxa* (Andersson) A.Camus, *Themeda quadrivalvis*, and *Themeda triandra* (Fig. 5.4). These species share a lack of spikelet pairs, but hairiness on homogamous and fertile spikelets, the reduction of glume, and awn characteristics (especially length) are different. Homogamous spikelets are greatly reduced to a single glume only in *T. arguens* while other species developed complete homogamous spikelets. Here, we proposed that *T. quadrivalvis* is a variety of *T. triandra* as supported by ecological, morphological, and phylogenetic data (Dunning et al., 2022). Climatic space of Australian and Middle eastern *T. quadrivalvis* populations overlaps with the pantropical climatic space of *T. triandra* (Arthan et al., 2022). Phylogenetic evidence shows close relationships between *T. quadrivalvis* and *T. triandra* (Fig. 5.4). Morphologically, only minor differences are observed between *T. quadrivalvis* and *T. triandra*. For example, *T. quadrivalvis* have smaller spikelet and spatheole than *T. triandra*.

5.4.4 TAXONOMIC TREATMENT

Key to genera of the subtribe Anthistiriinae

1. Terminal inflorescences unbranched…………………………………………………..2

1. Terminal inflorescences branched…………………………………………………..5

2. Lower glumes of the sessile spikelet with central pit…………………………..*Eremopogon*

2. Lower glumes of the sessile spikelet without central pit……………………………………3

3. Inflorescences not subtended by spathe……………………………………..*Heteropogon*

3. Inflorescences subtended by spathe……………………………………………………4

4. Leaves and spathe with glands, pedicels of basal homogamous pairs curved………*Iseilema*

4. Leaves and spathe without glands, pedicels of basal homogamous pairs straight….*Themeda*

5. Inflorescence branched in pair, internode with crater-like extension at the base of spikelet pairs…………………………………………………………………………*Cymbopogon*

5. Inflorescence branched more than 2, internode straight without crater-like extension at the base of spikelet pairs…………………………………………………………………...6

6. Habit annual…………………………………………………………………*Euclasta*

6. Habit perennial…………………………………………………………………………7

7. Inflorescence digitate or subdigitate…………….……………………………………8

7. Inflorescence not digitate………………………………………………………………9

8. Basal homogamous spikelet pairs absent, lower glume of the sessile spikelet with central pits…………………………………………………………………………*Bothriochloa*

8. Basal homogamous spikelet pairs present, lower glume of the sessile spikelet without central pits……………………………………………………………………*Dichanthium*

9. Inflorescence commonly comprising only a triad without spikelet pairs, pecidels and rachis internode with a translucent line………………………………………………*Capillipedium*

9. Inflorescence comprising of spikelet pairs, pecidels and rachis internode without a translucent line……………………………………………………………………………10

10. Basal homogamous spikelets absent, only one spikelet pair present, lower glumes not grooved..*Pseudanthistiria*

10. Basal homogamous spikelets present, several spikelet pairs present, lower glumes deeply grooved……………………………………………………………………...*Agenium*

Heteropogon Pers., Syn. Pl. 2: 533. 1807 – Lectotype: *Heteropogon glaber* Pers. (designated by Nash, 1912)

Diagnosis. – *Heteropogon* is a sister genus of *Themeda* as revealed by molecular data. The morphological distinction of *Heteropogon* from other Andropogoneae genera (except from *Themeda* and *Iseilema*) is spatheoles subtending racemes and paraclades (Kellogg, 2015) and the presence of homogamous spikelets (except from genera *Hyparrhenia*, *Iseilema*, and *Themeda*). However, *Heteropogon* is distinguished from *Themeda* by possessing numerous homogamous spikelets and fertile spikelet pairs.

Description. – Perennial; rhizomes present or absent; culms erect but sometimes geniculately ascending from the base, caespitose, glabrous; leaf sheaths glabrous or occasionally hairy; ligules truncate, ciliolate or eciliate; leaf blades plicate or non-plicate, abaxial and adaxial surfaces glabrous or hairy, lanceolate, margin scabrid, apex acute or attenuate. Inflorescence axillary and terminal, inflorescence paniculate; spatheoles glabrous or pubescent, lanceolate; rachis internodes fragile, pilose with white or yellow hairs, linear or cuneate, attached obliquely; raceme solitary, 8–51 sterile spikelets, 5–16 fertile spikelets; triads present; homogamous spikelets 6–46 in number, male or barren, a pair arranging at different levels, persistent, well developed, lanceolate; callus linear or cuneate, glabrous, attached obliquely, lower glume glabrous or pilose with tuberculate hairs, chartaceous, ovate or lanceolate, upper glume glabrous, chartaceous, lanceolate, lower lemma lanceolate, membranous, upper lemma linear or lanceolate, membranous; palea absent or minute; lodicules 2, cuneate, coriaceous. Fertile pairs separately deciduous from homogamous spikelets, 5–12 pairs, sessile spikelets different from pedicelled ones, sessile spikelet, well developed, pistillate or bisexual, elliptic; callus linear, hairy with brown hairs, lower glume densely pubescent with tawny hairs, coriaceous, lanceolate, two-grooved beside midvein; upper glume densely pubescent with tawny hairs, coriaceous, oblong; lower lemma lanceolate, membranous; upper lemma membranous, linear, attached at the base of awn, minute; palea membranous, ovate-oblong; lodicules 2, cuneate, coriaceous, companion spikelets, pedicelled, well developed, male, asymmetrical lanceolate; callus pubescent with dark brown hairs, linear; lower glume glabrous, coriaceous, lanceolate; upper glume glabrous, coriaceous, lanceolate; lower lemma membranous, lanceolate; upper lemma membranous, oblong; palea minute or absent; lodicules 3, cuneate, coriaceous; awn present, geniculate, column twisted and hirtellous; anthers 3; ovary 1; stigmas 2, plumose.

Habitat. – Tropical and subtropical savannas such as pine savannas (e.g., *P. kesiya*, *P. merkusii*,and *P. roxburghii*), deciduous broadleaf savannas, and fine-leafed and spiny savannas. *H. contortus* are sometimes found in rock outcrops and sand dunes.

Distribution. – Overall distribution of the genus is pantropical and some parts of subtropical regions in China and India and temperate zones in Europe (e.g., Austria, France, Germany, Italy) and America. This wide distribution range of the genus is caused by the distribution range of *H. contortus* alone. The other two species have relatively much less narrow than *H. contortus*. *H. triticeus* is distributed from India to Australia whereas *H. polystachyos* is endemic in India (see distribution maps in Appendix XV).

Themeda Forssk., Fl. Aegypt.-Arab. 178. 1775 – **Neotype (designated here)**: *Themeda triandra* Forssk.

Diagnosis. – *Themeda* represent unique raceme structures, strictly comprising 2 pairs of homogamous spiklets, only 0-4 pairs of fertile spikelets, and a triad at the top of raceme.

Description. – Annual or perennial; rhizomes usually present; stilt roots sometimes present; culms erect but sometimes geniculately ascending from the base, caespitose, glabrous or occasionally hairy; leaf sheaths glabrous to hairy; ligules truncate, mostly ciliolate but occasionally eciliate; leaf blades non-plicate, abaxial surface glabrous or hairy, adaxial surface glabrous to slightly hairy, glandular line sometimes present on the midrib, lanceolate. Inflorescences axillary and terminal or occasionally strictly terminal, inflorescence paniculate or fasciculate; spatheoles glabrous or pubescent, lanceolate; rachis internodes fragile or sometimes tough, glabrous or pilose with white, yellow, or tawny hairs, linear or cuneate, attached obliquely; raceme solitary or clustered, 6–9 sterile spikelets, 1–4 fertile spikelets; triad present; homogamous spikelets 4 in number, male or barren, a pair arranging at the same level or different levels, persistent, well developed, lanceolate; callus linear or squared, glabrous, lower glume glabrous or pilose with tuberculate hairs, glandular lines sometimes present, chartaceous, ovate lanceolate or lanceolate, upper glume glabrous or pubescent, chartaceous or subchartaceous, lanceolate to linear lanceolate, lower lemma lanceolate, membranous, upper lemma linear or lanceolate, membranous; palea absent or minute; lodicules 2, cuneate or oblong, coriaceous or membranous; fertile pairs deciduous separately from homogamous spikelets or together with homogamous spikelets, absent to up to 4 pairs, sessile spikelets different from pedicelled ones, well developed, bisexual, elliptic; callus cuneate or linear, pilose with white, yellow or tawny long hairs, lower glume densely pubescent all over or hirsute with short yellow or tawny hairs, coriaceous, elliptic lanceolate; upper glume glabrous or densely pubescent with tawny hairs, coriaceous, oblong or linear; lower lemma ovate or lanceolate, membranous; upper lemma membranous, linear, attached at the base of awn; palea sometimes absent, if present, membranous, ovate-oblong; lodicules 2, cuneate or oblong, coriaceous or membranous, companion spikelets, pedicelled, well developed, male or barren, lanceolate; callus glabrous or pubescent with white hairs, linear; lower glume glabrous or sparsely pilose with tuberculate hairs, chartaceous, lanceolate to linear lanceolate; upper glume glabrous, chartaceous to subchartaceous, lanceolate to linear lanceolate; lower lemma membranous, lanceolate; upper lemma sometimes absent, if present, membranous, ovate, lanceolate or linear; palea minute or absent; lodicules 2, oblong or cuneate, coriaceous; awn sometime absent, if present, geniculate or straight, column twisted or not, hispidulous or hirtellous; anthers 3; ovary 1; stigmas 2, plumose.

Habitat. – In general, species of *Themeda* occupy several savanna types and wetlands throughout the Tropics. Species distribution depend on habitat preferences, for example, *T. anathera* exists in chir pine forest in temperate zones, or *T. avenacea* is distributed in Melaleuca savannas in Australia. Occasionally, they are found in seasonally inundated habitats and wetlands in Southeast Asia and Australasia (e.g., *T. arundinacea*, *T. caudata*, *T. novoguineensis,* and *T. villosa*).

Distribution. – *Themeda* species are distributed throughout the tropics. The distribution range of *T. triandra* is the widest and cover temperate zones in Japan and Korea. However, most species are endemic to India and the rest of species are distributed in Southeast Asia (see distribution maps in Appendix XV).

Note: The holotype of *Themeda triandra* designated by Forskal was destroyed and there were not any types deposited in any herbaria. Thus, we designated the neotype of *Themeda triandra* from specimens collected in Yemen, which share similar localities to the original holotype.

Key to the species of *Heteropogon* and *Themeda*

1 Homogamous spikelet pairs more than 2 pairs…………………………………………...........2

1 Homogamous spikelet pairs less than 2 pairs………………………………………..............4

2 Inflorescences forming clusters and terminal………………………………..*H. polystachyos*

2 Inflorescences not forming clusters terminal and axillary……………………..........................3

3 Spikelets andromonoecious, homogamous spikelets shorter than 1.3 cm, awn diameter thinner than 0.4 mm ………………………………….*H. contortus* (including *H. fischerianus*)

3 Spikelet not andromonoecious, homogamous spikelet longer than 1.3 cm, awn diameter thicker than 0.4 mm……………………...…………………………………*H. triticeus*

4 Racemes in a inflorescence forming a cluster……………………………………………..5

4 Racemes in a inflorescence not forming a cluster………………………………………….13

5 Involucral spikelets inconspicuous or absent………………………………………*T. arguens*

5 Involucral spikelets conspicuous……………………………………………………………6

6 Fertile pairs present, triad present…………………………………………………………7

6 Fertile pairs absent, only triad present……………………………………………………9

7 Multiple spikelet pairs present in raceme……………………………………………*T. unica*

7 Only one spikelet pair present in raceme…………………………………………………8

8 Homogamous spikelets densely hairy all over…………...………….................*T. strigosa*

8 Homogamous spikelets glabrous…………………………………………………………...12

9 1 or 2 racemes present in a cluster, spikelets less than 1.2 mm…………...*T. sabarimalayana*

9 3 or more racemes present in a cluster, spikelets more than 1.2 mm…………….............10

10 Sessile spikelets awnless.…………………………………………………………...*T. minor*

10 Sessile spikelets awned……………………………………………………………………11

11 Sessile spikelets apically hirsute, sessile fertile spikelets 0.8‒0.9 mm long, awns 5.5‒7.0 cm long…………………………….. .. ..*T. triandra*

11 Sessile spikelets pilose all over, sessile fertile spikelets 0.5‒0.6 mm long, awns 2.5‒3.5 cm long……...*T. palakkadensis*

12 Sessile spikelets of fertile pairs sparsely hairy with brown hairs…….………….*T. tremula*

12 Sessile spikelets of fertile pairs densely hairy with long brown hairs…….*T. pseudotremula*

13 Raceme comprising 4 or more fertile spikelet pairs………………………………………14

13 Raceme comprising 1-2 fertile spikelet pairs…………………...................................15

14 Median glandular line on the glume present………………………………..*T. melanocarpa*

14 Median glandular line on the glume absent……………………………………*T. ritchiei*

15 Inflorescence strictly terminal……………………………………………………*T. saxicola*

15 Inflorescences both terminal and axillary…………………………………………………16

16 A pair of homogamous spikelets arrange at different levels………………………………17

16 A pair of homogamous spikelets arrange at the same level……………………...*T. trichiata*

17 Stilt roots present…………………………..18

17 Stilt roots absent……………………………………………………………………..........24

18 Awn present……………………………………………………………………………19

18 Awn absent…………………………………………………………………………...23

19 Basal leaf sheaths and innovations covered with dense white hairs…………….*T. avenacea*

19 Basal leaf sheaths and innovations not covered with hairs………………………………..20

20 Awn geniculate………………………………………………………………………... 21

20 Awn straight…………………………………………………………………………22

21 Involucral spikelets covered with dense tawny hairs; raceme persistent…………………………………………………………………...*T. arundinacea*

21 Involucral spikelets glabrous; raceme shed as a whole…………………………..*T. caudata*

22 Lower and upper glumes aristate……………………………………………*T. idjenensis*

22 Lower and upper glumes non-aristate……………………………………*T. novoguineensis*

23 Glumes glabrous…………………………………………………………...*T. villosa*

23 Glumes hairy with reddish brown hairs…………………………………………*T. gigantea*

24 More than 3 spikelet pairs present; awnless fertile lemma……………………...*T. anathera*

24 Only one spikelet pair present; awned fertile lemma…………………………….….25

25 Awn length less than 2 cm; culm height more than 1.5 metre…………………*T. cymbaria*

25 Awn length more than 2 cm; culm height less than 1.5 metre…………………………….26

26 Involucral spikelets covered with dense long tubercled white hairs; inflorescence bearing 1-2 raceme branches……………………...27

26 Involucral spikelets sparsely covered with tubercled white hairs; inflorescence bearing 3 raceme branches ………………..…………………………………………………….28

27 Non-tuberculate hairs on homogamous spikelets present; caryopses obovate……*T. hookeri*

27 Hairs on homogamous spikelets absent; caryopses oblanceolate ……………*T. huttonensis*

28 Sessile and pedicelled spikelets of fertile pair glabrous……………………..*T. yunnanensis*

28 Sessile and pedicelled spikelets of fertile pair covered with tubercled hairs……………...29

29 Keel of lower glume of involucral spikelets winged; lower glume hairy ………………………………………………………………………………*T. mooneyi*

29 Keel of lower glume of involucral spikelets non-winged; lower glume glabrous ……………………………………….……………………………..................*T. odishae*

Heteropogon contortus (L.) P.Beauv. ex Roem. & Schult. in Systema Vegetabilium 2: 836. 1817 ≡ ***Andropogon contortus*** L. in Species Plantarum. 2: 1045. 1753 — [***Andropogon contortum*** L. in Species Plantarum 2: 1045. 1753, orth. var.]. — [***Heteropogon hirtus*** Pers. in Synopsis Plantarum 2: 533. 1807, nom. illeg. superfl.] ≡ ***Sorghum contortum*** (L.) Kuntze in Revisio Generum Plantarum 2: 791. 1891 ≡ ***Holcus***

contortus (L.) Kuntze ex Stuck. in Anales del Museo Nacional de Buenos Aires. 11: 48. 1904 ≡ ***Holcus contortus*** var. ***secundus*** Hack. ex Stuck. in Anales del Museo Nacional de Buenos Aires 11: 48. 1904 — Lectotype (designated by Cope in Nasir & Ali (eds.), Flora of Pakistan. 143: 312. 1982): [illustration] "*Andropogon contortus*" in Plukenet, Phytographia: t. 191 f. 5. 1962 — **Epitype (designated here)**: Saudi Arabia, Jabal Fayfa, *J. S. Collette 5453* (K barcode K001426102!).

= ***Heteropogon allionii*** (Lam. ex DC.) Roem. & Schult. in Systema Vegetabilium 2: 835. 1817 ≡ ***Andropogon allionii*** Lam. ex DC. in Flore Française. Troisième Èdition 3: 97. 1805 — [***Heteropogon glaber*** Pers. in Synopsis Plantarum 2: 533. 1807, nom. illeg.] — [***Andropogon glaber*** (Pers.) Raspail in Annales des Sciences Naturelles (Paris) 5: 307. 1825, nom. Illeg.] — [***Andropogon messanense*** Biv. ex Parl. in Flora Italiana, ossia descrizione delle piante 1: 148. 1848, nom. inval.] ≡ ***Heteropogon contortus*** var. ***glaber*** (Pers.) Hack. in Flora Brasiliensis 2(4): 268. 1883 ≡ ***Andropogon contortus*** var. ***glaber*** (Pers.) Hack. in Monographiae Phanerogamarum 6: 587. 1889 ≡ ***Andropogon contortus*** var. ***allionii*** (Lam. ex DC.) Hack. in Boletim da Sociedade Broteriana 3: 137. 1885 ≡ ***Andropogon contortus*** subvar. ***allionii*** (Lam. ex DC.) Hack. in Monographiae Phanerogamarum 6: 587. 1889 — Holotype: [illustration] "*Andropogon allionii*" in Allioni, Florae Pedemontanae Icones accredit explanatio Nomenclaturae Botanicae 3: t. 91. f. 4. 1785 — **Epitype (designated here)**: France, Nice, *C. Allioni s.n.* (K barcode K000911729!).

= ***Heteropogon firmus*** J. Presl in Reliquiae Haenkeanae 1(4-5): 334. 1830 ≡ ***Heteropogon contortus*** var. ***hirtus*** (J. Presl) Fenzl ex Hack. in Flora Brasiliensis 2(4): 267. 1883 ≡ ***Andropogon firmus*** (J. Presl) Kunth in Enumeratio Plantarum 1: 486. 1933 — Holotype: Mexico, Veracruz, Orizaba, 1865, *Eugéne Bourgeau 2374* (MO barcode MO-144070!)

= ***Heteropogon roxburghii*** Arn. ex Nees in Nova Acta Physio-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum 19 (Suppl. 1): 183. 1843 ≡ ***Andropogon contortus*** subvar. ***roxburghii*** (Nees) Hack. in Botanisch Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 6: 238. 1885 ≡ [***Andropogon contortus*** subvar. ***roxburghii*** (Nees) Hack. in

Monographiae Phanerogamarum 6: 586–587. 1889, nom. illeg. hom.] — **Lectotype (designated here)**: India, Madras, September 1836, *R. Wight 2321* (K barcode K000245938!; isolectotype: NSW barcode NSW830730!).

= ***Andropogon besukiensis*** Steud. in Synopsis Plantarum Glumacearum 1: 367. 1854 ≡ ***Heteropogon besukiensis*** (Steud.) Miq. in Flora van Nederlandsch Indië 3: 494. 1857 — Holotype: Indonesia, Java, Besukie, Mount Arak-Ak, 5 April 1845, *H. Zollinger 2770* (P barcode P00745743!; isotype: P barcode P00745742!).

= ***Andropogon hohenackeri*** Hochst. ex Steud. in Synopsis Plantarum Glumacearum 1(4-5): 368. 1854 — **Lectotype (designated here)**: India, Tamil Nadu, Nilagiri, near Arangadu, 1847, *R. F. Hohenacker 1286* (G barcode G00165916!; isotypes: G barcode G00165917!, W barcode W0028300!)

= ***Andropogon hispidissimus*** Hochst. ex Steud. in Synopsis Plantarum Glumacearum. 1: 367. 1855 ≡ [***Heteropogon hispidissimus*** Hochst. ex A. Rich. in Tentamen Florae Abyssinicae 2: 453. 1850, nom. inval.] ≡ ***Andropogon contortus*** subvar. ***hispidissimus*** (Hochst. ex Steud.) Hack. in Monographiae Phanerogamarum. 6: 587. 1889 — Holotype: Ethiopia. Tigray, Gafta, 18 September 1838, *G. W. Schimper 1219* (P barcode P00446182!; isotypes: E barcode E00200291!, G barcode G00022293!, K barcode K000280099!, MO barcode MO-1742009!, TUB barcode TUB006325!, TUB006324!).

= ***Heteropogon contortus*** var. ***distichus*** C.E.C. Fisch in Flora of the Presidency of Madras 10: 1742–1743. 1934 — Lectotype (designated by Siddabathula et al., 2020): India, Tamil Nadu, Kodaikanal, Pulneys, Jesmond hill, 1 July 1901, *Bourne 2026* (K barcode K000245942!; isolectotypes CAL barcode CAL0000002306, MH barcode MH00002609).

= ***Heteropogon fischerianus*** Bor in Kew Bulletin 6(2): 170. 1951, **synon. nov**. — Holotype: India, Tamil Nadu, Kodaikanal, Pulneys (Palani), Jesmond Hill, 1 July 1901, *Bourne 2025* (K barcode K000245941!; isotypes CAL barcode CAL0000002320, G barcode G00165923, US barcode US00132611).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* absent. *Culms* erect, caespitose, intravaginal growth (branched), glabrous, 12–150 cm long, 0.15–2.56 mm thick. *Leaf sheaths* glabrous or sparsely hairy, keeled, 2.0–10.3 cm long. *Ligules* truncate, ciliolate, 0.1 cm long. *Leaf blades* phyllotaxy occasionally appearing spiral, plicate, abaxial and adaxial surfaces scabrid but occasionally glabrous, lanceolate, margin scabrid, apex obtuse or acuminate, 3.5–29(–30) cm long, (0.2–)0.3–0.8 cm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, racemes solitary, 2.0–7.0 cm long. *Spatheoles* wrapped around peduncle, surface glabrous, lanceolate, 1.2–16.2 cm long. *Rachis internodes* fragile at the node, pilose with white hairs at the base, linear, oblique at the apex, 0.1–0.2 cm long. *Racemes* solitary, 8–26 sterile spikelets, 8–16 fertile spikelets, 4.6–7.5 cm long (excluding awns). *Triad* absent. *Homogamous pairs* spikelets 6–34 in number, male or barren, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 0.5–1.0 cm long, 0.1–0.2cm wide; callus cuneate, lanceolate, pilose with yellowish brown hairs, attached obliquely, 0.20–0.25 cm long; lower glume glabrous or hairy with tubercled long white hairs, chartaceous, ovate or lanceolate, margins entire and partly enclose upper glume, apex obtuse (pedicelled) or acute (sessile), ca. 0.6 cm long, ca. 0.15 cm wide; upper glume glabrous, chartaceous, lanceolate, margin with fringed, apex acute, slightly shorter than the lower glume; lower lemma linear or ovate, membranous, margin fringed on the top, apex truncate, 0.40–0.80 cm long, < 0.1–0.1 cm wide; upper lemma lanceolate, membranous, margin fringed on upper half, apex truncate, 0.25–0.80 cm long, < 0.1–0.1 cm wide; palea absent, lodicules 2, cuneate, coriaceous, < 0.1 cm long. *Fertile pairs* female and barren, separately deciduous from homogamous spikelets, 7– 12 fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelet, well-developed, female, lanceolate, 0.4–0.7 cm long, < 0.10–0.15 cm wide; callus linear, pungent, curved, pilose with brown hairs, attached obliquely, 2–3 cm long; lower glume hirsute with short stiff hairs, coriaceous, elliptic-oblong, margin partly covering upper glume, apex obtuse or round, 1 spikelet long; upper glume hirsute with yellowish brown hairs in grooves, coriaceous, linear, margin entire, apex obtuse, 0.4–0.5 cm long, 0.5–0.6 mm wide; lower lemma lanceolate, membranous, margin entire, apex round, 2.0–3.0 mm long, 0.6–0.7 mm wide; upper lemma minute, linear, membranous, attached to the base of awn; palea absent, lodicules 2, cuneate, coriaceous, minute, companion spikelets deciduous with the fertile spikelet, pedicelled, well-developed, male, lanceolate, 0.5–1.5 cm long, 0.13–0.20 cm wide; callus glabrous, linear, 0.15 cm long; lower glume glabrous, chartaceous, lanceolate, margins partly enclose upper glume, apex acuminate, 1 spikelet wide and long; upper glume glabrous, chartaceous, lanceolate, margins inflexed and entire, apex acuminate, 0.75–0.9 cm long, 0.8–1.0 mm wide; lower lemma membranous, lanceolate, margin inflexed and ciliate, apex subacute, 0.50–0.85 cm long, 0.6–1.0 mm wide; upper lemma membranous, lanceolate, margin ciliate, apex obtuse, 0.4–0.8 cm long, 0.6–1.0 mm wide; palea membranous, oblong or lanceolate, < 0.1–0.25 cm long, < 0.1 cm wide, lodicules 2, cuneate, coriaceous, < 0.1 cm long. *Awn* present, geniculate, column twisted and pubescent, 5.0–9.2(–10) cm long, 0.30–0.36 cm wide. *Anthers* 3, 0.2–0.4 cm long. *Ovary and Stigma* ovary 1 < 0.1–0.1 cm long; stigmas 2, plumose. *Caryopsis* 0.25–0.50 cm long, 0.37–0.74 mm wide.

Etymology. – The specific epithet '*contortus*' refers to twisted hygroscopic awns when the plants are dry.

Vernacular names. – Huang mao (黄茅; Chinese name), spear grass (English name), Sarwala, Abdarka, Kursali (Pakistani names), Kali Kusali, Nanisunkhali, Pandhri Sukal (India), Oosipullu; Pani pullu; Karunsi pullu (Tamil Nadu, India), Ya nuad ruesi (หญ้าหนวดฤาษี; Thai name).

Geographic distribution. – *Heteropogon contortus* is distributed throughout the tropics, subtropics, and some parts of the temperate zones in Austria, China, France, Italy, Japan, and Switzerland. See distribution map in Appendix XV.

Phenology. – *Heteropogon contortus* flowers throughout the year as investigated from herbarium specimens.

Habitat & Ecology – This species occurs wide range of habitats, especially savanna-type habitats in Africa, America, Asia, and Australia. It is also found in open areas in the Mediterranean. In addition, nutrient-poor and arid habitats (e.g., rock outcrops) provide sub-optimal conditions for *H. contortus*. *Heteropogon contortus* co-occurs with other grasses, forbs, and trees in natural habitats. It is associated with congeneric species *H. triticeus* and other C_4 savanna grass genera such as *Hyparrhenia* (e.g., *H. diplanda*), *Themeda* (e.g., *Themeda anathera* and *Themeda triandra*), and *Cymbopogon* (e.g., *Cymbopogon flexuosus*). *H, contortus* is distributed in various savanna types such as *Acacia* savannas, Chir pine savannas, *Melaleuca* savannas, *Dipterocarp* savannas, and *Pinus merkusii* savannas. *Heteropogon contortus* is considered a species occupying wide precipitation regimes (Arthan et al., 2022) from arid (e.g., Oman and Yemen) to very wet regions (e.g., India and Southeast

Asia). Preadaptation to drought of *H. contortus* is reflected in morphology, anatomy, and physiology (Wang et al., 2016).

Phylogenetic position and morphological evolution. – Phylogenetic position of *H. contortus* is placed as an early-diverging species of *Heteropogon-Themeda* lineage and most closely related to *H. triticeus* (Arthan et al., 2021). *Heteropogon contortus* has been known to be the only species that expresses andromonoecy with male homogamous spikelets and female fertile spikelets (Malcomber & Kellogg, 2006) in the group. Variations in hairiness separate hairless temperate populations of *H. contortus* from haired tropical populations. However, the functionality of hairiness in relation to climate remains unknown.

Cytogenetics. – High variation in ploidy levels is documented for *Heteropogon contortus*, ranging from diploid (2n = 20) to nanoploid (2n = 90) (Tateoka, 1965; Tothill & Hacker, 1976). Ploidy levels are hypothesized to be associated with separate distributions of tropical and temperate populations. In addition, diploid individuals sexually reproduce whereas higher ploidy ones use the apomictic mode of reproduction (Emery & Brown, 1958).

Uses and ethnology. – *Heteropogon contortus* is of ecological importance such as phytoremediation and habitat restoration (Long et al., 2021). It is also known as promising source of fiber rich materials (Hyness et al., 2017).

Specimens examined. – Please see full list of specimens examined in Appendix XIV A.

Note. – Here, we treated *Heteropogon allionii,* described as separate species by Drisya & Pradeep (2020), and *Heteropogon fischerianus* as synonyms of *Heteropogon contortus*. Drisya & Pradeep (2020) specified the illustration of *Andropogon contortum* Allionii in Flora Pedemontana (1785: Tab. 91. Fig. 4) as the holotype. Although a scientific illustration is valid to be chosen as a holotype, we found that dried specimens should supplement the illustration. Here, we epitypified a type specimen from K herbarium as the epitype of *Heteropogon allionii*.

Heteropogon polystachyos (Roxb.) Schult. in Mantissa 2: 460. 1824 ≡ ***Andropogon polystachyos*** Roxb. in Flora Indica; or descriptions of Indian Plants 1: 265. 1820 ≡ [***Heteropogon polystachyos*** (Roxb.) Nees in Flora Brasiliensis seu Enumeratio Plantarum 2(1): 364. 1829, nom. inval.] ≡ ***Andropogon contortus***

subvar. ***polystachyos*** (Roxb.) Hack. in Monographiae Phanerogamarum 6: 588. 1889 ≡ ***Heteropogon contortus*** var. ***polystachyos*** (Roxb.) Deshp. in Bulletin of the Botanical Survey of India 30(1-4): 121. 1988 — **Lectotype (desginated here)**: India, Peninsula of India, *W. Roxburgh 2020* (K barcode K000246128!).

Description. – *Habit* annual. *Rhizome* absent. *Stilt root* absent. *Culm* erect, caespitose, glabrous, 15─25 cm long. *Leaf sheath* glabrous or occasionally hairy, 5 cm long. *Ligule* truncate, ciliolate, < 0.1 cm long. *Leaf blades* plicate, abaxial and adaxial surfaces hairy, lanceolate, apex acuminate, 5─10 cm long, 0.2─0.5 cm wide. *Inflorescences* terminal, inflorescence paniculate. *Spatheoles* glabrous, lanceolate. *Rachis internodes* fragile. *Racemes* compound, 2.0─2.5 cm long (excluding awns). *Triad* absent. *Homogamous pairs* spikelets male, a pair arranging at different levels, separately deciduous from fertile pairs, sessile spikelets similar to the pedicelled ones, well developed, lanceolate; callus glabrous; lower glume glabrous, chartaceous, lanceolate, apex acuminate; upper glume glabrous, chartaceous, lanceolate, shorter than the lower glume; lower lemma lanceolate, membranous; upper lemma membranous; lodicules 2, coriaceous, < 0.1 cm long. *Fertile pairs* female or barren, deciduous entirely, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, 0.50–0.65 cm long, 0.4–0.5 mm wide; callus broadened at the apex, pungent, pilose with dark brown hairs; lower glume hirsute with brown hairs, coriaceous, linear to narrowly oblong, margins partly enclosed upper glume, apex obtuse or round, 0.53–0.55 cm long, 0.5–0.7 mm wide; upper glume glabrous, coriaceous, narrowly obovate, margin entire, apex apiculate, 0.50–0.55 cm long, 0.6–0.7 mm wide; lower lemma glabrous, membranous, ovate, margin entire, apex acute, 0.13–0.15 cm long, 0.3–0.4 mm wide; upper lemma linear, membranous, attached to the base of awn, 0.35–0.40 cm long; palea absent; lodicules absent, companion spikelets, pedicelled, well developed, male, lanceolate, hairy on the margin, 0.55─0.60 cm long, 0.10─0.12 cm wide; callus linear; lower glume glabrous, chartaceous, narrowly elliptic-ovate, margins keeled and partly enclose upper glume, apex acute, 0.55─0.60 cm long, 0.10─0.12 cm wide; upper glume glabrous, chartaceous, narrowly ovate, margins inflexed and ciliate, apex acuminate, 0.53─0.58 cm long, 0.6─0.7 cm wide; lower lemma membranous, narrowly elliptic-ovate, margins ciliate, apex obtuse or round, 0.26─0.28 cm long, 0.5─0.6 mm wide; upper lemma oblong, membranous, < 0.1-0.1 cm long; palea absent; lodicules 2, cuneate, coriaceous, very tiny. *Awn* present, geniculate, column twisted, 4─5 cm long, 0.24─0.28 mm thick, *Anthers* 3, 0.13─0.15 cm long. *Ovary and Stigma* ovary 1; stigmas 2, plumose. *Caryopsis* 0.35─0.40 cm long, 0.5─0.6 mm wide.

Etymology. – The specific epithet '*polystachyos*' is derived from two Greek terms, 'polys' meaning many and 'stachys' meaning spike. This describes multiple racemes borne on the same branches which is different from the other two *Heteropogon* species.

Vernacular names. – No vernacular name for this species

Phenology. – July to November

Geographic distribution. – Endemic to India in Andaman & Nicobar Islands, Andhra Pradesh, Gujarat, Jharkhand, Maharashtra, and Telangana States.

Habitat & Ecology. – *Heteropogon polystachyos* can be found in open grasslands and dry deciduous savannas.

Phylogenetic position and morphological evolution. – No molecular data provided for *H. polystachyos* due to old materials.

Cytogenetics. – No cytogenetic data provided for *H. polystachyos*

Uses and ethnology. – No use data provided for *H. polystachyos*

Specimens examined. – **INDIA. Telangana State:** Kinnerasani Wildlife Sanctuary, Chatakonda Range, Gattumalla South Section and Beat, 17°39.003' N 80°36.138' E, 166 m, 15 November 2020, *J. Swamy 10868* (BSID).

Note. – Deshpande (1988) specified that the holotype of *H. polystachyos* was deposited in CAL; however, no record of type specimens could be found from the India Virtual Herbarium. Therefore, we designate the isotype of this species deposited at K herbarium as the lectotype.

Heteropogon triticeus (R.Br.) Stapf ex Craib in Bulletin of Miscellaneous Information, Royal Botanic Gardens, Kew 10: 432. 1912 ≡ ***Andropogon triticeus*** R. Br. in Prodromus Florae Novae Hollandiae 201. 1810. ≡ ***Sorghum triticeum*** (R. Br.) Kuntze in Revisio Generum Plantarum 2: 792. 1891 — Lectotype (designated by Siddabathula et al., 2020): Australia, East Coast, Carpentaria, Groote Eylandt, *R.*

Brown 6179 (BM barcode BM000991834; isolectotypes: BM barcodes BM000991830, BM000991829, BM000991831, BM000991833, BM000991832, E barcode E00691889, E00691888, E00691890, K barcodes K000911722!, K000911720!, K000911721!, P barcodes P00745740, P00745741, MEL barcode MEL1547816).

= ***Andropogon ischyranthus*** Steud. in Synopsis Plantarum Glumacearum 1: 367. 1855 ≡ ***Heteropogon ischyranthus*** (Steud.) Miq. in Flora van Nederlandsch Indië 3: 493. 1857 — **Lectotype (designated here)**: The Philippines, Luzon, Pangasinan, 1841, *Cumming 1003* (K barcode K000290016!; isotypes: K barcodes K000911724!, K000911723!, L barcode L0044510!, P barcode P00745739).

= ***Andropogon lianatherus*** Steud. in |Synopsis Plantarum Glumacearum 1: 367. 1854 ≡ ***Heteropogon lianatherus*** (Steud.) Miq. in Flora van Nederlandsch Indië 3: 493. 1857 — Holotype: Indonesia, Sulawesi, Maros, *H. Zollinger 1060* (P barcode P00745737!; isotype: GH barcode GH00091564!).

= ***Andropogon segaenensis*** Steud. in Synopsis Plantarum Glumacearum 1: 367. 1854 ≡ [***Heteropogon roylei*** Nees ex Steud. in Synopsis Plantarum Glumacearum 1: 367. 1854, nom. inval.] — Holotype: India, *s.d.*, October 1826, *Wallich* [Numer. List 8801] (K barcode K000245945!).

= ***Heteropogon insignis*** Thwaites in Enumeratio Plantarum Zeylaniae 5: 437. 1864 — **Lectotype (designated here)**: Sri Lanka, Mahning-galla, Matelle East, 1863, *G. H. K. Thwaites 3804* (K barcodes K000245945!; isotypes: BR barcode BR0000006862312!, K barcode K000245943!, K000245944!, GH barcode GH00023813!, P barcode P00745736!, W barcode W18890243747!, W19160028832!).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* absent. *Culms* erect, caespitose, glabrous, 100–300 cm long, 0.27–1.06 cm wide. *Leaf sheath* glabrous or occasionally hairy, 5.1–20.0 cm long. *Ligules* truncate, eciliate, 0.1 cm long. *Leaf blades* non-plicate, abaxial and adaxial surfaces glabrous or occasionally velvety, midrib widened, lanceolate, margin scabrid, apex attenuate, 20–80 cm long, 0.3–1.1 cm wide. *Inflorescences* axillary and terminal, inflorescence paniculate. *Spatheoles* pubescent on adaxial surface, lanceolate, 3.3–5.5 cm long. *Rachis internodes* fragile, hairy with yellowish brown hairs, cuneate, attached obliquely,

< 0.1-0.10 cm long. *Racemes* solitary, 27–51 sterile spikelets, 5–11 fertile spikelets, 8–20 cm long (excluding awns). *Triads* absent. *Homogamous pairs* spikelets 16–46 in number, male, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, asymmetrical, lanceolate, separately deciduous from fertile pairs, 1.30–2.20 cm long, 0.20-0.35 cm wide; callus cuneate, glabrous, attached obliquely, < 0.1 cm long; lower glume glabrous, coriaceous, lanceolate, margins entire and partly enclose upper glume, apex obtuse, 1 spikelet long; upper glume glabrous, coriaceous, lanceolate, margin fringe, apex acuminate, shorter than the lower glume, 0.9–1.8 cm long, 0.1–0.2 cm wide; lower lemma lanceolate, membranous, margin entire, apex acuminate, 0.8–1.5 cm long, 0.1–0.15 cm wide; upper lemma lanceolate, membranous, apex acuminate, 0.75–1.10 cm long, < 0.1 cm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1–0.1 cm long. *Fertile pairs* bisexual or barren, deciduous entirely, comprising 5–11 pairs of spikelets, fertile spikelets different from pedicelled ones, sessile spikelet, well developed, bisexual, linear, 0.60–1.10 cm long, about 0.1 cm wide; callus linear, hairy with brown hairs, attach obliquely, 0.45–0.60 cm long; lower glume densely pubescent with tawny hairs, coriaceous, lanceolate, two-grooved beside midvein, margins partly enclosed upper glume, apex obtuse, 1 spikelet long and wide; upper glume densely pubescent with tawny hairs, coriaceous, oblong, margin membranous, apex obtuse, 0.75–0.90 cm long, 0.13–0.14 cm wide; lower lemma lanceolate, membranous, margin entire, apex acuminate, 0.45–0.50 cm long, 0.6–0.7 mm wide; upper lemma membranous, linear, attached at the base of awn, minute; palea membranous, ovate-oblong, 0.20–0.26 cm long, 0.10–0.12 cm wide, apex ciliate; lodicules 2, cuneate, coriaceous, < 0.1–0.1 cm long, companion spikelets, pedicelled, well developed, male, hairy on the margin, asymmetrical lanceolate, 1.2–2.9 cm long, 0.3-0.4 cm wide; callus pubescent with dark brown hairs, linear, 0.2–0.3 cm long; lower glume glabrous, coriaceous, lanceolate, margins partly enclose upper glume, apex acuminate, 2.0–2.6 cm long, 0.40–0.45 cm wide; upper glume glabrous, coriaceous, lanceolate, margin inflexed and ciliate, apex acuminate, shorter than the lower glume, 0.16–0.36 cm long, 0.18–0.20 cm wide; lower lemma membranous, lanceolate, margin ciliate, apex acuminate, 1.30–1.85 cm long, 0.15–0.20 cm wide; upper lemma membranous, oblong, margins ciliate, apex acuminate, 1.0–1.5 cm long, 0.10–0.20 cm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1–0.1 cm long. *Awn* present, geniculate, column twisted and hirtellous, 7.4–14.8 cm long, 0.52–0.76 mm thick. *Anthers* 3, 0.5–1.2 cm long. *Ovary and Stigma* ovary 1, 0.15–0.30 cm long; stigmas 2, plumose. *Caryopsis* 0.5–0.7 mm long, 0.95–1.60 mm wide.

Etymology. – The specific epithet ‘triticeus’ refers to a resemblance of the inflorescences between *H. triticeus* and *Triticum* species.

Vernacular names. – Mai huang mao (麦黄茅; Chinese names), giant speargrass (English names), bhale kusal, patang (Indian names); ya nong (Thai names).

Phenology. – Flowering period spans from September to July. According to specimen examinations, Indian and Southeast Asian populations flower from September to December while phenological time of most Indonesian and Australian ones is from March to May.

Geographic distribution. – *Heteropogon triticeus* is distributed from India and Sri Lanka through Southeast Asia to Northeastern Australia and New Guinea. In Indonesia, this species only exists in Java, Lesser Sunda Islands, and Sulawesi.

Habitat & Ecology. – Open grasslands (Neldner et al., 1997) and different kinds of savannas, for example, pine savannas, dry deciduous savanna with *Dipterocarpus* spp. as dominant species (Ratnam et al., 2016), broadleaved woody savannas with *Corymbia* spp. (e.g., *C. tessellaris*) and *Eucalyptus* spp. (e.g., *E. miniata* and *E. tetrodonta*), and *Melaleuca* woodlands. Habitat preferences indicated that *H. triticeus* grows in highly precipitated regions (1400–1700 mm/year) with well-drained red loams but can also tolerate in the drier end of precipitation spectrum (e.g., sand dune). The abundance of *H. triticeus* depends on frequent fires (Williams et al., 2003). *H. triticeus* also co-occur with other C_4 Andropogoneae grasses such as *Heteropogon contortus*, *Hyparrhenia* spp., and *Themeda triandra*. In addition, *H. triticeus* provide seeds for native finches and rabbit-rat in Australia (Dostine et al., 2001, Firth et al., 2004).

Phylogenetic position and morphological evolution. – phylogenetic reconstructions based on nuclear-wide genes placed *H. triticeus* as a sister species of *H. contortus*. However, phylogenetic position of *H. triticeus* in plastome trees show more affinity with *Cymbopogon* spp. *H. triticeus* show primitive morphology as observed in *H. contortus* such as numerous homogamous spikelets and spikelet pairs.

Cytogenetics. – Pritchard & Gould (1964) documented hexaploidy (2n = 60) in Indian populations. This evidence might imply polyploid origin of this species, which requires more populations and data from orthologous markers to understand the origin polyploidization events.

Uses and ethnology. – No use data provided for *H. triticeus*.

Specimens examined. – Please see full list of specimens examined in Appendix XIV B.

Note. – Lectotypification of *Andropogon ischyranthus* Steud. was done in this study as the holotype was lost but the description was already provided for the taxa and one of isotypes was selected to replace the previous holotype.

Themeda anathera (Nees) Hack. in Monographiae Phanerogamarum 6: 669. 1889 ≡ ***Anthistiria anathera*** Nees in Synopsis Planatarum Glumacearum 1: 402. 1854 ≡ ***Androscepia anathera*** (Nees) Andersson in Nova Acta Regiae Societatis Scientiarum Upsaliensis, ser. 2 2: 249. 1856 — Holotype: India, Begala, November 1848, *N. Wallich 8773* (K barcode K000245971!; isotypes: G barcode G00176485!).

= *Themeda dacruzii* Birari in Journal of the Bombay Natural History Society 70(2): 346. 1973 — Holotype: India, Uttar Pradesh State, Dehra Dun, Mussoorie hill, 17 December 1969, *S. P. Birari I. 774* (FCP barcode unknown; isotypes: BSI barcode unknown, CAL barcode CAL0000002332!).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* absent. *Culms* erect, geniculately ascending from the base, caespitose, glabrous, 24–122 cm long, 0.60–1.98 cm wide. *Leaf sheaths* glabrous, 2.0–7.6 cm long. *Ligules* truncate, eciliate, < 0.1 cm long. *Leaf blades* non-plicate, abaxial surface glabrous to fairly hairy, adaxial surfaces glabrous to densely hairy, lanceolate, margin slightly scabrid, apex acuminate, 7–38 cm long, 0.2–0.4 cm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, 20–30 cm long. *Spatheoles* glabrous, lanceolate, 1.1–2.4 cm long. *Rachis internodes* tough, glabrous to hairy with white hairs, straight or slightly broadened at the apex, < 0.1–0.20 cm long. *Racemes* solitary, 7–9 sterile spikelets, 2–4 fertile spikelets, 0.9–1.4 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at different levels, deciduous with fertile pairs, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 0.45–0.75 cm long, 0.10–0.15 cm wide, larger than fertile pairs; callus linear broadened at the apex, glabrous, attached obliquely, < 0.1 cm long; lower glume pilose with white tuberculate hairs on the margin or all over, coriaceous, lanceolate, margins partly enclose upper glume, apex acuminate, 1 spikelet long and wide; upper glume glabrous, coriaceous, lanceolate, margin membranous keels, apex acute, shorter than the lower glume, 0.70─0.75 cm long, about 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin entire, apex acute, 0.35─0.50 cm long, < 0.1 mm wide; upper lemma glabrous, membranous, oblong, margin entire, apex acute, 0.1─0.2 cm long, < 0.1 mm wide; palea minute or absent; lodicules 2, cuneate, coriaceous, < 0.1 cm long. *Fertile pairs* bisexual and barren, deciduous entirely, 2─4 fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, 0.45─0.75 cm long, about 0.10 cm wide; callus linear, slightly broadened at the apex, hirsute at the top with tiny barbs, attach obliquely, < 0.1─0.1 cm long; lower glume glabrous, coriaceous, elliptic oblong, margins partly enclosed upper glume, apex obtuse, 1 spikelet long and wide; upper glume glabrous, coriaceous, oblong, apex obtuse, shorter and narrower than the lower glume, 0.35─0.60 cm long, about 0.1 cm wide; lower lemma lanceolate, membranous, margin inflexed, apex acute, 0.25─0.45 cm long, less than 1.0 mm wide; upper lemma oblong, membranous, margin entire, apex acute, < 0.1─0.2 cm long, < 0.1 mm wide; palea minute or absent; lodicules 2, cuneate, coriaceous, < 0.1 am long, companion spikelets, pedicelled, well developed, male or barren, lanceolate, 0.45─0.75 cm long, 0.10─0.15 cm wide; callus glabrous, linear, < 0.1 cm long; lower glume surfaces glabrous, hairy on the margin, coriaceous, lanceolate, margins partly enclose upper glume, apex acuminate, 1 spikelet long and wide; upper glume glabrous, coriaceous, lanceolate, margin inflexed and entire, apex acuminate, shorter than the lower glume, 0.40─0.75 cm long, < 0.1 mm wide; lower lemma membranous, lanceolate, margin entire, apex obtuse, 0.30-0.55 cm long, < 0.1 mm wide; upper lemma membranous, oblong, margin entire, apex obtuse, < 0.1-0.1 cm long, < 0.1 mm wide; palea absent; lodicules 2, cuneate, coriaceous, < 0.1 cm long. *Awn* absent, *Anthers* 3, 0.15─0.40 cm long. *Ovary and Stigma* ovary 1, < 0.1-0.15 cm long; stigmas 2, plumose. *Caryopsis* 1.00-3.27 mm long, 0.88-1.04 mm wide.

Etymology. – The specific epithet ‘anathera’ is composed of the word ‘ather’ meaning ‘without’, which describes a lack of awns in the racemes.

Vernacular names. – Loonder (English name), Liu jian (瘤菅; Chinese name), Bahari grass (Pakistan), Saryala Ghas (Pakistan)

Geographic distribution. – Distribution ranges cover Afghanistan and countries in Himalayan Mountain Ranges such as Pakistan, India, and Nepal.

Phenology. – July to November and occasionally in March.

Habitat & Ecology. – *Themeda anathera* exist at high elevation from 1200 to 1650 m above sea level in Subtropical pine savanna dominated by *Pinus roxburghii*, shrubland dominated by plants in genus *Carissa*, *Dodonaea*, *Myrsine*, and *Olea*, and high-altitude grasslands. Associated species in natural habitats indicated that *Themeda anathera* occupy xeric conditions.*Themeda anathera* coexist with *Arundinella* spp., *Bothriochloa* spp., *Chrysopogon* spp., *Heteropogon contortus*, *Ischaemum* spp., and *Themeda triandra*. This species provides nutritious fodder to native grazers at young stage.

Phylogenetic position and morphological evolution. – Phylogenetic position of *Themeda anathera* is among early-diverged *Themeda* species. In general, it possesses 3 pairs of fertile spikelets and less complex branching patterns.

Cytogenetics. – Birari (1980) documented diploid (2n = 20) and hexaploidy (2n = 60) varieties of *Themeda anathera*. The two ploidy varieties have different reproductive modes, sexual in diploid and facultative apomictic in hexaploidy. Morphologically, hexaploid plants have larger spikelets and hairier than the diploid ones.

Uses and ethnology. – *Themeda anathera* showed promising fodder grass for cattle due to high nutritive values (Bohra et al., 2008). Majeed et al. (2020) documented ethno-veterinary uses of *Themeda anathera* as refrigerant and blood purifier.

Specimens examined. – Please see full list of specimens examined in Appendix XIV C.

Note. – Specimens barcodes for the holotype of *Themeda dacruzii* cannot be accessed as no online database for FCP herbarium is not available.

Themeda arguens (L.) Hack. in Monographiae Phanerogamarum. 6: 657. 1889 ≡ ***Stipa arguens*** L. in Species Plantarum, Second Edition. 117. 1762 ≡ ***Anthistiria arguens*** (L.) Willd. in Species Plantarum, Forth Edition. 4: 901. 1806 ≡ ***Anthistiria ciliata*** Naezén var. ***major*** Thwaites in Enumeratio Plantarum Zeylaniae 366. 1864. ≡

Themeda forskalii Hack. var. ***major*** (Thwaites) Hack. in Monographiae Phanerogamarum. 6: 662. 1889 — Lectotype (designated by Merrill in Interpr. Herb. Amboin. 89. 1917): India, s.d., *J. Burman s.n.* (LINN barcode LINN 94.10!; epitype: K barcode K000911716).

= ***Anthistiria frondosa*** R.Br. in Prodromus Florae Novae Hollandiae. 1: 200. 1810 ≡ ***Themeda frondosa*** (R. Br.) Merr. in Dept. Agric. Nat. Res. Bur. Sci. Manila Publ. 9: 89. 1917 — Lectotype (designated by Veldkamp in Blumea 61: 32. 2016): Australia, *s.d.*, 24 February 1803, *R. Brown 6195* (BM barcode BM000991835!; isolectotypes: CANB barcode CANB378500.1!, E barcode E00393613!, K barcode K000911785!).

= ***Aristaria barbata*** Jungh. in Tijdschrift voor Natuurlijke Geschiedenis en Physiologie 7: 297. 1840 — **Type not found.**

= ***Anthistiria ciliata*** Naezén var. ***glabrescens*** Buse. in Plantae Junghuhnianae 3: 23. 1854 — Holotype: Indonesia. Java, Mountain of Madinang (‘G Madinang’), *F. W. Junghuhn s.n.* (L barcode L0329847!).

= ***Anthistiria pilifera*** Steud. in Synopsis Plantarum Glumacearum 1: 400. 1855 ***Anthistiria ciliata*** L. in Linnaea 7: 284 – Lectotype (designated by Veldkamp in Blumea 61: 32. 2016): Indonesia, Java, *H. Zollinger 373* (K barcode K000290005!; isolectotypes: G barcode G00219998!, L barcode L0329854!)

= ***Anthistiria junghuhniana*** Nees var. ***altior*** Andersson in Nova Acta Regiae Societatis Scientiarum Upsaliensis, series 2. 2: 233. 1856 — **Lectotype (designated here)**: Indonesia. Java, on the cliffs of Mount Gunong Mandjesinang (‘ In rupibus montis Gunong Mandjesinang’), *F. W. Junghuhn s.n.* (L barcode L0329850!).

= ***Anthistiria junghuhniana*** Nees var. ***minor*** Andersson in Nova Acta Regiae Societatis Upsaliensis, series 2. 2: 233. 1856 — **Lectotype (designated here)**: Indonesia. Java, Tijbogo, *F. W. Junghuhn s.n.* (L barcode L0064860!; isolectotypes: L barcodes L0329851!, L0329852!, L0329853!).

= ***Themeda arguens*** (L.) Hack. var. ***balinensis*** Jansen in Acta Botanica Neerlandica.

1(3): 479. 1952 — Holotype: Indonesia, Bali, Timor, *van Steenis 7763a* (BO barcode BO1901668).

Description. – *Habit* annual. *Rhizomes* absent. *Stilt roots* absent. *Culms* erect, caespitose, glabrous, 28–175 cm long, 1.00–5.03 mm thick. *Leaf sheaths* glabrous, 2.6–11.4 cm long. *Ligules* truncate, eciliate, 1 mm long. *Leaf blades* non-plicate, abaxial and adaxial surface mostly glabrous to fairly hairy, lanceolate, margin slightly scabrid, apex acuminate, 4.5–72.5 cm long, 0.2–0.8 cm wide. *Inflorescences* axillary and terminal, inflorescence paniculate. *Spatheoles* hairy at the base and on the margin with non-tuberculate hairs, lanceolate, 2.20–5.40 cm long. *Rachis internodes* fragile, glabrous or pilose with white hairs, shape linear, attached obliquely, < 0.1 cm long. *Racemes* clustered, 6 sterile spikelets, 1 fertile spikelet, 0.9–1.6 cm long (excluding awns). *Triad* present. *Homogamous pairs* reduced to minute glumes surrounded by spatheoles, 4 in number, barren, a pair arranging at the same level, persistent, sessile spikelets similar to the pedicelled ones, reduced to glumes, lanceolate, 0.45–1.00 cm long, < 0.1–0.1 cm wide, about the same size as fertile pairs; callus straight, glabrous attached obliquely, < 0.1 cm long; lower glume glabrous, membranous, lanceolate, margin membranous and entire, apex acuminate, 1 spikelet long and wide; upper glume glabrous, membranous, lanceolate, margin entire, apex acuminate, about the same size as the lower glume; lower lemma absent, upper lemma absent, palea absent; lodicules absent. *Fertile pairs* bisexual and barren, deciduous entirely, no fertile pairs (only triad present), fertile spikelets different from pedicelled ones, sessile spikelet, well developed, bisexual, elliptic, 0.55–0.80 cm long, 0.1–0.2 cm wide; callus linear, pilose with yellow to reddish brown hairs, attach obliquely, 0.15–0.45 cm long; lower glume hispidulous at the top, coriaceous, elliptic, margins partly enclosed upper glume, apex obtuse, 1 spiketlet long and wide; upper glume hirsute with short hairs on the top half, coriaceous, oblong, margin membranous and entire, apex obtuse, slightly shorter and narrower than the lower glume, 0.50–0.60 cm long, < 0.1–0.1 cm wide; lower lemma ovate, membranous, margin and entire, apex truncate, 0.25–0.35 cm long, 0.1–0.2 cm wide; upper lemma attached to awn, only a remnant; palea absent; lodicules absent, companion spikelets glabrous, pedicelled, well developed but mostly reduced to a single glume, barren, lanceolate, 0.55–1.00 cm long, < 0.1–0.1 cm wide; callus glabrous, linear, apex truncate, 0.2–0.3 cm long; lower glume glabrous, chartaceous, lanceolate, margins partly enclose upper glume, apex acuminate, 0.30–0.85 cm long, < 0.1–0.1 cm wide; upper glume glabrous, chartaceous, lanceolate, margin entire, apex acuminate, shorter than the lower glume, 0.70, cm long, < 0.1 cm wide; lower lemma absent; palea absent; lodicules absent. *Awn* present, geniculate, column twisted and hispidulous, 5.2-11.6

cm long, 0.37-0.70 mm long. *Anthers* 3, 0.1-0.2 cm long. *Ovary and Stigma* ovary 1, 0.1-0.2 cm long; stigmas 2, plumose. *Caryopsis* 0.30-0.50 cm long, 0.84-1.24 mm wide.

Etymology. – The specific epithet 'arguens' is from Latin word 'arguo' meaning the exposure of a flaw.

Vernacular names. – Christmas grass or lesser tasselgrass (English), Rumput merak (Malay), Misai adam (Malay), Ya chao choo (หญ้าเจ้าชู้; Thai).

Geographic distribution. – *Themeda arguens* is distributed in India and Sri Lanka through Southeast Asia to Northern and Northeastern Australia and New Guinea. It is also thought to be introduced in the Caribbean and North America (POWO, 2022).

Phenology. – Flowering time spans from October to January in Mainland Southeast Asia. Yet, this species commonly flowers from April to June in Peninsula regions in Indonesia, Malaysia, and New Guinea.

Habitat & Ecology. – Seasonally inundated grasslands and dry deciduous savannas with *Vachellia nilotica* (*Acacia nilotica*) and *Ziziphus* spp. as dominant trees, and *Eucalyptus* savanna. Main habitats of *Themeda arguens* are characterized by high seasonality and it depends on high precipitation during warmest season (Fierro, 2014).

Phylogenetic position and morphological evolution. – *Themeda arguens* is closely related to *Themeda triandra* in the terminal clade of the *Heteropogon-Themeda* nuclear and plastome trees. *T. arguens* lacks spikelet pairs and shows autapomorphy that homogamous spikelets are reduced to single glumes.

Cytogenetics. – Only diploid populations (2n = 20) were detected in *T. arguens* (Dell'Acqua et al., 2014), but higher ploidy levels have not been observed.

Uses and ethnology. – The Temuan Tribe, a native tribe of Ayer Hitam Forest, Selangor, Malaysia, used decoction from *T. arguens* root as aphrodisiac, blood cleansing, and body refreshing and poultice to treat lumbago (Hanum & Hamzah, 1999). Yoneyama et al. (2017) found that methanol extracts from *T. arguens* yielded active compounds that are toxic to cancer cells and can inhibit tumor formation.

Specimens examined. – Please see full list of specimens examined in Appendix XIV D.

Note. – Lectotypifications were done with *Anthistiria junghuhniana* Nees var. *altior*, and *Anthistiria junghuhniana* Nees var. *minor* by designating isotypes from L herbarium as lectotypes. In addition, the epitype of *Stipa arguens* was deposited in K herbarium was found as stated in the specimens 'Represents same species as specimen in the Linnean Herbarium, written up as *Stipa arguens* by Linnaeus.' by Tom Cope on 12 November 1948.

Themeda arundinacea (Roxb.) A. Camus in Flore Gènèrale de l'Indo-Chine 17: 363. 1922 ≡ ***Anthistiria arundinacea*** Roxb. in Flora Indica; or descriptions of Indian Plants 1: 256–257. 1820 ≡ ***Cymbopogon anrundinaceus*** (Roxb.) Schult. in Systema Vegetabilum, edition decima sexta 457. 1824 ≡ ***Themeda gigantea*** (Cav.) Hack. subsp. & var. ***arundinacea*** (Roxb.) Hack. in Monographiae Phanerogamarum 6: 674. 1889 ≡ ***Anthistiria gigantea*** Cav. subsp. ***arundinacea*** (Roxb.) Hack. in Monographiae Phanerogamarum 6: 674. 1889 ≡ ***Anthistiria gigantea*** Cav. var. ***arundinacea*** (Roxb.) Hack. ex Ridl. in Materials for a Flora of the Malayan Peninsula 3: 169. 1907 — Holotype: Bangladesh, *W. Roxburgh s.n.* (BM barcode BM000959817; isotypes: BR barcode BR0000006885601!, BR0000006883508!, K barcode K000245976!).

= ***Anthistiria subsericans*** Nees ex Steud. in Synopsis Plantarum Glumacearum 1: 401. 1854 ≡ ***Anthistiria arundinacea*** Roxb. var. ***subsericans*** (Nees ex Steud.) Andersson in Nova Acta Regiae Societatis Scientiarum Upsaliensis 2: 245. 1856 ≡ ***Anthistiria gigantea*** (Cav.) Hack. subvar. ***subsericans*** (Nees ex Steud.) Hack. in Monographiae Phanerogamarum. 6: 674. 1889 ≡ ***Themeda gigantea*** (Cav.) Hack. var. ***subsericans*** (Nees ex Steud.) Hack. in Monographiae Phanerogamarum. 6: 674. 1889 ≡ ***Themeda arundinacea*** (Roxb.) A.Camus var. ***subsericans*** (Nees ex Steud.) E.G.Camus & A.Camus in Flore Générale de l'Indo-Chine. 7: 363. 1992 ≡ ***Themeda subsericans*** (Nees ex Steud.) Ridl. (1925:212) — Holotype: India, *N. Wallich 8774-B* (K barcode K000245977!)

= ***Anthistiria vulpina*** Andersson in Nova Acta Regiae Societatis Scientiarum Upsaliensis. 2(2): 245. 1856 ≡ ***Themeda gigantea*** (Cav.) Hack. var. ***vulpina*** (Andersson) Hack. in Monographiae Phanerogamarum. 6: 673. 1889 — Lectotype (designated by Veldkamp in Blumea 61: 29—41. 2016): The Philippines, Luzon, Cagayan Province, *H. Cumming* 1272 (L barcode L0329848!; isolectotypes: E barcodes E00697732!, E00697733!, L barcodes L0063980!, L0063981!, L0063982, S barcode S-G-10539!, S09-30525!, W barcode W1889-0167395!).

= ***Themeda intermedia*** (Hack.) Bor var. ***intorta*** Jansen in Acta Botanica Neerlandica. 1(3): 481. 1952 — Holotype: Indonesia, Borneo, Martapoera, Riam Kiwa, Pengaron, February 1938, *F. C. van Loenen 16* (L barcode L0050256!; isotypes: BO barcode BO1901669).

Description. – *Habit* perennial. *Rhizomes* absent. *Stilt roots* present. *Culms* erect, caespitose, glabrous, 100─600 cm long, 0.57─1.50 cm thick. *Leaf sheaths* glabrous, 5.0─23.5 cm long. *Ligules* truncate, ciliolate, 0.5─2 mm long. *Leaf blades* non-plicate, abaxial surface mostly glabrous to occasionally hairy with tubercled hairs, adaxial surfaces mostly glabrous to occasionally hairy with tubercled hairs, midrib white and widened, lanceolate, margin slightly scabrid, apex acuminate, 30─120 cm long, 1.0─1.5 cm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, 30─60 cm long. *Spatheoles* glabrous, lanceolate, 2.8─5.1 cm long. *Rachis internodes* fragile, densely pilose with tawny hairs, straight, 0.1─0.2 cm long. *Racemes* solitary, drooping, 6─7 sterile spikelets, 2─3 fertile spikelets, 1.7─3.3 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a psir arranging at different levels, persistent, sessile spikelets shorter the the pedicelled ones, well developed, lanceolate, 1.0─1.65 cm long (sessile) and 1.15─2.05 cm long (pedicelled), 0.1─0.2 cm wide (sessile) and 0.1─0.2 cm wide (pedicelled), slightly larger than fertile pairs; callus pilose with tawny hairs, square, < 0.1─0.1 cm long; lower glume densely pilose with tawny tuberculate hairs, coriaceous, lanceolate, margins partly enclose upper glume, apex acuminate, 1 spikelet long and wide; upper glume glabrous, coriaceous, lanceolate, margin inflexed and entire, apex acute, slightly shorter than the lower glume, 0.75─1.55 cm long, 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin ciliate at the top, apex acuminate, 0.85─1.35 cm long (sessile spikelets) and 0.90─1.35 cm long (pedicelled spikelets), 0.1 cm wide (sessile spikelets) and 0.1 cm wide (pedicelled spikelets); upper lemma glabrous, membranous, lanceolate, margin entire, apex acuminate, 0.65─1.20 cm long (sessile spikelets) and 0.65─1.10 cm long (pedicelled spikelets), < 0.1 cm wide (sessile spikelets) and < 0.1 cm wide (pedicelled spikelets); palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1─0.1 cm long. *Fertile pairs* bisexual and barren, deciduous entirely, 1-2 fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic oblong, 0.75─1.00 cm long, 0.20─0.25 cm wide; callus cuneate, densely pilose with tawny hairs, attach obliquely, about 0.2 cm long; lower glume densely pubescent with tawny hairs, coriaceous, oblong, margins partly enclosed upper glume, apex obtuse, 1 spikelet long and wide; upper glume pubescent with tawny hairs, coriaceous, linear oblong, margin entire and inflexed, apex obtuse, slightly shorter and narrower than the lower glume, 0.70─0.90 cm long, about 0.15─0.20 cm wide; lower lemma glabrous, membranous, lanceolate, margin entire, apex acuminate, 0.40─0.65 cm long, 0.15─0.30 cm wide; upper lemma glabrous, membranous, oblong, margin entire, apex obtuse, 0.5─0.7 cm long, < 0.1 cm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1─0.15 am long, companion spikelets, pedicelled, well developed, male or barren, lanceolate, 1.20─2.00 cm long, 0.1─0.2 cm wide; callus hirsute with short yellow hairs at the base, linear, 0.10─0.3 cm long; lower glume hairy with tawny hairs, chartaceous, linear lanceolate, margins partly enclose upper glume, apex acute, 1 spikelet long and wide; upper glume glabrous, chartaceous, linear lanceolate, margin membranous, inflexed, ciliate at the top half, apex acute, slightly shorter than the lower glume, 1.00─1.80 cm long, 0.1 cm wide; lower lemma membranous, lanceolate, margin inflexed and ciliate, apex acute, 0.80─1.20 cm long, 0.15─0.5 cm wide; upper lemma membranous, lanceolate, margin entire, apex acuminate, 0.6─1.1 cm long, 0.2─0.55 mm wide; palea absent; lodicules 3, cuneate, coriaceous, < 0.1─0.15 cm long. *Awn* present, geniculate, column twisted and hispidulous, 3.3─11.1 cm long, 0.39─0.60 mm thick. *Anthers* 3, 0.15─0.70 cm long. *Ovary and Stigma* ovary 1, 0.1─0.2 cm long; stigmas 2, plumose. *Caryopsis* 3.0-6.5 mm long, 0.59-1.33 mm wide.

Etymology. – The specific epithet ‘arundinacea’ is derived from Latin words ‘arundo’ standing for a reed and ‘acea’ meaning like. This specific epithet described tall stature resembling a reed.

Vernacular names. – Tanga-bon (Assamese), wei jian (韦菅; Chinese), Ulla grass (English), Hathi grass (Hindi), rumput riong (Malay), sbouv (Khmer), Hierba Tarlaquena (Spanish), Tanglar/Talac grass (Tagalog; the Philippines), Kaem Luang (Thai).

Geographic distribution. – Distribution ranges cover India, Himalayan regions, Southern China, most parts of Southeast Asia excluding Sulawesi and New Guinea.

Phenology. – August to January

Habitat & Ecology. – *Themeda arundinacea* mainly inhabit in places with high precipitation or inundate conditions such as wetland, riverine forest, mangrove, alluvial grasslands, floodplains. It also exists in some types of savannas with high precipitation such as Pek savannas with *Vietnamosasa pusilla* as a dominant understorey and moist sal savannas with *Shorea robusta* as a main tree. *Themeda arundinacea* is associated with other tall grass species that also require high precipitation in genera *Arundo*, *Imperata, Narenga*, *Phragmites*, and *Saccharum*.

Phylogenetic position and morphological evolution. – *Themeda arundinacea* was placed in the wetland group (Fig. 5.4). Wetland species resemble in morphology and can be distinguished by inflorescence architecture, glume hairiness, and awn characteristics. Major differences between wetland species and other species within the clade are presence of stilt roots and climatic characteristics.

Cytogenetics. – Birari (1980) reported that *Themeda arundinacea* has chromosome number 60 (hexaploidy), which implies hybridization and polyploidy origins of this species (Dunning et al., 2017).

Uses and ethnology. – *Themeda arundinacea* is highly edible for native grazers and used as fodder and thatching for huts as documented in Himalayan regions in oak- and pine-dominated zones (Arya et al., 2011; Rawat et al., 2010). This species was also documented for important source of basketry, fodder, paper, and thatching in Chitwan, Nepal (Dangol, 2002).

Specimens examined. – Please see full list of specimens examined in Appendix XIV E.

Themeda avenacea (F. Muell.) Maiden & Betche in A Census of New South Wales Plants 15. 1916 ≡ ***Anthistiria avenacea*** F. Muell. in Fragmenta Phytographiæ Australiæ 5: 206. 1866 ≡ ***Themeda gigantea*** var. ***avenacea*** (F. Muell.) Hack. in Monographiae Phanerogamarum 6: 667. 1889 ≡ [***Themeda avenacea*** (F. Muell.) Durand & Jackson in Index Kewensis 1: 424. 1906, nom. inval.] ≡ ***Themeda avenacea*** (F. Muell.) C.A. Gardner in Flora of Western Australia 1: 344. 1952 — Holotype: Australia, Queensland, Peak Downs, *F. J. H. von Mueller s.n.* (MEL barcode MEL0682767A!; isotypes: K barcodes K000911781!, K000911784!).

= ***Themeda gigantea*** var. ***latifrons*** Domin in Bibliotheca Botanica 85: 277. 1915 — Holotype: Australia, Queensland, Flinders River, February 1910, *Dr. K. Domin 891* (PR barcode PR524106!).

= ***Anthistiria basisericea*** F. Muell. in Fragmenta Phytographiæ Australiæ 5: 207. 1866 — **Type not found.**

Description. – *Habit* perennial. *Rhizomes* absent. *Stilt roots* absent. *Culms* erect, caespitose, intravaginal growth, glabrous, 70‒250 cm long, 1.60‒4.80 cm wide. *Leaf sheaths* butt sheath at the base silky or woolly, upper sheath glabrous, 5.1-12.8 cm long (upper sheath). *Ligules* truncate, eciliate, 2‒7 mm long. *Leaf blades* plicate, abaxial and adaxial surfaces scaberulous, covered with tiny white barbs, leaf blade tapering to the midrib, lanceolate, margin slightly scabrid, apex acuminate, 22‒84 cm long, 1.0‒4.0 cm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, 15‒100 cm long. *Spatheoles* enclosing peduncle, glabrous, lanceolate, 3.9‒7.9 cm long. *Rachis internodes* fragile, densely hairy with ivory hairs, linear, 0.1‒0.40 cm long. *Racemes* solitary, 6 sterile spikelets, 1 fertile spikelet, 2.3‒3.9 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 1.7‒2.9 cm long (sessile) and 1.7‒2.9 cm long (pedicelled), 0.15‒0.30 cm wide (sessile) and 0.15‒0.30 cm wide (pedicelled), larger than fertile pairs; callus glabrous, square, attached obliquely, 0.10‒0.15 cm long; lower glume glabrous, coriaceous, lanceolate, margins partly enclose upper glume, apex acuminate, 1 spikelet long and wide; upper glume glabrous, coriaceous, lanceolate, margin membranous and slightly ciliate, apex acuminate, as long as the lower glume, 1.0‒1.90 cm long, 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin ciliate, apex acute, 0.35‒0.90 cm long (sessile spikelets) and 0.10‒1.40 cm long (pedicelled spikelets), < 0.1 cm wide (sessile spikelets) and < 0.1 cm wide (pedicelled spikelets); upper lemma glabrous, membranous, lanceolate, margin membranous and slightly ciliate, apex acuminate, 0.80‒1.70 cm long (sessile spikelets) and 1.0‒1.5 cm long (pedicelled spikelets), < 0.1 cm wide (sessile spikelets) and < 0.10 cm wide (pedicelled spikelets); palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1‒0.25 cm long. *Fertile pairs* bisexual and barren, deciduous entirely, no fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, 0.65‒1.10 cm long, 0.20‒0.25 cm wide; callus linear, densely hairy with ivory hairs, attach obliquely, 0.40‒0.85 cm long; lower glume densely pubescent with ivory hairs, coriaceous, elliptic oblong, margins partly enclosed upper glume, apex obtuse, 1 spikelet long and wide; upper glume pubescent with ivory hairs, coriaceous, straight, apex obtuse, slightly shorter and narrower than the lower glume, 0.85‒1.05 cm long, 0.1 cm wide; lower lemma membranous, lanceolate, margin ciliate at the top, apex acuminate, <0.10‒0.60 cm long, 0.10 cm wide; upper lemma membranous, attached to awn, oblong, very minute; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1‒0.25 am long, companion spikelets, pedicelled, well developed, barren, lanceolate, 1.50‒2.80 cm long, 0.15‒0.25 cm wide; callus glabrous, linear, 0.15‒0.40 cm long; lower glume glabrous, coriaceous, lanceolate, margins partly enclose upper glume, apex acute, 1 spikelet long and wide; upper glume glabrous, coriaceous, lanceolate, slightly shorter than the lower glume, 1.40‒2.0 cm long, 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin inflexed and ciliate, apex acute, 0.95‒1.75 cm long, 0.1 cm wide; upper lemma glabrous, membranous, lanceolate, margin ciliate at the top, apex acute and aristate, 0.10‒1.90 cm long, < 0.1 cm wide; palea absent; lodicules 3, cuneate, coriaceous, < 0.1‒0.25 cm long. *Awn* present, geniculate, column twisted and hirsute, 5.1‒11.0 cm long, 0.48‒0.74 cm thick. *Anthers* 3, 0.40‒0.85 cm long. *Ovary and Stigma* ovary 1, 0.10‒0.35 cm long; stigmas 2, plumose. *Caryopsis* 4.0‒7.5 mm long, 0.87‒1.61 mm wide.

Etymology. – The specific epithet ‘avenacea’ is from *Avena* and a Latin word ‘acea’ meaning like. This refers to *Avena*-like spikelets in *T. avenacea.*

Vernacular names. – Native oatgrass or tall oatgrass (English)

Geographic distribution. – Endemic to Australia in all mainland states of the country.

Phenology. – Mostly from February to April but occasionally early flowering in November, December and January.

Habitat & Ecology. – *Themeda avenacea* is highly associated with Australian native habitats, *Corymbia*, *Eucalyptus* and *Melaleuca* savannas and occasionally occurs in seasonally inundated grasslands. Frequent coexistence of *Themeda avenacea* with native plants in genera *Corymbia*, *Eucalyptus,* and *Melaleuca* indicates that it generally grows in moist to waterlogging conditions. Adaptations and responses to fire and grazers of this species remain understudied.

Phylogenetic position and morphological evolution. – *Themeda avenacea* is closely related to wetland *Themeda* species.

Cytogenetics. – No cytogenetic data for this species

Uses and ethnology. – O'Connell et al. (1983) stated that *T. avenacea* has no economic uses.

Specimens examined. – Please see full list of specimens examined in Appendix XIV F.

Themeda caudata (Nees) A. Camus in Flore Générale de l'Indo-Chine 7: 364. 1922 ≡ ***Anthistiria caudata*** Nees in the Botany of Captain Beechey's Voyage 245. 1838 ≡ ***Themeda gigantea*** (Cav.) Hack. subsp. ***caudata*** (Nees) Hack. in Monographiae Phanerogamarum 6: 676. 1889 ≡ ***Anthistiria gigantea*** subsp. ***caudata*** (Nees ex Hook. & Arn.) Hook.f. in the Flora of British India 7: 217. 1896 ≡ [***Themeda caudata*** (Nees) Hack. ex T.Durand & B.D. Jacks. in Index Kewensis 1: 424. 1906, nom. nud.] ≡ [***Themeda gigantea*** (Cav.) Hack. var. ***caudata*** (Nees) Keng in Claves Generum et Speciarum Graminearum Primarum Sinicarum Appendice Nomenclatione Systematica 247. 1957, nom. inval.] — Lectotype (designated by Veldkamp in Blumea 61: 36. 2016): China, Macao and the neighbouring islands, *G. H. Vachell 46* (CGE barcode CGE16260; isolectotype: CGE barcode CGE16261).

= ***Androscepia gigantea*** (Cav.) Brongn. var. ***armata*** Andersson in Nova Acta Regiae Societatis Scientiarum Upsaliensis, ser. 3. 2: 248. 1856 ≡ ***Anthistiria gigantea*** var. ***armata*** Andersson in Nova Acta Regiae Societatis Scientiarum Upsaliensis, ser. 3 2: 245. 1856 — **Lectotype (designated here)**: India, Assam, Churra Poonje, *F. de Silva & W. Gomez s.n. [Wallich Numer. List 8774]* (S barcode S-G-10540!).

= ***Themeda gigantea*** var. ***longispatha*** Hack. in Monographiæ Phanerogamarum 6: 677. 1889 — **Lectotype (designated here)**: Pakistan, Terai, foothills of the Himalayas, 15 December 1875, *C. E. O. Kuntze s.n.* (W barcode W19160028200 [photo!]).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* present. *Culms* erect, caespitose, intravaginal growth, glabrous, 100‒600 cm long, 0.61‒1.39 cm thick. *Leaf sheaths* glabrous, 5.8‒23.5 cm long. *Ligules* truncate, ciliolate, 0.7‒2.0 mm long. *Leaf blades* non-plicate, abaxial and adaxial surfaces glabrous to scabrous with tiny white barbs, midrib widened, lanceolate, margin scabrid, apex acuminate, 20─150 cm long, 2.5─16.0 cm wide. *Inflorescences* axillary and terminal, inflorescence paniculate. *Spatheoles* glabrous to slightly scabrous with non-tuberculate hairs, lanceolate, 2.9─5.7 cm long. *Rachis internodes* fragile, densely hairy with dark brown hairs, linear, 0.1 cm long. *Racemes* solitary, 7─8 sterile spikelets, 1─3 fertile spikelet, 2.1─3.2 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 1.10─1.85 cm long (sessile) and 1.10─1.70 cm long (pedicelled), 0.15─0.20 cm wide (sessile) and 0.15─0.20 cm wide (pedicelled), larger than fertile pairs; callus glabrous, square, attached obliquely, < 0.1 cm long; lower glume glabrous, chartaceous, lanceolate, margins partly enclose upper glume, apex acuminate, 1 spikelet long and wide; upper glume glabrous, chartaceous, lanceolate, margin inflexed and ciliate at the top half, apex acute, as long as the lower glume, 1.00─1.20 cm long, 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, 0.75─1.20 cm long (sessile spikelets) and 0.80─1.20 cm long (pedicelled spikelets), 0.2─0.3 mm wide (sessile spikelets) and 0.2─0.6 mm wide (pedicelled spikelets); upper lemma glabrous, membranous, lanceolate, 0.60─1.10 cm long (sessile spikelets) and 0.60─1.15 cm long (pedicelled spikelets); palea minute (0.15-0.40 cm long) or absent; lodicules 2, cuneate, coriaceous, < 0.1─0.1 cm long. *Fertile pairs* bisexual and barren, deciduous entirely, 1-2 fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, 0.70─0.95 cm long, 0.15─0.20 cm wide; callus linear, densely hairy with dark brown hairs, attach obliquely, 0.15─0.30 cm long; lower glume densely pubescent with yellow hairs, coriaceous, oblong, margins partly enclosed upper glume, apex obtuse, 1 spikelet long and wide; upper glume pubescent with yellow hairs, primary vein ciliate, coriaceous, oblong, apex obtuse, slightly shorter and narrower than the lower glume, 0.75─0.95 cm long, 0.1 cm wide; lower lemma membranous, lanceolate, margin entire and slightly ciliate at the top, apex acuminate, 0.30─0.75 cm long, 0.20─0.35 cm wide; upper lemma membranous, oblong, 0.15─0.70 cm long, < 0.1 cm wide; palea minute (0.15-0.40 cm long) or absent; lodicules 3, cuneate, coriaceous, 0.10─0.15 am long, companion spikelets, pedicelled, well developed, male or barren, lanceolate, 1.0─1.9 cm long, 0.15─0.20 cm wide; callus pilose with yellow hairs, linear, 0.15─0.20 cm long; lower glume glabrous to slightly hairy on the margin, coriaceous, linear lanceolate, margins partly enclose upper glume, apex acute, 1 spikelet long and wide; upper glume glabrous, coriaceous, lanceolate, margin entire, apex obtuse, slightly shorter than the lower glume, 1.25─1.45 cm long, < 0.1 cm wide; lower lemma membranous, lanceolate, margin entire and slightly ciliate at the top, apex obtuse, 0.75─1.10 cm long, 0.15─0.45 cm wide; upper lemma membranous, lanceolate, margin entire, apex obtuse, 0.55─1.05

cm long; palea minute (0.15-0.40 cm long) or absent; lodicules 3, cuneate, coriaceous, < 0.1–0.1 cm long. *Awn* present, straight, column twisted and hispidulous with white hairs, 3.0–5.7 cm long, 0.25–0.56 mm thick. *Anthers* 3, 0.20–0.65 cm long. *Ovary and Stigma* ovary 1, 0.10–0.35 cm long; stigmas 2, plumose. *Caryopsis* 3.0–4.5 mm long, 0.77–0.86 mm wide.

Etymology. – The specific epithet '*caudata*' is composed of two Latin words 'cauda' meaning tail and 'ata' meaning possessing, Lemma awn represents 'tail' in *T. caudata*.

Vernacular names. – Bao zi cao (苞子草; Chinese)

Geographic distribution. – Distribution ranges cover India, Himalayan regions, Southern China, most parts of Southeast Asia excluding Java, Lesser Sunda Islands and New Guinea. There are specimens collected from New Caledonia and this species is thought to be introduced there (POWO, 2022).

Phenology. – July to December and late flowering time in April and June

Habitat & Ecology. – *Themeda caudata* occurs moist deciduous and semi-evergreen forests dominated by *Shorea robusta* and native tree *Madhuca latifolia* in India and Sri Lanka. These habitats are characterized by monsoonal climate and receives annual precipitation from 1500–2900 mm. *Themeda caudata* is prevalent in seasonally inundated habitats such as riverine riparian forests, depressions, and alluvial grasslands.

Phylogenetic position and morphological evolution. – *Themeda caudata* is positioned in the wetland group.

Cytogenetics. – Birari (1980) reported that *Themeda caudata* is a tetraploid species (2n = 40).

Uses and ethnology. – No use data provided for *Themeda caudata*

Specimens examined. – Please see full list of specimens examined in Appendix XIV G.

Themeda cymbaria Hack. in Monographiae Phanerogamarum 6: 668. 1889 ≡

Themeda serratifolia (Hack.) Roberty in Boissiera 92. 1960 — **Lectotype** (designated by Chorghe, Dey & Lakshminarasimhan in the Journal of Japanese Botany 96(1): 31–

> 37. 2021): Sri Lanka, Tamil Nadu State, September 1875, *R. Wight 1707/175* (W barcode W1916-0028232!; isolectotypes: E barcode E00697625!; paralectotypes: W barcode W19160028232, W0028859).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* absent. *Culms* erect, caespitose, branched, glabrous, 136─250 cm long, 0.24─0.78 cm thick. *Leaf sheaths* basal leaf sheath present, overlappig, upper leaf sheath glabrous, 3.7─18.2 cm long. *Ligules* truncate, ciliolate, 1.0─1.2 mm long. *Leaf blades* non-plicate, abaxial and adaxial surfaces glabrous to scabrous, lanceolate, margin scabrid, apex acuminate, 30─60 cm long, 0.4─0.8 cm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, 48─90 cm long. *Spatheoles* glabrous occasionally hairy on the margin, lanceolate, 0.9─1.9 cm long. *Rachis internodes* fragile, glabrous hairs, linear, 0.1 cm long. *Racemes* solitary, 6-7 sterile spikelets, 1-2 fertile spikelet, 0.65─1.20 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at the same level, persistent, sessile spikelets similar to the pedicelled ones, well developed, oblong lanceolate, 0.4─0.8 cm long (sessile) and 0.45─0.75 cm long (pedicelled), <0.10─0.15 cm wide (sessile) and <0.10─0.15 cm wide (pedicelled), as long as fertile pairs; callus linear, glabrous, < 0.1 cm long; lower glume glabrous, chartaceous, oblong to lanceolate, margins partly enclose upper glume, apex acuminate, 1 spikelet long and wide; upper glume glabrous, chartaceous, oblong lanceolate, margin inflexed, apex acuminate, as long as the lower glume, 0.42─0.50 cm long, 0.8 mm wide; lower lemma glabrous, membranous, oblong lanceolate, margin inflexed and ciliate near the base, apex obtuse or acute, 0.28─0.40 cm long, < 0.1 cm wide; upper lemma glabrous, membranous, oblong, margin inflexed, apex obtuse or acute, 0.17─0.22 cm long, 0.5 mm wide; palea minute or absent; lodicules 2, cuneate, coriaceous, < 0.1 (ca. 0.4) cm long. *Fertile pairs* bisexual and barren, deciduous entirely, 1-2 fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelet, well developed, bisexual, elliptic, 0.35─0.55 cm long, <0.1─0.1 cm wide; callus cuneate, hairy with white and dark brown hairs, attach obliquely, 0.5─1.4 cm long; lower glume sparsely pubescent with white hairs, coriaceous, oblong, margins partly enclosed upper glume, apex obtuse, 1 spikelet long and wide; upper glume sparsely pubescent with white hairs, coriaceous, linear, margin inflexed, apex obtuse, slightly shorter and narrower than the lower glume, 0.30─0.38 cm long, 0.6 mm wide; lower lemma glabrous, membranous, oblong, margin ciliate towards the apex, apex obtuse, <0.10─0.30 cm long, 0.4 mm wide; upper lemma reduced to, membranous base of the awn, oblong, margin entire, apex obtuse, 0.2─0.4 cm long, 0.2 mm wide; palea minute or absent; lodicules 2, cuneate, coriaceous, < 0.10 (ca. 0.40 mm) cm long, companion spikelets, pedicelled, well developed, male, lanceolate, 0.4─0.7 cm long, <0.10─0.15 cm wide; callus hirsute or pilose with white hairs, linear, 0.10─0.15 cm long; lower glume glabrous, chartaceous, lanceolate, margins partly enclose upper glume, apex acuminate, 1 spikelet long abd wide; upper glume glabrous, chartaceous, oblong lanceolate, margin inflexexd, apex acuminate, slightly shorter than the lower glume, 0.45─0.55 cm long, 0.5 mm wide; lower lemma glabrous, membranous, oblong lanceolate, margin inflexed, apex obtuse or acute, <0.10─0.35 cm long, 0.5 mm wide; upper lemma glabrous, membranous, oblong, margin entire, apex obtuse, 0.2─0.5 cm long, 0.3 mm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1 cm long. *Awn* present, geniculate, column twisted and puberulous, 1.2─2.3 cm long, 0.08─0.29 mm wide. *Anthers* 3, 0.10─0.35 cm long. *Ovary and Stigma* ovary 1, <0.10─0.15 cm long; stigmas 2, plumose. *Caryopsis* 1.5─2.5 mm long, 0.50─0.60 mm wide.

Etymology. – The specific epithet '*cymbaria*' from two Greek words 'kymbe' meaning 'boat' and 'aria' meaning 'pertaining to'. This describes boat-like spathes subtending inflorescences.

Vernacular names. – Pothai pullu (Tamil), Noshia palai pullu (Tamil), Konda gaddi (Telugu), Karawata mana (Sinhala), Bhathdu (India).

Geographic distribution. – Distribution range of *Themeda cymbaria* is restricted to India and Sri Lanka

Phenology. – September to December

Habitat & Ecology. – *Themeda cymbaria* is present in both dry and moist deciduous savannas in association with dominant tree species in genera *Buchanania*, *Dillenia*, *Emblica*, *Pterocarpus*, *Tectona*, and *Terminalia*. It also forms C_4 grassland receiving high precipitation with *Apluda mutica*, *Apocopis* spp., *Capillipedium* spp., *Chrysopogon* spp., *Cymbopogon flexuosus*, *Eulalia trispicata*, *Heteropogon contortus*, *Ischaemum* spp., *Themeda triandra*, *Arundinella* spp., *Dimeria* spp.,

Phylogenetic position and morphological evolution. – *Themeda cymbaria* formed isolated position in the phylogenetic tree. This species retains a few spikelet pairs but develops complex inflorescence branching patterns (Fig. 5.4).

Cytogenetics. – Several studies only found that *Themeda cymbaria* is a diploid plant (2n = 20; Christopher & Abraham, 1978).

Uses and ethnology. – *Themeda cymbaria* naturally grows in hilly forest area of Sri Lanka. Fresh and dry plants are used as fodder in monsoonal and dry seasons as they have high amount of structural carbohydrates (Gandhi et al., 2011). Leaves of *Themeda cymbaria* were used as thatching materials in a tribal village Idamalakudy in India (Baijulal et al., 2017).

Specimens examined. – Please see full list of specimens examined in Appendix XIV H.

Themeda gigantea (Cav.) Hack. ex Duthie in The Fodder Grasses of Northern India 43. 1888 ≡ ***Anthistiria gigantea*** Cav. in Icones et Descriptiones Plantarum 5: 36 1799 ≡ ***Androscepia gigantea*** (Cav.) Brongn. in Voyage Autour du Monde 2(2): 78. 1831 — [***Androscepia gigantea*** (Cav.) Brongn. var. ***oligantha*** Buse. (1854: 364), nom. inval.]. — [***Androscepia gigantea*** (Cav.) Brongn. var. ***mutica*** Andersson. (1856: 248), nom. inval.]. — [***Themeda gigantea*** (Cav.) Hack. var. ***genuina*** Hack. (1889: 672), nom. inval.]. — ***Themeda gigantea*** (Cav.) Hack. var. ***amboinensis*** Hack. (1889: 673). — [***Anthistiria gigantea*** Cav. subsp. ***genuina*** Hack. ex Hook.f. (1896: 217), nom. inval.]. — [***Themeda gigantea*** (Cav.) Hack. subvar. ***mutica*** Roberty (1960: 91), nom. inval.]. — Lectotype (desginated by Garilleti in Fontqueria 38: 45. 1993): The Philippines, Luzon, Guaz, Née s.n. (MA barcode MA475296!).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* present. *Culms* erect, caespitose, glabrous, 100‒400 cm long, 0.52‒0.93 cm wide. *Leaf sheaths* glabrous, 6.7‒18.2 cm long. *Ligules* truncate, ciliolate, about 1 mm long. *Leaf blades* non-plicate, abaxial surfaces glabrous, adaxial surfaces scabrous, midrib widened, vein serrate, lanceolate, margin scabrid, apex acuminate, 30‒100 cm long, 5.0‒25.0 mm wide. *Inflorescences* axillary and terminal, inflorescence paniculate. *Spatheoles* enclosing inflorescence, glabrous, occasionally hairy on the margin, lanceolate, 1.0‒2.0 cm long. *Rachis internodes* tough, hairy with yellowish brown hairs, linear, very tiny < 0.1 cm long. *Racemes* solitary, 6-7 sterile spikelets, 1-2 fertile spikelet, 0.90‒1.90 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at the same level, deciduous with fertile, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 0.6‒1.0 cm long (sessile) and 0.55‒0.95 cm long (pedicelled), <0.10‒0.15 cm wide (sessile) and 0.10‒0.2 cm wide (pedicelled); callus cuneate, pilose with tuberculate tawny hairs, very tiny < 0.1 cm long; lower glume densely pilose with tuberculate tawny or dark brown hairs, coriaceous, lanceolate, margins partly enclose upper glume, apex acuminate, 1 spikelet long and wide; upper glume glabrous or occasionally hairy with tawny hairs, coriaceous, lanceolate, margin membranous and ciliate at the top half, apex acute, as long as the lower glume, 0.45─0.65 cm long rarely 0.95 or 1.0 cm, < 0.1─0.1 cm wide; lower lemma glabrous, membranous, lanceolate, 0.5─1.0 cm long (sessile spikelets) and 0.40─1.05 cm long (pedicelled spikelets), 0.1 cm wide; upper lemma glabrous, membranous, lanceolate, 0.4─1.0 cm long (sessile spikelets) and 0.45─1.00 cm long (pedicelled spikelets), < 0.1 cm wide; palea minute or absent; lodicules 2, cuneate, coriaceous, < 0.1─0.1 cm long. *Fertile pairs* bisexual and barren, deciduous entirely, 1-2 fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, 0.5─0.7 cm long, 0.10─0.15 cm wide; callus cuneate, densely pilose with tawny hairs, attach obliquely, 0.10─0.25 cm long; lower glume sparsely pubescent with tawny hairs, coriaceous, oblong, margins partly enclosed upper glume, apex obtuse, 1 spikelet long and wide; upper glume sparsely pubescent with tawny hairs, coriaceous, oblong, margin inflexed, apex acute, slightly shorter and narrower than the lower glume, 0.45─0.65 cm long rarely 1.0 cm, < 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin entire, apex acute, 0.40─0.65 cm long, < 0.1 cm wide; upper lemma glabrous, membranous, lanceolate, margin entire, apex acute, 0.40─0.65 cm long, < 0.1 mm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, about 0.10 cm long, companion spikelets, pedicelled, well developed, male, lanceolate, 0.6─1.1 cm long, 0.10─0.15 cm wide; callus pubescent with tawny hairs, linear, < 0.1─0.15 cm long; lower glume hairy with tawny hairs, coriaceous, lanceolate, margins partly enclose upper glume, apex acute, 1 spikelet long and wide; upper glume glabrous, coriaceous, lanceolate, margin inflexed, apex acute, slightly shorter than the lower glume, 0.50─0.65 cm long rarely 0.9 to 1.0 cm, < 0.1 cm wide; lower lemma glabrous, lanceolate, membranous, margin entire, apex acute, 0.4─0.7 cm long, about 0.1 cm wide; upper lemma glabrous, lanceolate, membranous, margin entire, apex acute, 0.40─0.65 cm long, about 0.1 cm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1─0.1 cm long. *Awn* absent. *Anthers* 3, 0.15─0.40 cm long. *Ovary and Stigma* ovary 1, <0.10─0.10 cm long; stigmas 2, plumose. *Caryopsis* 2.5─4.5 mm long, 0.71─1.18 mm wide.

1. Raceme shed as a whole, raceme 0.9─1.9 cm long……………………………..var. ***gigantea***
1. Raceme long persistent, raceme 1.8─2.8 cm long……………………………var. ***intermedia***

Themeda gigantea (Cav.) Hack. ex Duthie var. ***gigantea*** in The Fodder Grasses of

Northern India 43. 1888 ≡ ***Anthistiria gigantea*** Cav. in Icones et Descriptiones Plantarum 5: 36 1799 ≡ ***Androscepia gigantea*** (Cav.) Brongn. in Voyage Autour du Monde 2(2): 78. 1831 — [***Androscepia gigantea*** (Cav.) Brongn. var. ***oligantha*** Buse. (1854: 364), nom. inval.]. — [***Androscepia gigantea*** (Cav.) Brongn. var. ***mutica*** Andersson. (1856: 248), nom. inval.]. — [***Themeda gigantea*** (Cav.) Hack. var. ***genuina*** Hack. (1889: 672), nom. inval.]. — ***Themeda gigantea*** (Cav.) Hack. var. ***amboinensis*** Hack. (1889: 673). — [***Anthistiria gigantea*** Cav. subsp. ***genuina*** Hack. ex Hook.f. (1896: 217), nom. inval.]. — [***Themeda gigantea*** (Cav.) Hack. subvar. ***mutica*** Roberty (1960: 91), nom. inval.]. — Lectotype (desginated by Garilleti in Fontqueria 38: 45. 1993): The Philippines, Luzon, Guaz, Née s.n. (MA barcode MA475296!).

= ***Perobachne secunda*** J. Presl. in Reliquiae Haenkeanae 1(4-5): 348. 1830 — Holotype: The Philippines, Luzon, Port Sorsogon, *T. P. X. Haenke s.n.* (PR barcode PR450669!).

Etymology. – The specific epithet ‘*gigantea*’ is a Latin word which means ‘very large’. This species has tall culms compared to other related species.

Vernacular names. – Golagan hutan (Malay), baylad bantud (Hau; the Philippines), tanglang (Ifugao; the Philippines).

Geographic distribution. – This species is distributed in the Philippines, New Guinea and some Pacific Islands such as New Caledonia, Solomon Island, and Vanuatu.

Phenology. – Flowering time span throughout the year.

Habitat & Ecology. – *Themeda gigantea* was mainly found in seasonally inundated grasslands and wetlands with tall grasses in genera *Imperata* and *Phragmites* or in tropical semi-evergreen forest and pine savanna that are characterized by wet conditions. *Themeda gigantea* depends on high annual precipitation and precipitation of the driest month to grow. It remains unclear that fire and other savanna-regulating factors interact with this species.

Phylogenetic position and morphological evolution. – According to Dunning et al. (2017), *Themeda gigantea* was placed in the group with wetland species (e.g., *Themeda arundinacea* and *Themeda villosa*)

Cytogenetics. – No cytogenetic data provided for *T. gigantea*

Uses and ethnology. – Adhikari et al. (2010) reported medicinal uses of *Themeda gigantea* such as asthma, sores, and stomach ache.

Specimens examined. – Please see full list of specimens examined in Appendix XIV I.

Themeda gigantea (Cav.) Hack. var. ***intermedia*** Hack. in Monographiae Phanerogamarum 6: 675. 1889 ≡ ***Themeda gigantea*** (Cav.) Hack. subsp. ***intermedia*** Hack. in Monographiae Phanerogamarum. 6: 675. 1889 [***Themeda intermedia*** T. Durand & B. D. Jacks. in Index Kewensis 1: 424. 1901, nom. inval.] ≡ ***Themeda*** x ***intermedia*** (Hack.) Bor in Indian Forest Records 1: 3, 96. 1938 — Holotype: India, Meghalaya State, Khasia Hills, *J. D. Hooker & T. Thomson s.n.* (W barcode W0030636!; isotypes: L barcode L0064298!, L0064299!, K barcode K 000245974!, K000245975!).

= ***Themeda gigantea*** (Cav.) Hack. var. ***dubia*** Hack. in Monographiae Phaneroganarum. 6: 675. 1889 [***Themeda gigantea*** (Cav.) Hack. subvar. ***dubia*** (Hack.) Roberty in xxx 90. 1960, nom. inval.] — **Lectotype (secondarily designated here)**: The Philippines, *s.d., H. Cuming 1609* (MO barcode MO-2114794!; isolectotypes: K barcode K0002900001!, W barcode W0030637!, W1889-0071181!).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* present. *Culms* erect, caespitose, intravaginal growth, glabrous, 150–500 cm long, 5.1–15.0 mm wide. *Leaf sheaths* glabrous, 5.5–19.5 cm long. *Ligules* truncate, eciliate or ciliolate, 0.5–1.5 mm long. *Leaf blades* non-plicate, abaxial and adaxial surfaces glabrous, midrib widened, lanceolate, margin scabrid, apex acuminate, 50–100 cm long, 3–15 mm wide. *Inflorescences* axillary and terminal, inflorescence paniculate. *Spatheoles* glabrous, lanceolate, 2.0–3.5 cm long. *Rachis internodes* fragile, pilose with white hairs, oblong, slightly broadened at the apex, 0.15 cm long. *Racemes* solitary, drooping, 7–8 sterile spikelets, 2–3 fertile spikelets 1.8–2.8 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male or barren, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 0.95─1.40 cm long (sessile) and 1.10─1.50 cm long (pedicelled), 0.1─0.2 cm wide (sessile spikelets) and 0.10─0.20 cm wide (pedicelled spikelets); callus linear, slightly broaden at the apex, glabrous, < 0.1 cm long; lower glume hairy with tuberculate yellowish-brown hairs, coriaceous, lanceolate, margins partly enclose upper glume, apex obtuse, 1 spikelet long and wide; upper glume glabrous, coriaceous, lanceolate, margin membranous, apex acute, as long as the lower glume, 0.75─1.05 cm long, 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin entire, apex acute, 0.65─1.00 cm long (sessile spikelets) and 0.30─1.05 cm long (pedicelled spikelets), 0.1 cm wide; upper lemma glabrous, membranous, lanceolate, margin entire, apex acute, 0.60─1.10 cm long (sessile spikelets) and 0.25─1.00 cm long (pedicelled spikelets), 0.1 cm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.10─0.15 cm long. *Fertile pairs* bisexual and barren, deciduous entirely, 1─2 fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, 0.65─1.35 cm long, 0.15─0.20 cm wide; callus oblong, hairy with tawny hairs, attach obliquely, 0.10─0.25 cm long, lower glume fused with upper glume; lower glume densely pilose with reddish or yellowish hairs, coriaceous, lanceolate, margins partly enclosed upper glume, apex acuminate, 1 spikelet long and wide; upper glume pubescent with white hairs, coriaceous, lanceolate, margin membranous, apex acuminate, slightly shorter and narrower than the lower glume, 0.65─0.75 cm long, 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin ciliate, apex obtuse 0.30─0.65 cm long, < 0.1─0.1 cm wide; upper lemma glabrous, membranous, lanceolate, margin ciliate, apex obtuse, 0.30─0.65 cm long, < 0.1 cm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, 0.10─0.15 cm long, companion spikelets, pedicelled, well developed, male, lanceolate, 0.95─1.70 cm long, 0.1─0.2 cm wide; callus glabrous, oblong, 0.15─0.20 cm long; lower glume densely pilose with tawny hairs, coriaceous, lanceolate, margins partly enclose upper glume, apex acuminate, 1 spikelet long and wide; upper glume glabrous, coriaceous, lanceolate, margins entire, apex acuminate, slightly shorter than the lower glume, 0.80─1.1 cm long, 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin entire or ciliate, apex acute, 0.70-1.05 cm long, < 0.1 cm wide; upper lemma glarbous, membranous, lanceolate, margin entire, apex acute, 0.70─1.05 cm long, < 0.1 cm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1─0.1 cm long. *Awn* generally absent, if present, straight, column non-twisted and hispidulous, 0.4─2.9 cm long, 0.10─0.36 mm thick. *Anthers* 3, 0.15─0.45 cm long. *Ovary and Stigma* ovary 1, 0.10─0.20 cm long; stigmas 2, plumose. *Caryopsis* 2.0-5.0 mm long, 0.50-1.30 mm thick.

Etymology. – The specific epithet ‘*intermedia*’ refers to morphological similarity with other species in this case *T. gigantea*.

Vernacular names. – Ju zhong jian (居中菅; Chinese)

Geographic distribution. – Distribution ranges span from South Central China to mainland Southeast Asia, Indonesia and Australia, and also in the Philippines, New Guinea, and Vanuatu.

Phenology. – Flowering time mainly covers August to December but also in March to April

Habitat & Ecology. – Only seasonally inundated grasslands and wetlands were documented as main habitats of *Themeda intermedia*. It is present with other grasses generally growing in humid conditions such as *Imperata* and *Ischaemum*.

Phylogenetic position and morphological evolution. – *Themeda intermedia* is nested in the subclade of wetland species. Its morphological characteristics are similar to *Themeda gigantea* except larger reproductive structures in *Themeda intermedia*.

Cytogenetics. – *Themeda intermedia* has chromosome numbers of 40 (2n = 40) and it is tetraploid species (Löve, 1976).

Uses and ethnology. – No use data provided for *T. intermedia*.

Specimens examined. – Please see full list of specimens examined in Appendix XIV J.

Note. – Veldkamp (2016) specified that the holotype of *Themeda gigantea* var. *dubia* is deposited in W; however, no types were completely lectotypified. In addition, Veldkamp (2016) also specified isotypes from different collection numbers. Therefore, we selected specimen MO-2114794 as the lectotype and other specimens with the same collection number as isolectotypes. We also resurrected *Themeda gigantea* var. *intermedia* as a legitimate name of this taxa as evidence we provided agrees that it should be treated as a variety of *Themeda gigantea*.

Themeda hookeri (Griseb.) A. Camus in Bulletin du Muséum d’Histoire Naturelle 26:

425. 1920 ≡ ***Anthistiria hookeri*** Griseb. in Nachrichten von der Königlichen Gesellschaft der Wissenschaften und von der Georg-Augusts-Universität 3: 91. 1868 — Lectotype (designated by Veldkamp in Blumea. 61: 37. 2016): India, Sikkim State, Choongtang, *J. D. Hooker s.n.* (GOET barcode GOET9981!; isolectotypes: K barcode K001427978!, L barcode L1344978!).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* absent. *Culms* erect, base geniculately ascending, intravaginal growth, glabrous, 20–90 cm long, 0.74–1.99 mm wide. *Leaf sheaths* glabrous, 3.2–8.1 cm long. *Ligules* truncate, ciliolate, about 1 mm long. *Leaf blades* plicate, abaxial and adaxial surfaces glabrous or hairy with tuberculate hairs, lanceolate to filiform, margin scabrid, apex acuminate, 10.0–28.1 cm long, 2.0–4.0 mm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, lax. *Spatheoles* glabrous, linear to lanceolate, 1.0–2.9 cm long. *Rachis internodes* fragile, pilose with yellowish hairs on the margins, oblong, slightly broadened at the apex, < 0.10–0.15 cm long. *Racemes* solitary, 6–8 sterile spikelets, 1–3 fertile spikelets, 1.5–2.4 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 1.15–1.75 cm long (sessile) and 0.9–1.6 cm long (pedicelled), 0.10–0.20 cm wide (sessile) and 0.10–0.2 cm wide (pedicelled); callus linear, slightly broaden at the apex, glabrous, < 0.1–0.1 cm long; lower glume glabrous, coriaceous, lanceolate, margins partly enclose upper glume, apex acuminate, 1 spikelet long and wide; upper glume glabrous, subchartaceous, lanceolate, margin entire, apex acute, as long as the lower glume, 0.85–1.0 cm long, 0.10–0.15 cm wide; lower lemma glabrous, membranous, lanceolate, margin inflexed and ciliate at the top, apex acuminate, 0.7 cm long (sessile spikelets) and 0.6–0.7 cm long (pedicelled spikelets), < 0.10–0.25 cm wide (sessile spikelets) and < 0.10–0.25 cm wide (pedicelled spikelets); upper lemma glabrous, membranous, lanceolate, margin entire, apex acuminate, 0.5–0.9 cm long (sessile spikelets) and 0.45–0.90 cm long (pedicelled spikelets), < 0.1 cm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1 cm long. *Fertile pairs* bisexual and barren, deciduous entirely, 1–2 fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelet, well developed, bisexual, elliptic, 0.45–0.65 cm long, 0.10–0.2 cm wide; callus cuneate, densely pilose with yellowish brown hairs, attach obliquely, 0.20 cm long; lower glume pubescent with white hairs, coriaceous, lanceolate, margins partly enclosed upper glume, apex obtuse, 1 spikelet long and wide; upper glume pubescent with white hairs, coriaceous, oblong, margin inflexed and ciliate at the top, apex truncate, slightly shorter and narrower than the lower glume, 0.45–0.65 cm long, about 1.0 cm wide; lower lemma glabrous, membranous, lanceolate, very minute; upper lemma glabrous, membranous, lanceolate, 0.35─0.50 cm long, xx mm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1 cm long, companion spikelets, pedicelled, well developed, male or barren, lanceolate, 0.90─1.55 cm long, 0.1─0.2 cm wide; callus glabrous or pilose with yellow hairs, cuneate, 0.15 cm long; lower glume glabrous, chartaceous, lanceolate, margins partly enclose upper glume, apex acute, 1 spikelet long and wide; upper glume glabrous, subchartaceous, lanceolate, margins membranous and ciliate at the top half, apex acute, slightly shorter than the lower glume, 0.75─1.10 cm long, 1.0 mm wide; lower lemma glabrous, membranous, lanceolate, margins inflexed and membranous and ciliate on the top, apex acuminate, very minute, 0.60─0.80 cm long, about 0.1 cm wide; upper lemma glabrous, membranous, lanceolate, margins inflexed and membranous and ciliate on the top half, apex acuminate, 0.5─0.6 cm long, about 0.1 cm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1 cm long. *Awn* present, geniculate, column twisted and hispidulous, 2.0─4.0 cm long, 0.23─0.30 mm thick. *Anthers* 3, 0.25─0.50 cm long. *Ovary and Stigma* ovary 1, <0.10─0.10 cm long; stigmas 2, plumose. *Caryopsis* 2.0─4.5 mm long, 0.72─1.03 mm thick.

Etymology. – This species was names after Joseph Dalton Hooker, English botanist, traveller, and Garden's Director.

Vernacular names. – Xi nan jian cao (西南菅草; Chinese)

Geographic distribution. – *Themeda hookeri* has distribution ranges in Assam state in India, Nepal, Tibet, Southern China, and Thailand.

Phenology. – Flowering time span from July to December.

Habitat & Ecology. – *Themeda hookeri* exist in hot and dry habitats such as dry open woodland, desert shrubland, subtropical karst in China, and dry valleys. Associated species are good supporting indicators of dry habitats such as *Heteropogon contortus*.
This species is considered a subtropical species and exist at high elevation from 1100─3400 m (Shouliang & Philips, 2006; personal observations).

Phylogenetic position and morphological evolution. – *Themeda hookeri* is closely related with other Indian endemic species such as *Themeda anathera*, *Themeda huttonensis*, *Themeda* *mooneyi*, and *Themeda strigosa*. Reduced number of spikelet pairs and inflorescence with secondary branching are shared morphology of *Themeda hookeri* and its relatives.

Cytogenetics. – Only diploid level (2n = 20) was reported for *Themeda hookeri* (Birari, 1980, 1981; Löve, 1976).

Uses and ethnology. – No use data provided for *T. hookeri*.

Specimens examined. – Please see full list of specimens examined in Appendix XIV K.

Themeda huttonensis Bor in Indian Forest Records 1: 96. 1938 — Holotype: India, Nagaland State, Klahuri, Naga Hills, June 1935, *N. L. Bor 6717* (K barcode K000245981!; isotype: ASSAM barcode ASSAM0000000096!).

Description. – *Habit* perennial. *Stilt roots* absent. *Culms* erect, glabrous, 60–100 cm long. *Leaf sheaths* glabrous, keeled, 3.0–5.2 cm long. *Ligules* truncate, eciliate, 1.0–1.5 mm long. *Leaf blades* plicate, abaxial surface scabrous, adaxial surface pilose with tuberculate hairs, lanceolate to filiform, margin scabrid, apex acuminate, 8.5–20.0 cm long, 3.0–8.0 mm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, lax. *Spatheoles* glabrous, lanceolate, 1.9–3.0 cm long. *Rachis internodes* fragile, sparsely pilose with white hairs, oblong, about 0.1 cm long. *Racemes* solitary, 7 sterile spikelets, 2 fertile spikelets, 0.95–1.30 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, barren, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 0.95–1.20 cm long (sessile) and 0.8–1.1 cm long (pedicelled), 0.10–0.15 cm wide (sessile) and 0.10–0.15 cm wide (pedicelled); callus oblong, glabrous, < 0.1 cm long; lower glume sparsely pilose with tuberculate hairs, coriaceous, lanceolate, margins partly enclose upper glume, apex acuminate, 1 spikelet long and wide; upper glume glabrous, chartaceous, lanceolate, margins membranous and ciliate, apex acute, as long as the lower glume, 0.60–0.70 cm long, < 0.1–0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margins ciliate on the top, apex obtuse, 0.5–0.7 cm long (sessile spikelets) and 0.40–0.75 cm long (pedicelled spikelets), 0.1 cm wide; upper lemma glabrous, membranous, lanceolate, margin entire, apex acute, 0.45–0.60 cm long (sessile spikelets) and 0.40–0.65 cm long (pedicelled spikelets), < 0.1 cm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1 cm long. *Fertile pairs* bisexual and barren, deciduous entirely, 1 fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic oblong, 0.5─0.6 cm long, 0.10 cm wide; callus oblong, densely pilose with white hairs, attach obliquely, 0.10 cm long; lower glume mostly glabrous but pubescent at the apex with white hairs, chartaceous, lanceolate, margins partly enclosed upper glume, apex obtuse, 1 spikelet long and wide; upper glume mostly glabrous but pubescent at the apex with white hairs, subcoriaceous, oblong, margin entire, apex obtuse, slightly shorter and narrower than the lower glume, 0.50─0.55 cm long, < 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin entire, apex acuminate, 0.35─0.45 cm long, < 0.1 cm wide; upper lemma glarbous, membranous, lanceolate, < 0.1 cm long, xx mm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1 cm long, companion spikelets, pedicelled, well developed, male or barren, lanceolate, 0.75─0.90 cm long, xx cm wide; callus glabrous, linear, very narrow, 0.1 cm long; lower glume glabrous, chartaceous, lanceolate, margins fringe, partly enclose upper glume, apex acute, 1 spikelet long and wide; upper glume glabrous, chartaceous, lanceolate, margin membranous and ciliate, apex acute, slightly shorter than the lower glume, 0.7 cm long, <0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin membranous and ciliate, apex obtuse, 0.55 cm long, < 0.1 cm wide; upper lemma glabrous, membranous, lanceolate, 0.45─0.55 cm long, xx mm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1 cm long. *Awn* present, geniculate, column twisted and hispidulous, 2.0─2.7 cm long, 0.19─0.22 mm thick. *Anthers* 3, 0.20─0.25 cm long. *Ovary and Stigma* ovary 1, 0.10 cm long; stigmas 2, plumose. *Caryopsis* 0.3-0.4 mm long, 0.75 mm thick.

Etymology. – Specific epithet was named after John Henry Hutton, English anthropologist and administrator in the Indian Civil Service during the period of the British Raj.

Vernacular names. – No vernacular names provided for this species

Geograohic distribution. – *Themeda huttonensis* is endemic to India and it is restrictedly found in Nagaland Mountains in Assam state.

Phenology. – Phenological data from specimens informed that flowering time is around October.

Habitat & Ecology. – Themeda huttonensis was documented to occur on hillsides or near watercourse and stream banks at high altitude around 1,500 m above sea level (Fierro, 2014).

Phylogenetic position and morphological evolution. – *Themeda huttonensis* is sister and morphologically similar to *Themeda hookeri*.

Cytogenetics. – No cytogenetic data provided for *T. huttonensis*

Uses and ethnology. – No use data provided for *T. huttonensis*

Specimens examined. – Please see full list of specimens examined in Appendix XIV L.

Themeda idjenensis Jansen in Acta Botanica Neerlandica 1(3): 482. 1952 — Holotype: Indonesia, East Java, gregarious on the Northern slopes of the Idjen plateau and Mt. Tenger, 11 July 1916, *S. H. Koorders 42922* (L barcode L0329849!; isotype: BO barcode BO1460437).

Description. – *Habit* perennial. *Stilt roots* present. *Culms* erect, caespitose, intravaginal growth, glabrous, 300–500 cm long, 2.55–4.73 mm wide. *Leaf sheath* glabrous, 5.8–12.5 cm long. *Ligules* truncate, ciliolate, 2–3 mm long. *Leaf blades* plicate, abaxial surface glabrous to occasionally scabrous, adaxial surfaces glabrous, lanceolate, margin scabrid, apex acuminate, 50–100 cm long, 4–12 mm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, 50–100 cm long. *Spatheoles* glabrous, linear, 2.2–4.0 cm long. *Rachis internodes* fragile, glabrous, oblong, about 0.1 cm long. *Racemes* solitary, 6–7 sterile spikelets, 1 fertile spikelet or rarely 2, 1.6–2.3 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 1.1–1.5 cm long (sessile) and 1.10–1.45 cm long (pedicelled), 0.15–0.20 cm wide (sessile) and 0.15–0.20 cm wide (pedicelled); callus squared, slightly pilose, < 0.1 cm long; lower glume glabrous, coriaceous, lanceolate, margins partly enclose upper glume, apex aristate, 1 spikelet long and wide; upper glume glabrous, coriaceous, lanceolate, margin entire, apex acute, as long as the lower glume, 1.10–1.25 cm long, 1.0–1.5 mm wide; lower lemma glabrous, membranous, lanceolate, 0.35–1.20 cm long (sessile spikelets) and 0.70–1.35 cm long (pedicelled spikelets), <0.1–0.2 cm wide (sessile spikelets) and < 0.1–0.2 cm wide (pedicelled spikelets); upper lemma glabrous, membranous, lanceolate, 0.70–1.55 cm long (sessile spikelets) and 0.65–1.75 cm long (pedicelled spikelets), about 0.1 cm wide (sessile spikelets) and about 0.1 cm wide (pedicelled spikelets); palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1–0.1 cm long. *Fertile pairs* bisexual and barren, deciduous entreily, no fertile pairs or rarely 1, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, velvety with white hairs, elliptic, 0.60─0.90 cm long, 0.15─0.20 cm wide; callus cuneate, hairy with white hairs, attach obliquely, 0.10─0.30 cm long; lower glume pubescent with white hairs, coriaceous, lanceolate, margins partly enclosed, upper glume, apex truncate, 1 spikelet long and wide; upper glume pubescent with white hairs, coriaceous, oblong, margin entire, apex truncate, slightly shorter and narrower than the lower glume, 0.70─0.85 cm long, 1.0─1.5 mm wide; lower lemma glabrous, membranous, lanceolate, 0.5─0.7 cm long, < 0.1─1.0 mm wide; upper lemma glabrous, membranous, lanceolate, 0.20─0.65 cm long, 1.0 mm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1─0.1 cm long, companion spikelets, pedicelled, well developed, male, lanceolate, 1.05─1.50 cm long, 0.1─0.2 cm wide; callus glabrous, linear, about 0.1 cm long; lower glume glabrous, chartaceous, lanceolate, margins partly enclose upper glume, apex mucronate to aristate, 1 spikelet long and wide; upper glume glabrous, chartaceous, lanceolate, margin fringe, apex acuminate, slightly shorter than the lower glume, 1.00─1.25 cm long, 1.00─1.50 mm wide; lower lemma glabrous, membranous, lanceolate, 0.70─1.35 cm long, 1.00 mm wide; upper lemma glarbous, membranous, lanceolate, 0.9─1.8 cm long, 1.0 mm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.1─0.1 cm long. *Awn* present, straight, column twisted and hispidulous, 3.0─5.8 cm long, 0.19─0.44 mm thick. *Anthers* 3, 0.30─0.75 cm long. *Ovary and Stigma* ovary 1, 0.10─0.20 cm long; stigmas 2, plumose. *Caryopsis* 5.0─5.5 mm long, 0.58─1.05 mm thick.

Etymology. – The specific epithet ‘idjenensis’ refers to Idjin, Java, Indonesia where the species was first discovered.

Vernacular names. – No vernacular names provided for this species

Geographic distribution. – *Themeda idjenensis* is endemic to Java, Indonesia.

Phenology. – Flowering time spans from May to August

Habitat & Ecology. – *Themeda idjenensis* is found growing at high elevations (1120─1464 m) on mountain plateau or at the crater such as Idjen plateau and Mount Baluran. According to Veldkamp (2016), this species was found in grass-dominated habitats. Climatic space of *T. idjenensis* was described by high annual precipitation and precipitation of driest quarter (Arthan et al., 2022).

Phylogenetic position and morphological evolution. – No phylogenetic position confirmed for this species, but it is hypothesized to be included in the subclade with other wetland species, based on morphology and distribution range in Southeast Asia.

Cytogenetics. – No cytogenetic data provided for *T. idjenensis*

Uses and ethnology. – No use data provided for *T. idjenensis*

Specimens examined. – Please see full list of specimens examined in Appendix XIV M.

Themeda melanocarpa (Elliott) Arthan, Voronts. & Kellogg **comb. nov.** ≡ ***Andropogon melanocarpus*** Elliott in a Sketch of the Botany of South-Carolina and Georgia 1(2): 146. 1821 ≡ ***Cymbopogon melanocarpus*** (Elliott) Spreng. in Systema Vegetabilium 16(1): 289. 1824 ≡ ***Heteropogon melanocarpus*** (Elliott) Benth. in Journal of the Linnean Society, Botany 19(115–116): 71. 1881 ≡ ***Sorghum melanocarpum*** (Elliott) Kuntze in Revisio Generum Plantarum 2: 792. 1891 — **Lectotype (designated here)**: USA, Georgia, *s.d.*, *S. Elliott 3* (K barcode K000911719!).

= ***Stipa melanocarpa*** Muhl. in Descriptio uberior Graminum 183. 1817 ≡ [***Heteropogon melanocarpus*** (Muhl.) Coulter in Contributions from the United States National Herbarium 2(3): 493. 1894, nom. inval.] — Holotype: USA, Georgia, 1811, *S. Elliott 393* (PH barcode PH00032622!).

= ***Trachypogon scrobiculatus*** Nees in Flora Brasiliensis seu Enumeratio Plantarum 2(1): 347. 1829 ≡ ***Andropogon scrobiculatus*** (Nees) Kunth in Enumeratio Plantarum Omnium Hucusque Cognitarum 1: 507. 1833 ≡ ***Heteropogon scrobiculatus*** (Nees) E. Fourn. in Mexicanas Plantas 2: 64. 1886 — **Types not found.**

= ***Heteropogon acuminatus*** Trin. in Mémoires de l'Académie Imperiale des Sciences de St.-Pétersbourg. Sixième Série. Sciences Mathématique, Physique et Naturelles 2(3): 254. 1832 — Holotype: Brazil, *s.d.*, not traced.

= ***Andropogon polystictus*** Steud. in Synopsis Plantarum Glumacearum 1: 369. 1854 ≡ ***Heteropogon polystictus*** (Steud.) Hochst. in Flora 39: 28. 1856 ≡ **Lectotype**

(designated here): Ethiopia, Dscheladscheranne, 19 September 1840, *G. W. Schimper 2012* (E barcode E00200290!; isotypes: W barcode W18890263690!, W18890263691!, W19160028881!).

= ***Heteropogon betafensis*** A. Camus in Bulletin de la Société Botanique de France 71: 924. 1925 — Holotype: Madagascar, Betafo, May 1914, *H. Perrier de la Bâthie 10714* (P barcode P00450519!; isotype: P barcode P00450520!).

Description. – *Habit* annual. *Rhizomes* present. *Stilt roots* occasionally present. *Culms* erect, unbranched, glabrous, 50─250 cm long, 2.44─9.02 mm thick. *Leaf sheath* pilose with white hairs, midrib and veins with glands, 8.1─8.5 cm long. *Ligules* truncate, eciliate, 0.15 mm long. *Leaf blades* non-plicate, abaxial and adaxial surfaces scabrous, lanceolate, margin scabrid, apex acuminate, 10─50 cm long, 0.14─1.0 cm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, 10─30 cm long. *Spatheoles* glabrous, linear, midrib with glands, 7─12 cm long. *Rachis internodes* fragile, sparsely pilose with white hairs, linear, 0.2─0.3 cm long. *Racemes* solitary, 2─3 homogamous pairs rarely 4 pairs, 2─4 fertile spikelets, 3─6 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 2─6 in number or rarely 8, male or barren, a pair arranging at different levels, persistent, asymmetrical, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 1.15 cm long (sessile) and 1.40 cm long (pedicelled), 0.15 cm wide (sessile spikelets) and 0.20 cm wide (pedicelled spikelets); callus linear, glabrous, < 0.1─0.1 cm long; lower glume glabrous, glandular line on midrib, coriaceous, lanceolate, margins winged, apex attenuate, 1 spikelet long and wide; upper glume glabrous, subchartaceous, lanceolate, margins entire and membranous, apex acuminate, 0.55─1.45 cm long, < 0.10─0.20 cm wide; lower lemma glabrous, membranous, lanceolate, margin ciliate, apex acuminate, 0.40─0.80 cm long (sessile spikelets) and 0.40─0.80 cm long (pedicelled spikelets), < 0.1─0.1 cm wide (sessile spikelets) and 0.1 cm wide cm wide (pedicelled spikelets); upper lemma glarbous, membranous, oblong, margin entire, apex obtuse, 0.45 cm long (sessile spikelets) and 0.55 cm long (pedicelled spikelets), < 0.1 cm wide (sessile spikelets) and < 0.1 cm wide (pedicelled spikelets); palea absent; lodicules 2, oblong, coriaceous, hyaline, < 0.1 cm long. *Fertile pairs* bisexual and barren, deciduous entirely, 2─4 fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, 0.50─0.55 cm long, 0.10─0.13 cm wide; callus linear, hairy with reddish brown hairs, attach obliquely, 0.4 cm long; lower glume densely hirsute with brown hairs, coriaceous, elliptic, margins partly enclosed upper glume, apex truncate, 1 spikelet long and wide; upper glume densely hirsute with brown hairs, coriaceous, oblong, margin inflexed and entire, apex truncate, slightly shorter and narrower than the lower glume, 0.50–0.65 cm long, 0.10–0.15 cm wide; lower lemma glabrous, membranous, lanceolate, margin entire, apex acuminate, 0.3 cm long, 1.0 mm wide; upper lemma glabrous, membranous, much reduced, attached to awn; palea absent; lodicules 2, cuneate, coriaceous or membranous, hyaline, about 0.1 cm long, companion spikelets, pedicelled, well developed, male, lanceolate, asymmetrical, 1.6 cm long, 0.25 cm wide; callus glabrous, linear, 0.2–0.3 cm long; lower glume glabrous, glandular line on midrib, chartaceous, lanceolate, margins partly enclose upper glume, apex acute, 1 spikelet long and wide; upper glume glabrous or sparsely hirsute with short white hairs, subchartaceous, lanceolate, margin inflexed and ciliate, apex acute, slightly shorter than the lower glume, 0.65–1.55 cm long, < 0.1–0.15 cm wide; lower lemma glabrous, membranous, lanceolate, margins inflexed and ciliate, apex obtuse, 0.50–0.65 cm long, < 0.1–1.0 mm wide; upper lemma absent; palea absent; lodicules mostly absent, if present, hyaline, < 0.1 cm long. *Awn* present, geniculate, column twisted and hispidulous, 8.0–13.0 cm long, 0.33–0.49 mm thick. *Anthers* 3, < 0.1–0.1 cm long. *Ovary and Stigma* ovary 1, 0.1 cm long; stigmas 2, plumose. *Caryopsis* 4.0–4.5 mm long, 0.86–1.22 mm thick.

Etymology. – The specific epithet 'melanocarpus' come from two Greek words 'melas' meaning 'black' and 'karpos' meaning 'fruit', which describes mature black spikelets.

Vernacular names. – Sweet tanglehead (English)

Geographic distribution. – The distribution ranges of *Themeda melanocarpa* cover South Central China, South Asia, African tropical and subtropical sub-Saharan countries, Caribbean, North and South American tropical countries.

Phenology. – September to December but occasionally in March

Habitat & Ecology. – *Themeda melanocarpa* occupy both savannas and wetlands. These savannas include African savannas with dominant tree species in genera *Acacia*, *Brachystegia*, *Colophospermum*, *Commiphora, Julbernardia*, and *Pterocarpus*.

Phylogenetic position and morphological evolution. – *Themeda melanocarpa* (formerly *Heteropogon melanocarpus*) is morphologically unique as it is the only species producing specialized glands in midribs, spatheoles, and glumes. Its phylogenetic position is in the

Themeda clade and morphology also support *Themeda*-like characteristics. *Themeda melanocarpa* is closely related to *Themeda ritchiei*.

Cytogenetics. – Chromosome numbers of *Themeda melanocarpus* are 20 and 22 (Hoshino & Davidse, 1988; Moffett & Hurcombe, 1949).

Uses and ethnology. – No use data provided for *T. melanocarpa*.

Specimens examined. – Please see full list of specimens examined in Appendix XIV N.

Note. – Lectotypification of *Themeda melanocarpa* was carried out in this study as Elliott mentioned in the protologue "My specimens were too imperfect to enable me to examine accurately the corolla, stamens or style." We selected specimen from USA, Georgia collected by Elliott as the lectotype of *Themeda melanocarpa*.

Themeda minor L. Liu in Flora Xizangica 5: 343‒344. 1987 — Holotype: China, Xizang, Zayü, 10 July 1973, *L Liu 654* (PE barcode PE00615853!; isotype: PE barcode PE00615852!).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* absent. *Culms* erect, intravaginal, glabrous, 30‒50 cm long, 1.25‒1.70 mm thick. *Leaf sheaths* pilose on the margins, 2.5‒4.5 cm long. *Ligules* truncate, ciliate, about 1 mm long. *Leaf blades* non-plicate, abaxial and adaxial surfaces pilose with tuberculate hairs, lanceolate, margin scabrid, apex acute, 3‒8 cm long, 0.1‒0.2 cm wide. *Inflorescences* axillary and terminal, inflorescence paniculate. *Spatheoles* glabrous, lanceolate, 1.1‒1.5 cm long. *Rachis internodes* fragile, pilose with white hairs, oblong, < 0.1 cm long. *Racemes* solitary, 6 sterile spikelets, 1 fertile spikelet, 0.80‒0.95 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male or barren, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 0.4‒0.5 cm long, < 0.1‒0.1 cm wide; callus squared, slightly pilose, < 0.1 cm long; lower glume pilose with white tuberculate hairs, chartaceous, lanceolate, margins entire and partly enclose upper glume, apex acute, 1 spikelet long and wide; upper glume glabrous, chartaceous, lanceolate, margin entire, apex acute, as long as the lower glume, 0.45‒0.5 cm long, 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, 0.35‒0.40 cm long, about 0.1 cm wide ; upper lemma glabrous, membranous, lanceolate, 0.45‒0.50, about 0.1 cm wide; palea minute or absent; lodicules 2, cuneate, coriaceous, < 0.10 cm long. *Fertile pairs* bisexual and barren, deciduous entirely, no fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, about 0.40 cm long, < 0.1–0.1 cm wide; callus cuneate, pilose with white hairs, attach obliquely, 0.10 cm long; lower glume pilose with white hairs at the apex, coriaceous, lanceolate, margins entire and partly enclosed upper glume, apex acute, 1 spikelet long and wide; upper glume pubescent with white hairs, coriaceous, oblong, margin entire, apex acuminate, slightly shorter and narrower than the lower glume, 0.4 cm long, < 0.1–0.1 cm wide; lower lemma slightly pilose, membranous, lanceolate, 0.25 cm long, < 1.0 mm wide; upper lemma glabrous, membranous, lanceolate, 0.30–0.35 cm long, 1.0 mm wide; palea minute or absent; lodicules 2, cuneate, coriaceous, companion spikelets, pedicelled, well developed, barren or male, lanceolate, about 0.5, 0.5, 0.55 cm long, < 0.1 cm wide; callus pilose with white hairs, oblong, < 0.1 cm long; lower glume densely hirsute with white hairs, chartaceous, lanceolate, margins partly entire and enclose upper glume, apex acute, 1 spikelet long and wide; upper glume pubescent, chartaceous, lanceolate, margin entire, apex acuminate, slightly shorter than the lower glume, 0.4–0.5 cm long, < 0.1 cm wide; lower lemma glarbous, membranous, lanceolate, 0.30 cm long, < 1.0 mm wide; upper lemma glabrous, membranous, lanceolate, 0.40 cm long, < 1.0 mm wide; palea minute or absent; lodicules 2, cuneate, coriaceous. *Awn* poorly developed, about 0.4 cm long. *Anthers* 3, 0.15 cm long. *Ovary and Stigma* ovary 1; stigmas 2, plumose.

Etymology. – The specific epithet ‘minor’, a Latin word meaning small, is a comparative term explaining that this species is smaller than other related species.

Vernacular names. – Xiao jian cao (小菅草; Chinese)

Geographic distribution. – *Themeda minor* is endemic to China

Phenology. – Flowering time spans from June to September.

Habitat & Ecology. – A report from Liu et al. (2004) described the habitat of *Themeda minor* to be semi-arid region and dominated by *Robinia pseudoacacia*.

Phylogenetic position and morphological evolution. – *Themeda minor* is closely related to Indian endemic species *T. hookeri* and *T. huttonensis*.

Cytogenetics. – No cytogenetic data provided for *T. minor*

Uses and ethnology. – No use data provided for *T. minor*

Specimens examined. – **CHINA. Tibet:** Nyingchi, Zayü County, 2000 m, 10 July 1973, *Qinghai-Tibet team 654* (PE)

Themeda mooneyi Bor in Kew Bulletin in 1951: 451. 1952 — Holotype: India, Odisha, near Pottangi, Koraput District, 4100 ft. alt., *H. F. Mooney 4064* (K barcode K00245982!; isotype: K barcode K00911697!).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* absent. *Culms* erect, caespitose, intravaginal growth, glabrous, 20–50 cm long, 0.72–1.10 mm wide. *Leaf sheaths* glabrous, keeled, 3.6–5.5 cm long. *Ligules* truncate, ciliolate, 1.5 mm long. *Leaf blades* non-plicate, abaxial surface glabrous, adaxial surface pubescent with white hairs, lanceolate, margin scabrid, apex acuminate, 12.6–30.0 cm long, 2–4 mm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, lax. *Spatheoles* glabrous, lanceolate, 2.2–5.0 cm long. *Rachis internodes* fragile, densely pilose with yellow hairs, linear, about 0.1 cm long. *Racemes* solitary, 7 sterile spikelets, 2 fertile spikelets, 1.7–2.1 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 1.00–1.40 cm long (sessile) and 1.0–1.1 cm long (pedicelled), 0.15–0.20 cm wide (sessile spikelets) and 0.15 cm wide (pedicelled spikelets); callus square, glabrous, very short and narrow, < 0.1 cm long; lower glume densely pilose with tuberculate white hairs, coriaceous, lanceolate, margins partly enclose upper glume, apex obtuse, 1 spikelet long and wide; upper glume glabrous, chartaceous, lanceolate, margins membranous and ciliate, apex acute, shorter than the lower glume, 0.65–0.80 cm long, 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin membranous and ciliate, apex acuminate, 0.70–0.75 cm long (sessile spikelets) and 0.70–0.75 cm long (pedicelled spikelets), < 0.1 cm wide; upper lemma glabrous, membranous, lanceolate, margin entire, apex acuminate, 0.60–0.70 cm long (sessile spikelets) and 0.60 cm long (pedicelled spikelets), very narrow, < 0.1 cm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.10 cm long. *Fertile pairs* bisexual and barren, deciduous entirely, 1 fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, oblong, 0.50 cm long, 0.10 cm wide; callus oblong, hairy with tawny hairs, attach obliquely, 0.15 cm long; lower glume glabrous and setose at the apex, coriaceous, lanceolate, margins partly enclosed upper glume, apex obtuse, 1 spikelet long and wide; upper glume glabrous, coriaceous, oblong, slightly obtuse at the apex, margin inflexed, apex obtuse, as long as the lower glume, 0.45–0.60 cm long, < 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, 0.35–0.40 cm long, < 0.1 cm wide; upper lemma glabrous, membranous, lanceolate, 0.20 cm long, xx mm wide; palea minute or absent; lodicules 3, cuneate, coriaceous, < 0.10 cm long, companion spikelets, pedicelled, well developed, male, lanceolate, 1.1–1.3 cm long, 0.1 cm wide; callus sparsely pilose with yellow hairs, linear, slightly broadened at the apex, 0.10–0.20 cm long; lower glume glabrous, coriaceous, lanceolate, margins partly enclose upper glume, apex acuminate, 1 spikelet long and wide; upper glume glabrous, chartaceous, lanceolate, margins inflexed, membranous and ciliate, apex acuminate, slightly shorter than the lower glume, 0.70–0.85 cm long, 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margins membranous and ciliate, apex acuminate, 0.40–0.70 cm long, < 0.1 cm wide; upper lemma glabrous, membranous, lanceolate, margins membranous and entire, apex acuminate, 0.50–0.60 cm long, < 0.1 cm wide; palea minute or absent; lodicules 2, cuneate, coriaceous, < 0.1 cm long. *Awn* present, geniculate, column twisted and hispidulous, 2.5–4.5 cm long, 0.16–0.27 mm thick. *Anthers* 3, 0.35–0.40 cm long. *Ovary and Stigma* ovary 1, < 0.10–0.15 cm long; stigmas 2, plumose. *Caryopsis* 2.5 mm long.

Etymology. – The species was named in honour of Herbert Francis Mooney, Irish-born Indian forester and plant collector.

Vernacular names. – No vernacular names provided for *T. mooneyi*

Geographic distribution. – *Themeda mooneyi* is endemic to India

Phenology. – Flowering time span from August to October

Habitat & Ecology. – *Themeda mooneyi* exists in moist savannas of India such as semi-evergreen forest and moist mixed deciduous forests or montane grassland with wet conditions as indicated by coexistence with sedge species in genera *Cyperus* and *Fimbristylis*.

Phylogenetic position and morphological evolution. – *Themeda mooneyi* belong to the subclade including Indian endemic species such as *Themeda hookeri*, *Themeda huttonensis*, and *Themeda strigosa*.

Cytogenetics. – Birari (1980, 1981) investigated that *Themeda mooneyi* is a diploid species (2n = 20).

Uses and ethnology. – No use data provided for *T. mooneyi*

Specimens examined. – Please see full list of specimens examined in Appendix XIV O.

Themeda novoguineensis (Reeder) Jansen (1952: 483). ≡ ***Themeda gigantea*** (Cav.) Hack. var. ***novoguineensis*** Reeder (1948: 374). ≡ Holotype: Papua New Guinea, Central Province, Nakeo District, Baroka, 50 m. alt., April 1933, *L. J. Brass 3710* (GH barcode GH00024496!; isotypes: BRI barcode BRI-AQ0304787!, K barcode K000290049!, US barcode US04358554!).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* present. *Culms* erect, caespitose, intravaginal growth, glabrous, 140–400 cm long, 3.95–8.48 mm wide. *Leaf sheaths* glabrous, keeled, 5.2–12.8 cm long. *Ligules* truncate, ciliolate, 1.0–1.2 mm long. *Leaf blades* non-plicate, abaxial surface glabrous and scabrous, adaxial surface glabrous, lanceolate, margin scabrid, apex acuminate, 30–100 cm long, 2–7 mm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, 30–40 cm long. *Spatheoles* glabrous, lanceolate, 1.0–2.9 cm long. *Rachis internodes* fragile, pilose with white hairs, linear, < 0.1–0.1 cm long. *Racemes* solitary, 6 sterile spikelets, 1 fertile spikelets, 1.15–1.60 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 0.75–0.90 cm long (sessile) and 0.70–0.90 cm long (pedicelled), 0.10 cm wide (sessile spikelets) and 0.10 cm wide (pedicelled spikelets); callus square, sparsely pilose with white hairs, attached obliquely, 0.2–0.3 cm long; lower glume glabrous, coriaceous, lanceolate, margins partly enclose upper glume, apex acuminate, 1 spikelet long and wide; upper glume glabrous, coriaceous, lanceolate, margin membranous and ciliate, apex acuminate, shorter than the lower glume, 0.65–0.90 cm long, 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin membranous and ciliate at the top, apex acuminate, (0.10–0.40) 0.6–0.9 cm long (sessile spikelets) and <0.10–0.40 cm long (pedicelled spikelets), < 0.1–0.1 cm wide; upper lemma glabrous, membranous, lanceolate, margin entire, apex acute, 0.55–0.80 cm long (sessile spikelets) and 0.50–0.80 cm long (pedicelled spikelets), < 0.1 cm wide; palea irregular shape, membranous, hyaline, 0.3–0.45 cm long; lodicules 2, cuneate, coriaceous, < 0.10–0.10 cm long. *Fertile pairs* bisexual and barren, deciduous entirely, no fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, 0.50─0.70 cm long, 0.10 cm wide; callus linear, pilose with yellow hairs, attach obliquely, 0.20─0.30 cm long; lower glume puberulous, coriaceous, oblong, margins partly enclosed upper glume, apex acuminate, 1 spikelet long and wide; upper glume hirsute with short hairs, coriaceous, oblong, margin inflexed and entire, apex obtuse, slightly shorter the lower glume, 0.45─0.65 cm long, < 0.1─0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin ciliate at the apex, apex acuminate, 0.50─0.60 cm long, < 0.1 cm wide; upper lemma reduced and attached to the awn, glabrous, membranous, lanceolate, very minute; palea linear, membranous, hyaline, 0.20─0.3 cm long; lodicules 2, cuneate, membranous, < 0.10─0.10 cm long, companion spikelets, pedicelled, well developed, male or barren, lanceolate, 0.60─0.95 cm long, 0.1 cm wide; callus glabrous, linear, 0.20 cm long; lower glume glabrous, chartaceous, lanceolate, margins partly enclose upper glume, apex acuminate, 1 spikelet long and wide; upper glume glabrous, chartaceous, lanceolate, margins membranous and ciliate, apex acuminate, slightly shorter than the lower glume, 0.60─0.90 cm long, < 0.1─0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margins ciliate, apex acuminate, 0.50─0.75 cm long, < 0.1─0.1 mm wide; upper lemma glabrous, membranous, lanceolate, margins entire, apex acute, 0.40─0.65 cm long, < 0.1 mm wide; palea irregular shape (bifid), hyaline, 0.15─0.3 cm long; lodicules 2, oblong, coriaceous, < 0.1─0.10 cm long. *Awn* present, straight, column twisted and hispidulous, 0.85─4.00 cm long, 0.25─0.43 mm thick. *Anthers* 3, 0.17─0.45 cm long. *Ovary and Stigma* ovary 1, 0.10─0.15 cm long; stigmas 2, plumose. *Caryopsis* 2.0 mm long, 0.56 mm thick.

Etymology. – The specific epithet '*novoguineensis*' refers to New Guinea where the species was first discovered.

Vernacular names. – No vernacular names provided for this species

Geographic distribution. – *Themeda novoguineensis* is endemic to New Guinea.

Phenology. – Mostly from April to June and occasionally from January to March.

Habitat & Ecology. – *Themeda novoguineensis* is present in Eucalyptus savannas, especially in transition zone to interfluves area or tall grassland dominated by grasses in genera *Cymbopogon* and *Imperata.*

Phylogenetic position and morphological evolution. – *Themeda novoguineensis* is grouped with the subclade containing species lacking spikelet pairs in the raceme such as *Themeda tremula* and *Themeda triandra*.

Cytogenetics. – No cytogenetic data for *T. novoguineensis*

Uses and ethnology. – No use data provided for *T. novoguineensis*

Specimens examined. – Please see full list of specimens examined in Appendix XIV P.

Themeda odishae Chorghe, K. Prasad, Prasanna & Y. V. Rao in Phytotaxa 245(2): 183. 2016 — Holotype: India, Orissa, Gajapati District, Mahendragiri Hills, 17 September 2014, *Alok Chorghe & K. Prasad 4209* (BSID barcode BSID0017186!, isotypes: BSID barcode BSID0017187!, CAL barcodes CAL0000025358!, CAL0000025359!).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* absent. *Culms* decumbent, caespitose, intravaginal growth, glabrous, up to 35 cm long. *Leaf sheaths* glabrous, keeled, margin winged with tuberculate hairs, 2.0–5.0 cm long. *Ligules* truncate, ciliolate, 1.0 mm long. *Leaf blades* non-plicate, abaxial and adaxial surfaces glabrous and scabrous, margin scabrid, apex attenuate, 5–12 cm long, 2–2.5 mm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, lax, 3 racemes subtended by spathe. *Spatheoles* glabrous, lanceolate, 3.0–7.0 cm long. *Rachis internodes* fragile. *Racemes* solitary, 7 sterile spikelets, 2 fertile spikelets, 1.5–2.0 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 0.70–0.90 cm long, 0.12–0.15 cm wide; callus linear, glabrous, about 0.1 cm long; lower glume sparsely pilose with tuberculate white hairs, coriaceous, lanceolate, margins 2-keeled, keels winged and scabrid, apex acute, 1 spikelet long and wide; upper glume glabrous, chartaceous, lanceolate, shorter than the lower glume, apex acute; lower lemma glabrous, membranous, lanceolate, margin ciliate, apex obtuse, 0.70–0.75 cm long, 0.10–0.12 cm wide; upper lemma glabrous, membranous, linear, 0.65–0.70 cm long, 0.5 mm wide; palea absent; lodicules 2, linear, apex truncate, coriaceous, very minute. *Fertile pairs* bisexual and barren, deciduous entirely, 1 fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, 0.50–0.55 cm long, 0.10–0.12 cm wide; callus linear, pilose with whitish brown hairs, attach obliquely, 0.20 cm long; lower glume glabrous, coriaceous, lanceolate, scabrid, margins partly enclosed upper glume, apex obtuse, 1 spikelet long and wide; upper glume glabrous, chartaceous, lanceolate, apex obtuse, margin ciliate, slightly shorter the lower glume, 0.50–0.55 cm long, 0.8–1.0 mm wide; lower lemma glabrous, membranous, linear, 0.40–0.45 cm long, 0.7–0.8 mm wide; upper lemma glabrous, membranous, linear, 0.25–0.30 cm long, xx mm wide; palea absent; lodicules 2, coriaceous, very minute. companion spikelets, pedicelled, well developed, male, lanceolate, 0.80–0.90 cm long, 0.12–0.15 cm wide; callus glabrous, linear, about 0.15 cm long; lower glume pilose with white hairs in upper half, coriaceous, lanceolate, margins partly enclose upper glume, apex acute, 1 spikelet long and wide; upper glume glabrous, chartaceous, lanceolate, margin membranous, apex acute, slightly shorter than the lower glume, 0.75–0.85 cm long, 0.10–0.12 cm wide; lower lemma glabrous, membranous, linear, 0.65–0.70 cm long, 0.8–1.0 mm wide; upper lemma glabrous, membranous, linear, 0.54–0.60 cm long, 0.5–0.7 mm wide; palea absent; lodicules 2, coriaceous, very minute. *Awn* present, geniculate, column twisted and hispidulous, 3.0–3.5 cm long, xx mm thick. *Anthers* 3, 0.38–0.40 cm long. *Ovary and Stigma* ovary 1, stigmas 2, plumose. *Caryopsis* unknown.

Etymology. – The specific epithet ‘*odishae*’ refers to Odisha State, India where the species was first discovered.

Vernacular names. – No vernacular names for this species

Geographic distribution. – This species is endemic to Gajapati District, India.

Phenology. – Information based on a single specimen is September

Habitat & Ecology. – Chorghe et al. (2016) reported that *T. odishae* was found on rock outcrops at the Mahendragiri hills at elevation between 1300 to 1400 m.

Phylogenetic position and morphological evolution. – No phylogenetic position of *T. odishae* has not been investigated. Morphological differences between *T. odishae* and closely related species, *T. mooneyi* and *T. saxicola* are the number of pedicelled spikelets and inflorescence structure.

Cytogenetics. – No cytogenetic data for *T. odishae*.

Uses and ethnology. – No use data provided for *T. odishae*.

Specimens examined. – **INDIA. Odisha State:** Gajapati District, Mahendragiri Hills, 1393 m, 18°58'5.3"N, 84°22'8.6"E, 17 September 2014, *A. Chorge & K. Prasad 4209* (BSID, CAL).

Themeda palakkadensis Chorghe, K. Prasad & Lakshmin. in Taiwania 64(3): 231.
2019 — Holotype: India, Kerala, Palakkad District, Elvai Malai, 12 November 2016, *K. Prasad 8485* (CAL barcode CAL0000033967!; isotypes: BSI barcode BSI0000001616!, CAL barcodes CAL0000033968!).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* absent. *Culms* erect, caespitose, intravaginal growth, glabrous, 30‒60 cm long. *Leaf sheaths* glabrous, keeled, 1.0‒5.0 cm long. *Ligules* truncate, eciliate, 2.0 mm long. *Leaf blades* non-plicate, abaxial and adaxial surfaces glabrous, lanceolate, margin scabrid, apex attenuate, 2‒15 cm long, 2.0‒5.0 mm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, 5.0‒20.0 cm long. *Spatheoles* densely pilose with tuberculate hairs, lanceolate, 2.0‒5.0 cm long, 0.3‒0.6 cm wide. *Rachis internodes* fragile, linear, slightly broadened at the apex, about 0.2 cm long. *Racemes* clustered, 6 sterile spikelets, 1 fertile spikelets, about 1.0 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at the same levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 0.80‒1.00 cm long, 0.15‒0.20 cm wide; callus square, glabrous, attached obliquely, very short and narrow; lower glume sparsely pilose with tuberculate white hairs, chartaceous, lanceolate, margins 2-keeled, keels broadly winged, apex obtuse, 1 spikelet long; upper glume glabrous, membranous, lanceolate, as long as the lower glume, apex acute, 0.80‒0.90 cm long, 0.10‒0.15 cm wide; lower lemma glabrous, membranous, lanceolate, margin ciliate, 0.80‒0.85 cm long, 0.10 cm wide; upper lemma absent; palea absent. *Fertile pairs* bisexual and barren, deciduous entirely, no fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, oblong, 0.50‒0.60 cm long, 0.15‒0.20 cm wide; callus cuneate, pilose with reddish brown hairs, attach obliquely, 0.20 cm long; lower glume densely pilose with reddish brown hairs, coriaceous, oblong, margins partly enclosed upper glume, apex obtuse, 1 spikelet long; upper glume densely pilose with reddish brown hairs, chartaceous, lanceolate, margin inflexed, apex obtuse, slightly shorter the lower glume, 0.45‒0.55 cm long, about 1.0 mm wide; lower lemma glabrous, ovate, membranous, margin ciliate at the top, apex truncate, 0.40‒0.45 cm long, 0.8‒0.1 mm wide; upper lemma glabrous, membranous, 0.15‒0.25 cm long, 0.25‒0.30 cm wide; palea absent; companion spikelets, pedicelled, well developed, male, lanceolate, 0.70‒0.80 cm long, 0.10‒0.15 cm wide; callus glabrous, cuneate, about 0.10 cm long; lower glume glabrous, chartaceous, lanceolate, margins keeled, keels winged, partly enclose upper glume, apex acuminate, 1 spikelet long; upper glume glabrous, membranous, lanceolate, margins ciliate, apex acute, slightly shorter than the lower glume, 0.70–0.75 cm long, 0.10–0.15 cm wide; lower lemma glabrous, membranous, lanceolate, margins membranous and ciliate, 0.65–0.70 cm long, about 1.0 mm wide; upper lemma absent; palea absent. *Awn* present, geniculate, column twisted and hispidulous, 2.5–3.5 cm long. *Anthers* 3, 0.4–0.5 cm long. *Ovary and Stigma* ovary 1, stigmas 2, plumose. *Caryopsis* 0.25–0.30 cm long, about 0.5 mm wide.

Etymology. – The specific epithet '*palakkadensis*' refers to Palakkad District, Kerala State, India where the species was first discovered.

Vernacular names. – No vernacular names for this species

Geographic distribution. – This species is endemic to Palakka District, Kerala State, India (Chorge et al., 2019).

Phenology. – September to December

Habitat & Ecology. – *Themeda palakkadensis* was found growing on rock outcrops at elevation from 1600 to 1900 m (Chorge et al., 2019).

Phylogenetic position and morphological evolution. – Phylogenetic position remained unknown; however, its morphology suggests that it be a close relative to *Themeda triandra* as raceme comprises of

Cytogenetics. – No cytogenetic data provided for *T. palakkadensis*.

Uses and ethnology. – No use data provided for *T. palakkadensis*.

Specimens examined. – **INDIA. Kerala State:** Palakkad District, Elivai Malai, 1858 m, 10°56′06.34″N, 76°38′20.76″E, 12 November 2016, *K. Prasad 8480, 8485* (BSI, CAL); 1570 m, 10°56′41.98″N, 76°38′40.81″E, 12 November 2016, *K. Prasad 8465* (CAL); 1561 m, 10°56′42.41″N, 76°38′41.60″E, 12 November 2016, *K. Prasad 8463* (CAL)

Themeda pseudotremula Potdar, Salunkhe & S. R. Yadav in Kew Bulletin 58(1): 243. 2003 — Holotype: India, Maharashtra, Tillari ghat, Kolhapur District, 12 November 2001, *G. G. Potdar 801* (CAL barcode CAL0000002336!; isotypes: BSI barcode BSI0000000674!, BSI0000000675!, K! barcode K001089705!).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* absent. *Culms* erect, base geniculately ascending, caespitose, intravaginal growth, glabrous, 80–200 cm long, about 02 cm thick. *Leaf sheaths* hairy with tuberculate hairs, 2.9–3.6 cm long. *Ligules* truncate, ciliolate, 1.5 mm long. *Leaf blades* non-plicate, abaxial glabrous or hirsute, adaxial surfaces pilose with tuberculate hairs, lanceolate, margin scabrid, apex attenuate, 30–60 cm long, 5.0–12.0 mm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, fasciculate, 20–50 cm long. *Spatheoles* surface glabrous, pilose with tuberculate hairs on the margin, lanceolate, 1.4–1.7 cm long. *Rachis internodes* fragile, pilose with tawny hairs, linear, about 0.1 cm long. *Racemes* clustered, 6 sterile spikelets, 2 fertile spikelets rarely 3, 0.5–1.0 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at slightly different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 0.70–0.90 cm long, 0.5–1.7 mm wide; callus oblong, pilose with tawny hairs, attached obliquely, very short; lower glume pilose with tuberculate white hairs, membranous, lanceolate, margins with tuberculate hairs, apex acute, 0.70–0.85 cm long, 1.2–1.5 mm wide; upper glume surface glabrous, membranous, lanceolate, margin ciliate, apex acuminate, slight shorter than the lower glume, 0.65–0.75 cm long, 0.80–1.0 cm wide; lower lemma glabrous, membranous, oblong, margin ciliate, apex obtuse, 4.0–5.0 mm long, 0.5–0.7 mm wide; upper lemma glabrous, membranous, linear, margin ciliate, apex acute, about 0.3 cm long, very narrow, < 1.0 mm wide; palea absent; lodicules cuneate, coriaceous, very short, < 1 mm long. *Fertile pairs* bisexual and barren, deciduous entirely, 1 fertile pair rarely 2, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, lanceolate, 0.25–0.35 cm long, 0.80–1.00 mm wide; callus oblong, pilose with reddish brown hairs, attach obliquely, < 0.1 cm long; lower glume densely pilose with reddish brown hairs, coriaceous, lanceolate, deeply channelled on dorsal side, margins partly enclosed upper glume, apex obtuse, 1 spikelet long; upper glume densely pilose with reddish brown hairs, coriaceous, lanceolate, deeply 2-channelled, apex obtuse, as long as the lower glume, 0.25–0.30 cm long, 0.50–0.60 mm wide; lower lemma glabrous, membranous, lanceolate, margin ciliate, apex acute, 0.20–0.25 cm long, 0.3–0.5 mm wide; upper lemma reduced to membranous base of awn; palea absent; lodicules 2, cuneate, coriaceous, companion spikelets, pedicelled, well developed, male, lanceolate, 0.50–0.60 cm long, 0.60–0.80 mm wide; callus glabrous, linear, 0.20–0.25 cm long; lower glume pilose with tuberculate white hairs, chartaceous, lanceolate, margins with tuberculate hairs, partly enclose upper glume, apex acute, 0.50–0.60 cm long, 0.80–0.10 mm wide; upper glume pilose with tuberculate white hairs, membranous, lanceolate, margin ciliate, apex obtuse, slightly shorter than the lower glume, 0.45–0.60 cm long, 0.40–0.70 mm wide; lower lemma glabrous, membranous, lanceolate, margin ciliate, apex obtuse, 0.25–0.40 cm long, 0.50–0.60 mm wide; upper lemma absent; palea absent; lodicules 2, cuneate, coriaceous. *Awn* present, geniculate, column twisted and hispidulous, 2.0–3.0 cm long, 0.22–0.31 mm wide. *Anthers* 3, 0.12–0.15 cm long. *Ovary and Stigma* ovary 1, 0.3–0.5 mm long, stigmas 2, plumose. *Caryopsis* 0.25–0.30 cm long, 0.8–1.0 mm wide.

Etymology. – The specific epithet '*pseudotremula*' is composed of two Latin words, 'pseudo' and 'tremula'. The word 'pseudo' was used to distinguish this species with closely related species, *T. tremula*.

Vernacular names. – No vernacular names provided for *T. pseudotremula*.

Geographic distribution. – *Themeda pseudotremula* is endemic to Kolhapur District, Maharashtra State, India (Potdar et al., 2003).

Phenology. – The specimens only recorded that flowering time is November.

Habitat & Ecology. – *Themeda pseudotremula* grows in moist conditions such as moist deciduous forests or moist to wet microhabitats at medium elevations (Potdar et al., 2003).

Phylogenetic position and morphological evolution. – Phylogenetic position remained unknown

Cytogenetics. – No cytogenetic data provided for *T. pseudotremula*

Uses and ethnology. – No use data provided for *T. pseudotremula*

Specimens examined. – **INDIA. Maharashtra State:** Kolhapur District, Tillari Ghat, 400-800 m, 12 November 2001, *G. Potdar 801* (CAL, K).

Note. – *T. pseudotremula* isotype deposited in BLAT herbarium cannot be accessed online.

Themeda ritchiei (Hook. f.) Arthan, Voronts. & Kellogg **comb. nov.** ≡ ***Andropogon ritchiei*** Hook. f. in The Flora of British India 7(21): 201. 1896 ≡ ***Heteropogon ritchiei*** (Hook. f.) Blatt. & McCann in Journal of the Bombay Natural History Society 32: 623. 1928 — Holotype: India, the Deccan, Karnataka Belgaum, South of Ghats hills, *s.d, D. Ritchie 884* (K barcode K000245946!; isotype: CAL barcode CAL0000002307, photograph!).

Description. – *Habit* annual. *Rhizomes* absent. *Stilt roots* occasionally present. *Culms* erect, glabrous, 90–120 cm long, 0.78–5.85 mm thick. *Leaf sheaths* glabrous, 3.7–10.0 cm long. *Ligules* truncate, eciliate, 0.4–0.6 cm long. *Leaf blades* non-plicate, abaxial and adaxial surfaces pilose with tuberculate yellow hairs, lanceolate, margin scabrid, apex acuminate, 15–45 cm long, 0.8–1.0 cm wide. *Inflorescences* axillary and terminal, inflorescence paniculate. *Spatheoles* glabrous, lanceolate, 1.6–6.9 cm long. *Rachis internodes* fragile, pilose with tawny hairs, linear, 0.1–0.2 cm long. *Racemes* solitary, unilateral, 10–14 sterile spikelets, 5–7 fertile spikelets, 2.5–4.9 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 2–4 in number, male, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, asymmetrical, lanceolate, 0.70–1.15 cm long, 0.20–0.35 cm wide; callus linear, pilose with tawny hairs, attached obliquely, 0.20 cm long; lower glume surface pilose with tuberculate tawny hairs throughout or at the apex, chartaceous, lanceolate, margins keeled, winged keels, apex obtuse, 1 spikelet long and wide; upper glume surface glabrous, chartaceous, lanceolate, margin fringe, apex obtuse, slightly shorter than the lower glume, 0.70–1.05 cm long, 0.2 cm wide; lower lemma glabrous, membranous, lanceolate, margin entire, apex obtuse, 0.70–0.90 mm long, < 0.1 cm wide; upper lemma glabrous, membranous, linear, margin entire, apex acute, 0.50–0.80 cm long, < 0.1 cm wide; palea absent; lodicules 3, cuneate, coriaceous, < 1.0–1.0 mm long. *Fertile pairs* bisexual and barren, deciduous entirely, 4–8 fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, linear, 0.40–0.60 cm long, 0.15–0.25 cm wide; callus linear, pilose with tawny hairs, attach obliquely, 0.20 cm long; lower glume pubescent with tawny hairs throughout, coriaceous, elliptic, margins partly enclosed upper glume, apex obtuse, 1 spikelet long and wide; upper glume pubescent with tawny hairs, coriaceous, oblong, margin inflexed and ciliate, apex obtuse, slightly shorter than the lower glume, 0.45–0.60 cm long, < 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin entire, apex acute, 0.30–0.35 cm long, < 0.1–0.1 cm wide; upper lemma glabrous, membranous, linear, margin entire, apex obtuse, 0.10 cm long, < 0.10 cm wide; palea absent or minute; lodicules 2, cuneate, coriaceous, < 0.1─0.1 cm long, companion spikelets, pedicelled, well developed, male, lanceolate, 0.80─1.20 cm long, 0.25─0.35 cm wide; callus glabrous, linear, 0.1 cm long; lower glume pilose with tuberculate tawny hairs on wings, chartaceous, lanceolate, margins keeled, apex acute, 1 spikelet long; upper glume glabrous, chartaceous, lanceolate, margins inflexed, membranous and ciliate, apex acute, 0.85–1.05cm long, 0.10–0.15 cm wide; lower lemma glabrous, membranous, lanceolate, margin ciliate at the top, apex acute, 0.50─1.00 cm long, 0.1 cm wide; upper lemma glabrous, membranous, lanceolate, margins ciliate at the top, apex acute, 0.60–0.90 cm long, < 0.1 cm wide; palea absent; lodicules 3, cuneate, coriaceous, < 0.1─0.1 cm long. *Awn* present, geniculate, column twisted and hispidulous, 3.0─6.7 cm long, 0.40─0.46 mm thick. *Anthers* 3, 0.55─0.80 cm long. *Ovary and Stigma* ovary 1, 0.1 cm long, stigmas 2, plumose. *Caryopsis* 0.40 cm long, 0.87 mm thick.

Etymology. – The specific epithet '*ritchiei*' was named after David Rirchie (1809─1866) who was a physician and plant collector in India.

Vernacular names. – Simena (Antakarana - Madagascar); Fatakambe (Tsimihety - Madagascar)

Geographic distribution. – *Themeda ritchiei* is endemic to India.

Phenology. – Flowering time covers September to November, based on three specimens.

Habitat & Ecology. – *Themeda ritchiei* occurs in both dry and moist deciduous savannas or open grasslans in marshy areas.

Phylogenetic position and morphological evolution. – *Themeda ritchiei* was placed in the *Themeda* clade in both nuclear and plastome trees and is sister species to *Themeda melanocarpus* (Arthan et al., 2021). Both species represent *Themeda* characteristics such as reduced number of homogamous spikelets and spikelet pairs.

Cytogenetics. – Only single report from Marhold (2008) documented that chromosome number of *H. ritchiei* is 54.

Uses and ethnology. – Gorade & Datar (2014) evaluated that *Themeda* (*Heteropogon*) *ritchiei* belong to palatability grade B, which is a good fodder grass species.

Specimens examined. – Please see full list of specimens examined in Appendix XIV Q.

Themeda sabarimalayana Sreek. & V.J. Nair in Bulletin of the Botanical Survey of India 29: 127. 1989 — Holotype: India, Kerala, Pathanamthitta District, on the way to Sabarimala, 1500 ft. alt., *P. V. Sreekumar 69433* (CAL barcode unknown; isotype: K barcode K000245984!, MH barcode MH unknown).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* present. *Culms* erect, caespitose, intravaginal growth, glabrous, 50‒200 m long, 3.04‒7.87 mm thick. *Leaf sheaths* glabrous, 4.7‒16.6 cm long. *Ligules* truncate, eciliate, 0.1 mm long. *Leaf blades* non-plicate, abaxial and adaxial surfaces glabrous, lanceolate, margin scabrid, apex acute, 15‒40 cm long, 0.4‒1.0 cm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, 30‒60 cm long. *Spatheoles* glabrous, lanceolate, 1.6‒2.1 cm long. *Rachis internodes* fragile, glabrous, linear, < 0.1 cm long. *Racemes* clustered, 6 sterile spikelets, 1 fertile spikelet, 0.8‒1.1 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at the same level, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 0.65‒0.70 cm long, 0.15‒0.20 cm wide; callus square, glabrous, attached obliquely, < 0.1 cm long. lower glume asymmetrical, glabrous, chartaceous, lanceolate, margins winged on one side, margin partly covered upper glume, apex acuminate, 1 spikelet long and wide; upper glume glabrous, chartaceous, lanceolate, margin fringe, apex acute, slightly shorter than the lower glume, 0.6‒0.7 cm long, 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin fringe at the top, apex acute, 0.5‒0.6 cm long, < 0.1 cm wide; upper lemma glabrous, membranous, linear-lanceolate, margin entire, apex acute, 0.10‒0.25 cm long, < 0.1 cm wide; palea absent or minute; lodicules 3, cuneate, coriaceous, < 0.1 cm long. *Fertile pairs* bisexual and barren, deciduous entirely, 1 fertile pair, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, lanceolate, 0.50‒0.60 cm long, about 1.0 mm wide; callus linear, pilose with tawny hairs, attach obliquely, < 0.1‒0.10 cm long; lower glume hirsute with tawny hairs throughout, coriaceous, lanceolate, margins partly enclosed upper glume, apex truncate, 1 spikelet long and wide; upper glume hirsute with tawny hairs, coriaceous, oblong, margin inflexed and entire, apex obtuse, slightly shorter than the lower glume, 0.60‒0.65 cm long, < 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin entire, apex obtuse, 0.40‒0.45 cm long, < 0.1 cm wide; upper lemma glabrous, membranous, linear, margin entire, apex acute, very narrow, minute about 0.1 cm long; palea absent or minute; lodicules 2, oblong, membranous, < 0.1 cm long, companion spikelets, pedicelled, well developed, male, lanceolate, 0.55–0.60 cm long, 0.10 cm wide; callus pubescent, linear, 0.10–0.15 cm long; lower glume glabrous, chartaceous, lanceolate, margins entire and partly enclose upper glume, apex acute, 1 spikelet long; upper glume glabrous, chartaceous, lanceolate, margin ciliate, apex acute, 0.50–0.55 cm long, about 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margins entire, apex acute, 0.45–0.55 cm long, < 0.1 cm wide; upper lemma absent; palea bifid, hyaline, membranous, < 0.1 cm long; lodicules 2, cuneate, coriaceous, very minute, < 0.1 cm long. *Awn* present, geniculate, column twisted and hispidulous, 1.5–3.0 cm long, 0.31–0.33 mm thick. *Anthers* 3, 0.15–0.30 cm long. *Ovary and Stigma* ovary 1, 1.0–1.5 mm long, stigmas 2, plumose. *Caryopsis* 0.66–2.0 mm long, 0.19–0.26 mm thick.

Etymology. – The specific epithet '*sabarimalayana*' was coined from Sabarimala, Kerala, India where this species was discovered.

Vernacular names. – No vernacular names provided for *T. sabarimalayana*

Geographic distribution. – This species is endemic to India and found in Pathanamthitta District, Kerala State and Kodaikanal District, Tami Nadu State (Sreekumar & Nair, 1987).

Phenology. – November to December is flowering time, based on two specimens.

Habitat & Ecology. – No natural habitats described for this species.

Phylogenetic position and morphological evolution. – Phylogenetic position of *Themeda sabarimalayana* is placed in a group of species lacking spikelet pairs such as *Themeda tremula* and *Themeda triandra*.

Cytogenetics. – No cytogenetic data provided for *T. sabarimalayana*

Uses and ethnology. – No use data provided for *T. sabarimalayana*

Specimens examined. – **INDIA. Kerala State:** Pathanamthitta District, on the way to Sabarimala, 1500 ft, 23 December 1980, *P. V. Sreekumar 69433* (CAL, K), **Tamil Nadu State:** Kodaikanal District, Dindigul, Vadakavunchi─Panneikkadu path, 1600 m, 03 November 1987, *K. M. Matthew & K. T. Mathew 51031* (K).

Note. – The holotype of *Themeda sabarimalayana* cannot be found in CAL through Indian Virtual Herbarium, but we examined the isotype with the same collector's name and number in K.

Themeda saxicola Bor in Kew Bulletin 1951: 452. 1951 — Holotype: India, Odisha (Orissa) State, Koraput District, Raisili Village, alt. 3,200 ft., 25 October 1950, *H. F. Mooney 4241* (K barcode K000245985!).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* absent. *Culms* erect or decumbent, caespitose, intravaginal growth, glabrous, 20─36 m long, 0.48─0.99 mm thick. *Leaf sheaths* glabrous, 2.1─4.45 cm long. *Ligules* truncate, ciliolate, < 0.1 cm long. *Leaf blades* non-plicate, abaxial surface glabrous, adaxial surfaces hairy with tuberculate hairs, lanceolate, margin scabrid, apex attenuate, 5.0─9.0 cm long, 0.1─0.3 mm wide. *Inflorescences* strictly terminal, inflorescence solitary. *Spatheoles* glabrous, lanceolate, 3.7─5.2 cm long. *Rachis internodes* fragile, pilose with tawny hairs at the top, linear, 0.15 cm long. *Racemes* solitary, 7 sterile spikelets, 2 fertile spikelets, 1.40─1.80 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 1.10─1.50 cm long, 0.10─0.13 cm wide; callus cuneate, pilose with red hairs, attached obliquely, about 0.2 cm long; lower glume surface glabrous, chartaceous, lanceolate, margins partly covered upper glume, apex acute, 1 spikelet long and wide; upper glume surface glabrous, chartaceous, lanceolate, margin ciliate, apex acute, shorter than the lower glume, 0.6─0.7 cm long, 0.9─1.1 mm wide; lower lemma glabrous, membranous, lanceolate, margin ciliate, apex acuminate, 5.0─6.0 mm long, about 0.5 mm wide; upper lemma glabrous, membranous, linear, margin ciliate, apex acuminate, 5.0─5.5 mm long, 0.2─0.4 mm wide; palea absent; lodicules 3, cuneate, coriaceous, < 1.0 mm long. *Fertile pairs* bisexual and barren, deciduous entirely, 1 fertile pair, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, 0.50─0.80 cm long, about 1.0 mm wide; callus cuneate, pilose with red hairs, attach obliquely, 2.0 mm long; lower glume pilose with tuberculate hairs at the apex, coriaceous, elliptic oblong, margins partly enclosed upper glume, apex truncate, 1 spikelet long and wide; upper glume glabrous, coriaceous, oblong, margin membranous and ciliate, apex obtuse, slightly shorter than the lower glume, 0.45‒0.50 cm long, about 0.5 mm wide; lower lemma glabrous, membranous, lanceolate, margin membranous and ciliate, apex obtuse, 0.30‒0.45 cm long, 0.30‒0.50 mm wide; upper lemma glabrous, membranous, linear, margin entire, apex acute, very minute; palea linear, membranous, 0.20‒0.25 cm long, 0.20 mm wide; lodicules 2, cuneate, coriaceous, < 0.1 cm long, companion spikelets, pedicelled, well developed, male, lanceolate, 1.00‒1.05 cm long, 0.10‒0.15 mm wide; callus pilose with red hairs, linear, 0.2 cm long; lower glume glabrous, chartaceous, lanceolate, margins winged and partly enclose upper glume, apex acute, 1 spikelet long; upper glume glabrous, chartaceous, lanceolate, margin ciliate, apex acute, 0.58‒0.65 cm long, 0.80‒1.00 mm wide; lower lemma glabrous, membranous, lanceolate, margin ciliate, apex acuminate, 0.50‒0.60 cm long, 0.70‒0.90 mm wide; upper lemma glabrous, membranous, lanceolate, margin entire, apex acuminate, 0.50‒0.55 cm long, about 0.2 mm wide; palea glabrous, linear, 0.1 cm long; lodicules 2, cuneate, coriaceous, < 0.1 cm long. *Awn* present, geniculate, column twisted and hispidulous, 2.0‒4.8 cm long, 0.30‒0.40 mm thick. *Anthers* 3, 3.5‒4.0 cm long. *Ovary and Stigma* ovary 1, 0.20 mm long, stigmas 2, plumose. *Caryopsis* about 0.30 cm long, 0.79‒0.86 mm thick.

Etymology. – The specific epithet ‘saxicola’ from ‘saxum’ meaning ‘rock’ and ‘cola’ meaning ‘dweller’ explain that this species grows on rocks.

Vernacular names. – No vernacular names for *T. saxicola*.

Geographic distribution. – *Themeda saxicola* is endemic to Koraput District, Odisha State, India.

Phenology. – October to December

Habitat & Ecology. – *Themeda saxicola* was found growing on granite rock outcrops or cervices in habitats with long dry seasons and extreme temperature (Chorghe & Kulloli, 2022).

Phylogenetic position and morphological evolution. – Molecular data of this species is not provided as the specimens are poorly preserved, thus, phylogenetic position is still elusive. It represents unique solitary terminally borne inflorescence and spikelets with a few spikelet pairs.

Cytogenetics. – No cytogenetic data provided for *T. saxicola*.

Uses and ethnology. – No use data provided for *T. saxicola*.

Specimens examined. – **INDIA. Odisha State:** Koraput District, near Laxmipur, near Raisili Village, 945 m, 25 October 1950, *H. F. Mooney 4241* (K).

Conservation status. – According to Chorghe & Kulloli (2022), *Themeda saxicola* was assessed to be a critically endangered species as its distribution range is restricted in Raisili Hill. Threats to this species include mining and invasive alien species.

Themeda strigosa (Buch.-Ham. ex Hook.f.) A. Camus (1920: 423). ≡ ***Anthistiria strigosa*** Buch.-Ham. ex Hook.f. (1896: 214). — Lectotype (designated by Karthigeyan & Murugan in Phytotaxa 372(2): 176‒178. 2018): India, Assam, Camrup District, 'habitat in Camrupa orientalis arundinetis', 4 December 1800, *F. Buchanan-Hamilton s.n.* [Buchanan-Hamilton's (1822) catalogue no. 2321] (E barcode E00393919!).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* absent. *Culms* erect, glabrous, 100‒150 cm long, 2.78‒3.65 mm thick. *Leaf sheaths* glabrous, keeled, 4.2‒6.7 cm long. *Ligules* truncate, ciliolate, < 0.1 cm long. *Leaf blades* non-plicate, abaxial surface glabrous, adaxial surfaces hairy with tuberculate hairs, lanceolate, margin scabrid, apex attenuate, 10.2‒40.3 cm long, 0.2‒0.4 cm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, 30‒60 cm long. *Spatheoles* glabrous, lanceolate, 0.8‒1.3 cm long. *Rachis internodes* fragile, pilose with white hairs, linear, about 0.1 cm long. *Racemes* solitary, 6 sterile spikelets, 2‒3 fertile spikelets, 0.55‒0.80 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at the same level, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 0.40 cm long, < 0.10‒0.10 cm wide; callus square, pubescent, attached obliquely, about 0.5 mm long; lower glume surface pilose with tuberculate tawny hairs, chartaceous, lanceolate, margins partly covered upper glume, apex acute, 1 spikelet long and wide; upper glume surface glabrous, chartaceous, lanceolate, margin entire, apex acute, shorter than the lower glume, 0.40 cm long, < 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin entire, apex acuminate, 0.3‒0.4 mm long, < 0.1 cm wide; upper lemma glabrous, membranous, linear-lanceolate, margin entire, apex acuminate, 0.35‒0.40 mm long, < 0.1 cm wide; palea absent or minute; lodicules

3, cuneate, coriaceous, < 1.0 mm long. *Fertile pairs* bisexual and barren, deciduous entirely, 1─2 fertile pair, fertile spikelets different from pedicelled ones, sessile spikelet, well developed, bisexual, elliptic, 0.25─0.35 cm long, about 1.0 mm wide; callus square, pilose with white hairs, attach obliquely, 0.5 mm long; lower glume hirsute with hairs at the apex, coriaceous, elliptic oblong, margins partly enclosed upper glume, apex obtuse, 1 spikelet long and wide; upper glume glabrous, coriaceous, oblong, margin ciliate at the top, apex obtuse, slightly shorter than the lower glume, about 0.3 cm long, < 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin sparsely ciliate, apex acuminate, 0.20─0.25 cm long, < 0.1 cm wide; upper lemma glabrous, membranous, linear, fused at the base of awn, 0.10─0.20 cm long, < 0.10 cm wide; palea absent or minute; lodicules 3, cuneate, coriaceous, < 0.1 cm long, companion spikelets, pedicelled, well developed, male or barren, lanceolate, 0.30─0.40 cm long, < 0.10─0.10 cm wide; callus pilose with white hairs, linear, 0.1 cm long; lower glume pilose with tuberculate white hairs over the surface or on the margin, chartaceous, lanceolate, margins entire, apex acute, 1 spikelet long; upper glume glabrous, chartaceous, lanceolate, margin entire, apex acute, 0.35─0.40 cm long, < 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin ciliate at the top, apex acute, 0.30─0.40 cm long, < 0.10 cm wide; upper lemma glabrous, membranous, lanceolate, margin ciliate at the top, apex acute, 0.25─0.35 cm long, < 0.10 cm wide; palea glabrous, ovate, < 0.1 cm long; lodicules 2, cuneate, coriaceous, < 0.1 cm long. *Awn* present, geniculate, column twisted and hispidulous, 1.0─1.1 cm long, 0.06─0.11 mm thick. *Anthers* 3, 0.10─0.20 cm long. *Ovary and Stigma* ovary 1, < 0.1 cm long, stigmas 2, plumose. *Caryopsis* 0.66─1.00 mm long, 0.19─0.26 mm thick.

Etymology. – The specific epithet '*strigosa*' means that spikelets of this species are covered with short, bristle-like hairs.

Vernacular names. – No vernacular names provided for *T. strigosa*.

Geographic distribution. – *Themeda strigosa* is endemic to India.

Phenology. – *T. strigosa* was recorded to flower in October based on information on specimen labels.

Habitat & Ecology. – No ecological data provided for *Themeda strigosa.*

Phylogenetic position and morphological evolution. – *Themeda strigosa* is placed as a sister species of *Themeda anathera*.

Cytogenetics. – Birari (1980, 1981) found that *Themeda strigosa* is diploid (2n = 20).

Uses and ethnology. – No use data provided for this species.

Specimens examined. – **INDIA**. **Bihar State**: Munger District, October 1894, Mokim 1444 (K), **Bihar State**: Munger District, October 1894, Mokim 1516 (K)

Themeda tremula (Nees) Hack. in Monographiae Phanerogamarum 6: 667. 1889 ≡ ***Anthistiria tremula*** Nees in Synopsis Plantarum Glumacearum 1: 401. 1854 ≡ ***Androscepia tremula*** (Nees) Andersson in Nova Acta Regiae Societatis Scientiarum Upsaliensis, ser. 2 2: 247. 1856 — **Lectotype (designated here)**: Sri Lanka, *s.d., N. Wallich s.n.* [num. list. no. 8765] (K barcode K000245968!).

= ***Anthistiria thwaitesii*** Hook. f. in The Flora of British India 7(21): 215. 1896 ≡ ***Anthistiria tremula*** var. ***thwaitesii*** (Hook. f.) Trimen in A Hand-book to the Flora of Ceylon 5: 250. 1900 ≡ ***Themeda thwaitesii*** (Hook. f.) A. Camus in Bulletin du Muséum d'Histoire Naturelle 26: 267. 1920 — **Lectotype (designated here)**: Sri Lanka, *G. H. K. Thwaites 961* (BR barcode BR0000006884925!; isolectotypes: CAL barcode CAL0000002335!, K barcode K000245969!).

= ***Anthistiria tremula*** Nees var. ***brunnea*** Hook. f. in A Hand-book to the Flora of Ceylon 5: 250. 1900 ≡ ***Themeda tremula*** var. ***brunnea*** (Hook.f.) Senaratna (1956: 198). — Type: Sri Lanka, near Moragala, *Trimen s.n.* [numer. List Wallich 8765] not traced.

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* occasionally present. *Culms* base decumbent, erect, caespitose, glabrous, 15–204 cm long, 0.68–6.18 mm thick. *Leaf sheaths* glabrous or occasionally hairy with tuberculate hairs, 2.0–8.5 cm long. *Ligules* truncate, ciliolate, < 0.1 cm long. *Leaf blades* non-plicate, abaxial surface glabrous or occasionally hairy on the margin, adaxial surfaces glabrous and sparsely hairy with tuberculate hairs, lanceolate, margin scabrid, apex acute, 6–30 cm long, 0.3–0.8 cm wide. *Inflorescences* axillary and terminal, inflorescence fasciculate, 5–30 cm long. *Spatheoles* hairy with tuberculate hairs throughout or on the margin rarely glabrous, lanceolate, 0.9–2.2 cm long. *Rachis internodes* fragile, pilose with tawny hairs, linear, about 0.1 cm long. *Racemes* solitary, 7 sterile spikelets, 2 fertile spikelets, 0.70─1.20 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 0.50─0.85 cm long, 0.10─0.20 cm wide; callus square, glabrous, attached obliquely, < 0.1 cm long; lower glume surface pilose with tuberculate tawny hairs, chartaceous, lanceolate, margins partly covered upper glume, apex acute, 1 spikelet long and wide; upper glume surface glabrous, chartaceous, lanceolate, margin fringe, apex acute, shorter than the lower glume, 0.45─0.55 cm long, about 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin entire, apex obtuse, 0.45─0.55 mm long, about 0.1 cm wide; upper lemma glabrous, membranous, linear, margin ciliate, apex acute, 0.15─0.45 mm long, < 0.1 cm wide; palea absent; lodicules 2, cuneate, coriaceous, < 1.0 mm long. *Fertile pairs* bisexual and barren, deciduous entirely, 1 fertile pair, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, 0.25─0.40 cm long, < 0.1─0.1 mm wide; callus oblong, pilose with tawny hairs, attach obliquely, < 0.1 cm long; lower glume pubescent with tawny hairs throughout, coriaceous, elliptic oblong, margins partly enclosed upper glume, apex obtuse, 1 spikelet long and wide; upper glume pubescent with tawny hairs, coriaceous, oblong, margins entire, apex obtuse, slightly shorter than the lower glume, about 0.3 cm long, < 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margins entire, apex acuminate, 0.10─0.30 cm long, < 0.1 cm wide; upper lemma glabrous, membranous, linear, fused at the base of awn, < 0.10─0.15 cm long, < 0.10 cm wide; palea absent or minute; lodicules 3, cuneate, coriaceous, < 0.1 cm long, companion spikelets, pedicelled, well developed, male, lanceolate, 0.45─0.80 cm long, < 0.10 cm wide; callus pilose with tawny hairs, linear, 0.1 cm long; lower glume pilose with tuberculate tawny hairs throughout, chartaceous, lanceolate, margins entire, apex acute, 1 spikelet long; upper glume glabrous, chartaceous, lanceolate, margin entire, apex acute, 0.35─0.50 cm long, < 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin inflexed, apex acute, 0.10─0.45 cm long, < 0.10 cm wide; upper lemma glabrous, membranous, lanceolate, margins entire, apex acute, < 0.10─0.30 cm long, < 0.10 cm wide; palea absent; lodicules 2, cuneate, coriaceous, < 0.1 cm long. *Awn* present, geniculate, column twisted and hispidulous, 1.2─3.5 cm long, 0.12─0.25 mm thick. *Anthers* 3, 0.10─0.30 cm long. *Ovary and Stigma* ovary 1, < 0.1─0.15 cm long, stigmas 2, plumose. *Caryopsis* 0.15─0.25 cm long, 0.37─0.70 mm thick.

Etymology. – The specific epithet '*tremula*' is derived from a Latin word '*tremulus*' and describes inflorescence subject to movement in a slight breeze.

Vernacular names. – Pinibara tana (Sinhala; Nepal), Barki, Bhatandi

Geographic distribution. – South Asia including Bangladesh, India, and Sri Lanka, is native distribution range of *Themeda tremula.*

Phenology. – Flowering period of *T. tremula* is common in October to December but some populations can flower from January to May.

Habitat & Ecology. – *Themeda tremula* occurs in both lowland and upland savannas, especially in basin and wet placed that receive annual rainfall from 1450 to 2250 mm per year.

Phylogenetic position and morphological evolution. – *Themeda tremula* is placed in the subclade containing species without spikelet pairs (e.g., *Themeda triandra*) in both nuclear and plastome trees (Arthan et al., 2021).

Cytogenetics. – Themeda tremula was reported to be diploid (2n =20) and octoploid (2n = 80) plants (Birari, 1980, 1981; Mehra, 1975).

Uses and ethnology. – *Themeda tremula* is used as a fodder grass in Sri Lanka (Premaratne et al., 2003) and India (Gorade & Datar, 2014). It is suitable to use as a fodder when they are young.

Specimens examined. – Please see full list of specimens examined in Appendix XIV R.

Note. – Syntypes of *Anthistiria tremula* Nees var. *brunnea* are documented in the protologue under two collections, Pearson s.n. and Trimen s.n., but lectotypification could not be finished due to limited access to herbarium specimens in Sri Lanka. This name could be valid as a synonym of *Themeda tremula* but requires further investigation from the specimens.

Themeda triandra Forssk. in Flora Aegyptiaco-Arabica 178. 1775 ≡ [***Themeda polygama*** J.F. Gmel. in Systema Naturae 2: 149. 1791, nom. illeg. superfl.] ≡ [***Anthistiria forskalii*** Kunth in Révisoin des Graminées 1: 162. 1829, nom. illeg. superfl.] ≡ ***Themeda forskalii*** (Kunth) Hack. ex Duthie in The Fodder Grasses of Northern India 43. 1888 ≡ [***Themeda forskalii*** (Kunth) Hack. in Monographiae

Phanerogamarum 6: 659. 1889, nom. illeg. hom.] — **Neotype (designated here)**: Yemen Al Hadiyah, *Forsskål s.n.* (holotype C, destroy; neotype K barcode K).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* absent. *Culms* erect, caespitose, intravaginal growth, glabrous, 25─274 cm long, 0.81─4.96 mm thick. *Leaf sheaths* glabrous, 4─15 cm long. *Ligules* truncate, ciliolate, 0.1─0.3 cm long, rarely 0.4 cm long. *Leaf blades* non-plicate, abaxial and adaxial surfaces glabrous or pilose with tuberculate hairs, linear ovate, margin scabrid, apex acute, 5─50 cm long, 0.1─1.0 cm wide. *Inflorescences* axillary and terminal, inflorescence fasciculate, 10─30 cm long, rarely 50 cm long. *Spatheoles* scarious, margins with bristles, lanceolate, 0.8─3.5 cm long. *Rachis internodes* fragile, glabrous or densely pilose with tawny hairs, cuneate, <0.1─0.15 cm long. *Racemes* clustered, 6 sterile spikelets, 1 fertile spikelet, 6.0 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at same level, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 0.8─1.0 cm long, , 0.20─0.22 cm wide; callus square, glabrous, 0.20─0.4 cm long; lower glume pilose with tuberculate hairs on the margin, at the apex, on the top half, or throughout, chartaceous, oblong-lanceolate, margins with one-sided winged keel, partly enclosed upper glume, apex acute, 1 spikelet long and wide; upper glume surface glabrous, chartaceous, narrowly ovate, margin membranous and ciliate, apex acute, slightly shorter than the lower glume, 0.7─1.0 cm long, 0.18─0.20 cm wide; lower lemma glabrous, membranous, narrowly elliptic, margin cilate at the upper part, apex acuminate, about 1.0 cm long, (< 1.0) 2.0 mm wide; upper lemma glabrous, membranous, ovate, margin inflexed and ciliate, apex acute, 0.1 cm long, 0.5 mm wide; palea absent; lodicules 2, cuneate, coriaceous, < 1.0─1.0 mm long. *Fertile pairs* bisexual and barren, deciduous entirely, no fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, 0.80─0.90 cm long, rarely 0.5 cm long, 0.10─0.12 cm wide; callus cuneate, densely pilose with tawny hairs, pungent, attach obliquely, < 0.1─0.1 cm long; lower glume hirsute with short bristles at the top, coriaceous, ovate, margins partly enclosed upper glume, apex truncate, 1 spikelet long and wide; upper glume sparsely hairy/hirsute with short hair at the top, coriaceous, narrowly oblong, margin membranous and ciliate at the top, apex acute, slightly shorter than the lower glume, 0.60─0.80 cm long, 0.8─1.0 mm wide; lower lemma glabrous, membranous, elliptic, margin entire, apex acute, 0.35─0.42 cm long, 0.5─0.7 mm wide; upper lemma glabrous, membranous, reduced and attached to awn, margin entire, 0.3 cm long, 0.15 cm wide; palea absent; lodicules 2, cuneate, coriaceous, < 0.1─0.1 cm long, companion spikelets pedicelled, well developed, male, lanceolate, 0.80─1.40 cm long, 0.80─1.0 mm wide; callus glabrous, linear, 0.10–0.12 cm long; lower glume pilose with tuberculate hairs, chartaceous, narrowly ovate, margins inflexed, serrulate on the top, one-sided winged, apex acuminate, 1 spikelet long and wide; upper glume glabrous, chartaceous, oblong-lanceolate, margins inflexed and ciliate, apex acute, 0.54–1.0 cm long, < 0.1 cm wide; lower lemma glabrous, membranous, oblong-lanceolate, margin ciliate, apex acute, 0.25–0.65 cm long, about 0.1 cm wide; upper lemma absent or glabrous, membranous, oblong-lanceolate, margin entire, apex acute; palea absent; lodicules 2, oblong, coriaceous, < 0.1–0.1 cm long. *Awn* present, geniculate, column twisted and hispidulous, (3.0–) 5.5–7.0 cm long, 0.14–0.29 mm thick. *Anthers* 3, 0.25–0.28 cm long. *Ovary and Stigma* ovary 1, 0.12–0.14 cm long, stigmas 2, plumose. *Caryopsis* 0.35–0.40 cm long, rarely 0.30 cm long, 1.0 mm thick.

1.Perennial, homogamous spikelet 0.6–1.4 cm long, sessile spikelet 0.80–0.90 cm long, pedicelled spikelet 0.80–1.40 cm long, awn 5.5–7.8 cm long, caryopsis 0.35–0.40 cm long…………………………………………………………………………..var. ***triandra***
1.Annual, homogamous spikelet 0.4–0.7 cm long, sessile spikelet 0.35–0.50 cm long, pedicelled spikelet 0.40–0.70 cm long, awn 1.0–5.8 cm long, caryopsis 0.20–0.35 cm long. ……………………………………………………………………...var. ***quadrivalvis***

Themeda triandra Forssk. var. ***triandra*** ≡ ***Themeda triandra*** Forssk. in Flora Aegyptiaco-Arabica 178. 1775 ≡ [***Themeda polygama*** J.F. Gmel. in Systema Naturae 2: 149. 1791, nom. illeg. superfl.] ≡ [***Anthistiria forskalii*** Kunth in Révisoin des Graminées 1: 162. 1829, nom. illeg. superfl.] ≡ ***Themeda forskalii*** (Kunth) Hack. ex Duthie in The Fodder Grasses of Northern India 43. 1888 ≡ [***Themeda forskalii*** (Kunth) Hack. in Monographiae Phanerogamarum 6: 659. 1889, nom. illeg. hom.] — **Neotype (designated here)**: Yemen Al Hadiyah, *Forsskål s.n.* (holotype C, destroy; neotype K barcode K001427937).

= ***Anthistiria imberbis*** Retz. in Observationes Botanicae. 3: 11. 1783 ≡ [***Anthistiria vulgaris*** Hack. var. ***imberbis*** (Retz.) Hack. ex Wawra in Itin. Princ. S. Cobugi. 2: 102. 1888, nom. illeg.] ≡ ***Calamina imberbis*** (Retz.) Roem. & Schult. in Systema Vegetabilium 2: 810. 1817 ≡ ***Themeda forskalii*** var. ***imberbis*** (Retz.) Hack. in Monographiae Phanerogamarum 6: 661. 1889 ≡ ***Themeda imberbis*** (Retz.) Cooke in The Flora of the Presidency of Bombay 2: 993. 1908 ≡ ***Themeda triandra*** var. ***imberbis*** (Retz.) Hack. 7: 63. 1908 ≡ ***Themeda triandra*** var. ***imberbis*** (Retz.) Thell. (1912: 74). — ***Themeda triandra*** var. ***imberbis*** (Retz.) A. Camus in in Proceedings and Transactions of the Rhodesia Scientific Association 7: 63. 1908 ≡ Holotype: South Africa, Cape Province, Cape of Good Hope, *A. Sparrmann s.n.* (LD barcode LD1241177!).

= ***Anthistiria australis*** R.Br. in Prodromus Florae Novae Hollandiae 1: 200. 1810 ≡ Anthesteria australis (R.Br.) R.Br. ex Spreng. (1824: 291) ≡ ***Themeda australis*** (R.Br.) Stapf in Flora of Tropical Africa 9: 420. 1919 — Holotype: Australia, South Australia, Port Lincoln, *s.d., R. Brown 6194* (BM barcode BM000885880!, BM000885883!, BM; isotypes: E barcode E00393611!, E00393612!, K barcode K000911787!, K000911788!).

= ***Anthistiria punctata*** Hochst. ex A. Rich. in Tentamen Florae Abyssinicae 2: 448. 1850 ≡ ***Themeda forskalii*** var. punctata (Hochst. ex A. Rich.) Hack. in Monographiae Phanerogamarum. 6: 662. 1889 ≡ ***Themeda triandra*** Forssk. var. punctata (Hochst. ex A. Rich.) Stapf in Flora of Tropical Africa 9: 419. 1919 — Lectotype (designated by Chase & Niles in Index to grass species 3: 397. 1962): Ethiopia, Mount Scholoda, 3 October 1837, *G. H. W. Schimper 73* (P barcode P00446187 photo!; isolectotypes: K barcode K000280101!, L barcode L1339577!, US barcode US00139280!).

= ***Anthistiria subglabra*** Buse in Plantae Junghuhnianae. 363. 1854 — Holotype: Indonesia, Sumatra, Padang Lawas, near Pertibi, *Dr. Horner 110* (L barcode L0329846!).

= ***Anthistiria vulgaris*** Hack. in Die Natürlichen Pflanzenfamilien 2(2): 29. 1887 ≡ ***Themeda forskalii*** var. ***vulgaris*** (Hack.) Hack. in Monographiae Phanerogamarum 6: 660. 1889. — **Types not found**.

= ***Themeda barbata*** (Desf.) Veldk. in Journal of Japanese Botany 90: 293‒297. 2015 ≡ ***Andropogon ciliatus*** Thunb. in Murray in Systema Vegetabilium 14: 903. 1784 ≡ ***Anthistiria ciliata*** L. f. var. β. Geartn. in De Fructibus et Seminibus Plantarum 2: 465. 1791 ≡***Anthistiria barbata*** Desf. in Journal de Physique, de Chimes, d'Histoire Naturelle et des Arts 40: 294. 1792 ≡ [***Anthesteria barbata*** (Desf.) C. Presl in Repert. Bot. Syst. 1: 305. 1833, pro comb.] ≡ [Anthistiria japonica Willd. in Species Plantarum 4: 901. 1806, nom. superfl.] ≡ [Anthestiria japonica Willd. ex Spreng. in Systema Vegetabilium 1: 290. 1824, nom. superfl.] ≡ [Anthistiria arguens (L.) Willd.

f. japonica Andersson in Nova Acta Reagiae Societatis Scientiarum Upsaliensis, ser. 3 B: 236. 1856] ≡ Anthistiria arguens (L.) Willd. var. japonica (Andersson) Andersson ex Miq. in Prolus. Fl. Jap. 178. 1866 ≡ Themeda forskalii Hack. subvar. Japonica (Andersson) Hack. in DC. in Monographiae Phenerogamarum 6: 662. 1889 ≡ Themeda triandra Forssk. subvar. japonica (Andersson) Hack. ex Rendle in Journal of Linnean Society 36: 378. 1904 ≡ Themeda triandra Forssk. var. japonica (Andersson) Makino in Botanical Magazine, Tokyo 26: 213. 1912 ≡ [***Themeda japonica*** (Willd.) Tanaka in Bulteno Scienca de la Fakultato Terkultura Kjusu Imperia Universitato 4: 194, 207. 1925] ≡ [Themeda japonica Tanaka var. typica Honda in Journal of the Faculty of Science, University of Tokyo, Section 3 3: 349. 1930, nom. inval.] ≡ [***Themeda arguens*** L. subvar. ***japonica*** (Andersson) Roberty in Boissiera 6: 91. 1960, nom. inval] ≡ Themeda triandra Forssk. subsp. japonica (Andersson) T. Koyama in Gr. Japan 452, 532. 1987 — Lectotype (designated by Veldkamp (2015) in Journal of Japanese Botany 90: 293–297. 2015): Japan, Kyushu, mountains of Nagasaki, *C. P. Thunberg 23927* (UPS barcode V-143174!; isolectotypes:

= ***Anthistiria japonica*** Willd. in Species Plantarum. Edtio quarta 4: 901. 1806 ≡ ***Anthistiria arguens*** var. ***japonica*** (Willd.) Andersson in Nova Acta Regiae Societatis Scientiarum Upsaliensis, ser. 2 2: 236. 1856 ≡ ***Themeda triandra*** var. japonica (Willd.) Makino in Botanical Magazine, Tokyo 26: 213. 1912 ≡ ***Themeda japonica*** (Willd.) Tanaka in Bulteno Scienca de la Fakultato Terkultura Kjusu Imperia Universitato 1: 194. 1925 ≡ ***Themeda triandra*** subsp. ***japonica*** (Willd.) T. Koyama in Grasses of Japan and its Neighbouring Regions 532. 1987 — **Types not found**.

= ***Themeda helferi*** Munro ex Hack in Monographiae Phenerogamarum. 6: 665. 1889 ≡ [Anthistiria helferi Munro ex Hack. (1889: 665), nom. inval.] ≡ ***Anthistiria ciliata*** var. ***helferi*** (Munro ex Hack.) Hook.f. in The Flora of British India. 7(21): 214. 1897 ≡ ***Themeda ciliata*** subsp. ***helferi*** (Munro ex Hack.) A. Camus in Bulletin du Muséum d'Histoire Natutelle. 26: 424. 1920 ≡ ***Themeda quadrivalvis*** var. ***helferi*** (Munro ex Hack.) Bor in Grasses of Burma, Ceylon, India and Pakistan (excluding Bambuseae). 252. 1960 — Lectotype (designated by A. S. Thomas in Phytotaxa. 416(2): 197–199. 2019): Myanmar, Tenasserim and Andamans, *J. W. Helfer 6809* (W barcode W 1916-0028238 digital photo!; isolectotypes: E barcode E00393921!, K barcode K000245965!, L barcode L0064303!, MO barcode MO2114793!, US barcode

US00603530 digital photo!, US01231721 digital photo!, W barcode W1886-0008854!, W0030635!).

= ***Themeda laxa*** (Andersson) A. Camus in Bulletin de Muséum d'Histoire Naturelle 26: 266, 423. 1920 ≡ ***Anthistiria laxa*** Andersson in Nova Acta Regiae Societatis Scientiarum Upsaliensis, ser. 2 2: 243. 1856 ≡ ***Themeda forskalii*** var. ***laxa*** (Andersson) Hack. in Monographiae Phanerogamarum 6: 663. 1889 ≡ ***Themeda triandra*** var. ***laxa*** (Andersson) Noltie in Edinburgh Journal of Botany 56(3): 402. 2000 — **Lectotype (designated here)**: Nepal, *N. Wallich 8775* (K barcode K000245947!; isolectotypes: E barcode E00393914!).

= ***Themeda acaulis*** B.S. Sun & S. Wang in Journal of the Yunnan University. Series A. 21(2): 96. 1999 — Holotype: China, Longling, river valley, Longzhen bridge, 18 December 1991, *S. Bi-Xin & S. Wang 91197* (YUKU barcode YUKU0093084).

Etymology. – The specific epithet 'triandra' was rooted in two Greek words 'treis' (three) and 'aner' (man), which refers to a structure in the raceme comprised of a sessile bisexual spikelet with three male spikelets.

Vernacular names. – Thaemed, Themed, Alak (Arabic name); Megarukaya (Japanese name for *Themeda barbata*); Solsae (Korean name); Erigai thattu pullu (Tamil Name, India).

Geographic distribution. – *Themeda triandra* is distributed throughout tropical zones in Africa, Asia, and Australia but it is absent in North and South America. Its distribution range is extended to subtropical regions in South Africa and Australia, and temperate regions in Japan.

Phenology. – *Themeda triandra* flowers throughout the year, depending on regions they occur.

Habitat & Ecology. – *Themeda triandra* exists in wide ranges of habitats from wet savannas in Southeast Asia (Ratnam et al., 2016) to drier habitats in Africa and Australia (Snyman, Ingrid & Kirkman, 2013).

Phylogenetic position and morphological evolution. – *Themeda triandra* is placed in the phylogenetic tree with sister species that lacks spikelet pairs and have three or more inflorescence branching orders. Analyses by Dunning et al. (2017, 2022) showed that the *Themeda triandra* complex includes *Themeda laxa* and *Themeda quadrivalvis* in the clade.

Cytogenetics. – Ploidy levels of *Themeda triandra* range from diploid (2n = 20) to decaploid (2n = 100); however, common ploidy levels are diploid, tetraploid and hexaploid (Hayman, 1960; Ahrens et al., 2020).

Uses and ethnology. – *Themeda triandra* is considered valuable fodder for cattle in many parts of the world due to high nutrients (Snyman, Ingram & Kirkman, 2013).

Specimens examined. – Please see full list of specimens examined in Appendix XIV S.

Note. – We treated *Themeda laxa* and *Themeda helferi* as synonyms and *Themeda quadrivalvis* as a variety of *Themeda triandra* for their overlapping geographic distributions with *Themeda triandra* with inconspicuous or minor differences in sizes. We also revised the morphological description to cover morphological variation in this species.

Tropicos database specified that the holotype of *Anthistiria laxa* was deposited in S herbarium, but the specimen was absent from online database. Therefore, we designated the isotype from K herbarium as the lectotype of *Anthistiria laxa*.

Type specimens of *Themeda triandra* specified in the protologue were not found (Hepper & Friis, 1994) and might be destroyed. The specimen was collected by Pehr Forsskål during the expedition to Yemen in 1763. The latest investigation of type specimens was done by Veldkamp (2016), but the neotype was not designated. Here, neotypification was done by selecting specimens in K herbarium from Yemen where the first specimen was collected.

In addition, Veldkamp (2015) made taxonomic combinations with *Themeda barbata* and *Themeda japonica.* We recognized *Themeda barbata* as a correct name but not *Themeda japonica* and treated it as a synonym of *Themeda triandra*.

= ***Themeda triandra*** var. ***quadrivalvis*** (L.) Arthan, Kellogg & Voront., **comb. nov.** ≡

[***Andropogon nutans*** L. in Mantissa Plantarum 2: 303. 1771, nom. illeg. hom] ≡ ***Andropogon quadrivalvis*** L. in Systema Vegetabilium. Editio decima tertia 13: 758. 1774 ≡ [***Anthistiria ciliata*** L. f. in Supplementum Plantarum 113. 1782, nom. illeg. superfl.] ≡ [***Themeda ciliata*** (L. f.) Hack. ex Duthie in Monographiae Phanerogamarum 6: 664. 1889] ≡ [***Themeda ciliata*** Hack. in Monographiae Phanerogamarum 6: 664. 1889] ≡ ***Themeda quadrivalvis*** (L.) Kuntze in Revisio Generum Plantarum 2: 794. 1891 — Lectotype (designated by T. Cope in Cafferty et al. in Taxon 49(2): 246. 2000): India, *s.d.*, *Anonymous s.n.* (LINN barcode LINN1211.5).

= ***Anthistiria scandens*** Roxb. in Flora Indica; or description of Indian Plants 1: 253. 1820 — **Types not found**.

= ***Themeda echinata*** Keng in Sinensia 10: 329. 1939 — **Holotype**: China, Yunnan, 28 November 1906, *J. Esquirol 1112* (P barcode P00745735!).

= ***Themeda ciliata*** subsp. ***chinensis*** A. Camus in Bulletin de Muséum d'Histoire Naturelle in 26: 424. 1920 ≡ ***Themeda chinensis*** (A. Camus) S.L. Chen & T.D. Zhuang in Bulletin of Botanical Research, Harbin 9(2): 59–60. 1989 — **Lectotype (designated here)**: China, Yunnan, Kaiyuan (Ami Chow), 'tunnel de O mi tcheou', 28 November 1906, *J. Esquirol 1112* (P barcode P00745734!; isotype: P barcode P00745735!).

= ***Themeda yuanmounensis*** S.L. Chen & T.D. Zhuang in Bulletin of Botanical Research, Harbin 9(2): 60–61. 1989 — Holotype: China, Yunnan, Yuanmoun, *Jinsha Jiang Exped. 63-6833* (JSBI barcode unknown; isotypes: PE barcode unknown, KUN barcode unknown, YUNU barcode unknown).

Description. – *Habit* annual. *Rhizomes* present. *Stilt roots* absent. *Culms* erect, base geniculately ascending, caespitose, intravaginal growth, glabrous, 30–200 cm long, 1.44–4.96 mm thick. *Leaf sheaths* glabrous, 1.5–6.8 cm long. *Ligules* truncate, eciliate, 2.0–3.0 mm long. *Leaf blades* non-plicate, abaxial and adaxial surfaces glabrous rarely sparsely hirsute, lanceolate, margin serrulate, apex acute, 5–31 cm long, 0.3–1.0 cm wide. *Inflorescences* axillary and terminal, synflorescence paniculate, fasciculate, 10–50 cm long. *Spatheoles* glabrous, lanceolate, margins with tuberculate hairs, apex acuminate, 1.1–2.8 cm long. *Rachis* *internodes* fragile, about 0.1 cm long. *Racemes* clustered, 6 sterile spikelets, 1 fertile spikelet, 0.5–1.2 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male or barren, a pair arranging at the same level, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 0.45–0.65 cm long, < 0.1–0.2 cm wide; callus linear; lower glume surface glabrous except margins, chartaceous, lanceolate, margins with tuberculate hairs, apex acute, 0.40–0.70 cm long, about 1.5 mm wide; upper glume surface glabrous, chartaceous, lanceolate, margin ciliate, apex acute, slightly shorter than the lower glume, 0.5–0.6 cm long, 0.8–1.0 mm wide; lower lemma glabrous, membranous, lanceolate, apex acute, 1.0–6.5 mm long, 0.8–1.0 mm wide; upper lemma glabrous, membranous, lanceolate, margin scaberuloous, apex acute, 1.5–6.0 mm long, 0.8–1.0 mm wide; palea absent; lodicules 2, cuneate, coriaceous, < 1.0–1.0 mm long. *Fertile pairs* bisexual and barren, deciduous entirely, no fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, 0.35–0.50 cm long, < 1.0–1.0 mm wide; callus oblong, pilose with reddish brown hairs, attach obliquely, 0.5–1.0 mm long; lower glume glabrous or scaberulous with tuberculate hairs at the apex, coriaceous, narrowly ovate-oblong, margins partly enclosed upper glume, apex truncate, 1 spikelet long; upper glume glabrous, coriaceous, oblong, margin inflexed, apex obtuse, slightly shorter than the lower glume, 0.40–0.45 cm long, 0.8–1.0 mm wide; lower lemma glabrous, membranous, lanceolate, margin ciliate, apex acute, 0.25–0.40 cm long, 0.8–1.0 mm wide; upper lemma glabrous, membranous, linear; palea absent; lodicules 2, cuneate, coriaceous, 0.8–1.0 mm wide, companion spikelets, separately deciduous, pedicelled, well developed, barren, linear, 0.40–0.70 cm long, 0.10–0.15 mm wide; callus pilose with reddish brown hairs, oblong; lower glume glabrous, chartaceous, linear, margins scaberulous, partly enclose upper glume, apex acute, 1 spikelet long; upper glume glabrous, chartaceous, linear, margin ciliate, apex acute, slightly shorter than the lower glume; lower lemma glabrous, membranous, lanceolate, apex acute, 0.10–0.50 cm long, < 1.0 mm wide; upper lemma glabrous, membranous, lanceolate, margin scaberulous, apex acute, < 0.10–0.20 cm long; palea absent; lodicules 2, cuneate, coriaceous, < 0.1 cm long. *Awn* present, geniculate, column twisted and hispidulous, 1.0–5.8 cm long, 0.13–0.43 mm thick. *Anthers* 3, < 0.10–0.25 cm long. *Ovary and Stigma* ovary 1, 0.5–2.0 mm long, stigmas 2, plumose. *Caryopsis* 0.20–0.35 cm long, 0.47–0.97 mm thick.

Etymology. – The specific epithet ‘quadrivalvis’ was formed from two Latin words, ‘quatour’ and ‘valva’ meaning ‘four doors.’ This refers to four male homogamous spikelets at the base of raceme.

Vernacular names. – Grader grass or Habana grass (English), Bhati, Fulora, Kusali gavat, Zini, Ya Kai (Thai).

Geographic distribution. – According to POWO (2022), native distribution of *Themeda quadrivalvis* is from South India to Myanmar and Thailand. This species is also introduced in many parts of the world such as northeastern Australia, Carribean, Middle Eastern, South Africa, New Guinea, and South-Central China.

Phenology. – Flowering time of most populations span from August to December except Australian populations that flower from February to May.

Habitat & Ecology. – The species was found in arid environments in Africa, the Caribbean, and Middle East.

Phylogenetic position and morphological evolution. – Phylogenetic position of *Themeda quadrivalvis* is nested with *Themeda triandra* in the plastome and nuclear phylogenetic trees by Arthan et al. (2021). Broader *T. quadrivalvis* and *T. triandra* populations were sampled by Dunning et al. (2017, 2022) and revealed that *T. quadrivalvis* populations were nested within the *T. triandra* clade. Most of their morphological differences are trivial as only size of reproductive structures can distinguish these two taxa except for annuality in *T. quadrivalvis*.

Cytogenetics. –Three ploidy levels, tetraploid (2n = 40), hexaploidy (2n = 60), and octoploid (2n = 80), were documented for *Themeda triandra* var. *quadrivalvis* (Birari, 1980, 1981; Christopher, 1978)

Uses and ethnology. – *T. quadrivalvis* is used as fodder to feed Sheep in Madhya Pradesh, India (Arora et al., 1972).

Specimens examined. – Please see full list of specimens examined in Appendix XIV T.

Note. – Long debate about species status of *T. quadrivalvis* and *T. triandra* is concluded here by treating *T. quadrivalvis* as a subspecies of *T. triandra*. It was hypothesized that *T. quadrivalvis* is under speciation process. Both taxa share distribution ranges from Australia to Middle East, but only *T. quadrivalvis* migrated to the New World.

Arthan et al. (2022) demonstrated that the climatic space of Australian and Middle eastern *T. quadrivalvis* populations overlaps with the pantropical climatic space of *T. triandra*. This could be a consequence from niche conservatism in diverging species. Phylogenetic reconstructions from nuclear and plastome markers yielded the solid conclusion at population level that *T. quadrivalvis* was nested among *T. triandra* populations. Concordant results were shown in previous studies with less effort in sampling (Arthan et al., 2021; Dunning et al., 2017).

Tropicos mentioned that the holotype and isotypes of *Themeda yuanmounensis* were deposited in NAS or formerly known as JSBI (holotype), PE, KUN, and YUNU (isotypes); however, they were not found in Chinese Virtual Herbarium. Here, we did not specify any barcodes until they are properly checked.

Themeda trichiata S.L. Chen & T.D. Zhuang in Bulletin of Botanical Research, Harbin 9(2): 58. 1989 — Holotype: China, Guangxi, Bose, 14 December 1955, *Bose Exped. 01109* (JSBI(NAS) barcode JSBI(NAS)00112038!; isotypes: IBK barcode IBK00182487!).

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* absent. *Culms* erect, caespitose, hairy, 150─195 cm long, 0.50─0.70 cm thick. *Leaf sheaths* hairy with non-tuberculate hairs, 6.6─15.0 cm long. *Ligules* truncate, ciliolate, 0.10─0.15 cm long. *Leaf blades* non-plicate, abaxial surface hirsute and densely hairy, adaxial surfaces less hairy, lanceolate, margin scabrid, apex acuminate, 40─80 cm long, 0.4─0.7 cm wide. *Inflorescences* axillary and terminal, inflorescence fasciculate. *Spatheoles* hairy with non-tuberculate hairs, lanceolate, 2.50─4.30 cm long. *Rachis internodes* fragile, pilose with tawny hairs, cuneate, 0.1 cm long. *Racemes* solitary, 7 sterile spikelets, 2 fertile spikelets, 1.70─2.40 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male or barren, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, narrowly lanceolate, 1.15─1.50 cm long, 0.15─0.20 cm wide; callus cuneate or occasionally linear, glabrous, attached obliquely, < 0.10─0.10 cm long; lower glume surface glabrous, chartaceous, lanceolate, margins narrowly keeled, winged keels, apex acuminate, 1 spikelet long and wide; upper glume surface glabrous, chartaceous, lanceolate, margin fringe, apex acuminate, slightly shorter than the lower glume, 0.95─1.1 cm long, 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin fringe, apex acuminate, 0.80─0.90 mm long, 0.1 cm wide; upper lemma glabrous, membranous, lanceolate, margins entire, apex obtuse, 0.60‒0.80 cm long, < 0.1 cm wide; palea absent or minute; lodicules 3, cuneate, coriaceous, < 0.1 cm long. *Fertile pairs* bisexual and barren, deciduous entirely, 1 fertile pair, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, 0.70‒0.75 cm long, 0.20 cm wide; callus cuneate, pilose with tawny hairs, attach obliquely, about 0.2 cm long; lower glume pilose with tawny hairs throughout, coriaceous, elliptic, margins partly enclosed upper glume, apex obtuse, 1 spikelet long and wide; upper glume pubescent with tawny hairs, coriaceous, oblong, margins entire, apex obtuse, slightly shorter than the lower glume, 0.80 cm long, < 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margins sparsely ciliate at the top, apex acuminate, 0.25‒0.50 cm long, < 0.10 cm wide; upper lemma glabrous, membranous, stipitiform, margins entire, apex acuminate, 0.25‒0.45 cm long, < 0.10 cm wide; palea absent or minute; lodicules 2, cuneate, coriaceous, 0.1 cm long, companion spikelets, pedicelled, well developed, male or barren, lanceolate, 1.20‒1.40 cm long, 0.20 cm wide; callus glabrous, linear, 0.1 cm long; lower glume glabrous or occasionally sparsely hairy, chartaceous, lanceolate, margins entire, apex acute, 1 spikelet long; upper glume glabrous, chartaceous, lanceolate, margin fringe, apex acute, 0.90‒1.00 cm long, 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margins ciliate, apex acute, 0.75‒1.00 cm long, < 0.1 cm wide; upper lemma glabrous, membranous, lanceolate, margin entire, apex acute, 0.65‒0.85 cm long, < 0.1 cm wide; palea absent or minute; lodicules 3, cuneate, coriaceous, < 0.1‒0.1 cm long. *Awn* present, geniculate, column twisted and hispidulous, 2.0‒5.1 cm long, 0.16‒0.39 mm thick. *Anthers* 3, 0.35‒0.60 cm long. *Ovary and Stigma* ovary 1, 0.1 cm long, stigmas 2, plumose. *Caryopsis* 0.45‒0.50 cm long, 1.20‒1.32 mm thick.

Etymology. – The specific epithet '*trichiata*' is derived from two words, '*thrix*' (Greek) and 'ata' (Latin) meaning hair and possessing, respectively. This refers to dense hairs on leaves and culms.

Vernacular names. – Mao jian (毛菅; Chinese name)

Geographic distribution. – *Themeda trichiata* is endemic to South Central China.

Phenology. – Flowering spans from August to December

Habitat & Ecology. – Shouliang & Phillips (2006) documented that *T. trichiata* occur on dry mountain slopes.

Phylogenetic position and morphological evolution. – *Themeda trichiata* is closely related to *Themeda avenacea* and its phylogenetic position show strong affinity to wetland species (Arthan et al., 2021).

Cytogenetics. – No cytogenetic data provided for *T. trichiata*

Uses and ethnology. – No use data provided for *T. trichiata*

Specimens examined. – **CHINA. Guangxi Zhuang Autonomous Region:** 14 December 1955, *Baise 01109* (NAS); **Hainan Province:** Yaichow, 1100 ft., 1932–1933, *N. K. Chun & C. L. Tso 44678* (K).

Note. – *Themeda trichiata* morphologically resembles to *T. caudata* but can be separated from one another in that the former has hairy stem and leaf, homogamous spikelet inserting at the same level, and greater size of homogamous spikelets. However, hairiness is considered an insignificant character to separate species as it could be labile under environmental stress (e.g., herbivory or humidity; Hou & Simpson, 1992).

Themeda unica S.L. Chen & T.D. Zhuang in Bulletin of Botanical Research, Harbin 9(2): 56. 1989 — Holotype: China, Anhui, Jing Xian Pan Cun, 200-1000 m. alt., 17 October 1915, *P. Courtois 13169* (JSBI(NAS) barcode JSBI(NAS)00112039!).

Description. – *Habit* perennial. *Stilt roots* absent. *Culms* erect or geniculate at the base, caespitose, glabrous, 100‒250 cm long, 0.4‒1.0 cm thick. *Leaf sheaths* loosely hispid with tuberculate hairs. *Ligules* truncate, ciliolate, 0.2‒0.7 cm long. *Leaf blades* non-plicate, abaxial and adaxial surfaces glabrous or pilose with tuberculate hairs on adaxial surface, lanceolate, margin scabrid, apex acuminate, 30‒60 cm long, 0.4‒1.0 cm wide. *Inflorescences* axillary and terminal, inflorescence fasciculate. *Spatheoles* glabrous, lanceolate, 4‒9 cm long. *Rachis internodes* fragile. *Racemes* clustered, 9‒11 sterile spikelets, 4‒6 fertile spikelets. *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, margins pilose with white tuberculate hairs, apex acuminate, 2.5‒4.0 mm long; callus linear, pilose with hairs; lower glume surface pilose with tuberculate hairs on the margins, chartaceous, lanceolate, apex acuminate, 1 spikelet long and wide; upper glume surface glabrous, chartaceous, lanceolate, apex acute, slightly shorter than the lower glume; lower lemma glabrous, membranous; upper lemma glabrous, membranous; lodicules 2, cuneate, coriaceous, < 1.0 mm long. *Fertile pairs* bisexual and barren, deciduous entirely, 3─5 fertile pairs, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic-oblong, 0.7─1.0 cm long; callus acute, about 0.25 cm long; lower glume densely strigose with brown hairs, coriaceous, elliptic-oblong, 1 spikelet long and wide; upper glume pubescent coriaceous, oblong, slightly shorter than the lower glume; lower lemma glabrous, membranous; upper lemma glabrous, membranous; lodicules 2, cuneate, coriaceous, < 0.1 cm long, companion spikelets, pedicelled, well developed, male, lanceolate, 2.0 cm long; callus hairy, linear; lower glume pilose with hairs, chartaceous, lanceolate, apex acute, 1 spikelet long and wide; upper glume glabrous, chartaceous, lanceolate; lower lemma glabrous, membranous; upper lemma glabrous, membranous; lodicules 2, cuneate, coriaceous, < 0.1 cm long. *Awn* present, geniculate, column twisted and hispidulous, 2─4 cm long. *Anthers* 3. *Ovary and Stigma* ovary 1, stigmas 2, plumose. *Caryopsis* 0.53 cm long, 1.63 mm thick.

Etymology. – The specific epithet ‘unica’ is from a Latin word ‘unicus’ meaning singular referring to single nerve on lower glume.

Vernacular names. – Zhe wan jian (浙皖菅; Chinese name)

Geographic distribution. – *Themeda unica* is endemic to Tibet.

Phenology. – Flowering time spans from August to October.

Habitat & Ecology. – Shouliang & Phillips (2006) documented that *T. unica* exist on hill slopes.

Phylogenetic position and morphological evolution. – *Themeda unica* is placed in a subclade with late-diverging *T. tremula*.

Cytogenetics. – No cytogenetic data provided for *T. unica*

Uses and ethnology. – No use data provided for *T. unica*

Specimens examined. – **CHINA. Yunnan**, 08 October 1914, *C. C. Courtois 10607* (NAS); **Yunnan**, 16 September 1920, *C. C. Courtois 26724* (NAS).

Themeda villosa (Poir.) A.Camus in Flore Générale de l'Indo-Chine 7: 364. 1922 ≡ ***Anthistiria villosa*** Poir. in Encyclopédie Méthodique, Botanique 1: 396. 1810 ≡ ***Themeda gigantea*** (Cav.) Hack. subsp. & var. ***villosa*** (Poir.) Hack. in Monographiae Phanerogamarum 6: 675. 1889 ≡ ***Anthistiria gigantea*** Cav. subsp. ***villosa*** (Poir.) Hook. xx: 217. 1896 — Lectotype (designated by Veldkamp in Blumea 61: 29–40. 2016): Indonesia, Java, 5 September 1768, *P. Commerson s.n.* (P barcode micro IDC 6207!; isolectotype: L barcode L0329772!).

= ***Androscepia gigantea*** (Cav.) Brongn. var. ***armata*** Andersson in Nova Acta Regiae Societatis Scientiarum Upsaliensis, ser. 2 2: 248. 1856 — **Lectotype (designated here)**: India, s.d., *F. de Silva & W. Gomez s.n.* [numer. list. Wallich no. 8776a] (S barcode S-G-10540!; isolectotypes: E barcode E00697829!).

= ***Androscepia gigantea*** (Cav.) Brongn. var. ***sundaica*** Buse in Plantae Junghuhnianae 364. 1854 ≡ ***Themeda gigantea*** (Cav.) Hack. var. ***sundaica*** (Buse) in unknown publication 26: 428. 1920 — Lectotype (designated by Veldkamp in Blumea 61: 29–40. 2016): Indonesia, Java, Cibogo (Tjibogo), *F. W. Junghuhn s.n.* (L barcode L0064300!; isolectotypes: L barcodes L0064301!, L0064302!).

= ***Heterelytron scabrum*** Jungh. in Tijdschrift voor Natuurlijke Geschiedensis en Physiologie 7: 295. 1840 —**Types not found**: Indonesia, Java, *F. W. Junghuhn s.n.*.

Description. – *Habit* perennial. *Rhizomes* present. *Stilt roots* present. *Culms* erect, caespitose, glabrous, 150–350 cm long, 0.52–2.3 cm thick. *Leaf sheaths* glabrous, 8.0–18.7 cm long. *Ligules* truncate, ciliolate, 0.10–0.15 cm long. *Leaf blades* non-plicate, abaxial and adaxial surfaces glabrous, midrib widened and prominent towards the apex, lanceolate, margin slightly scabrid, apex acuminate, 58–250 cm long, 0.6–2.0 cm wide. *Inflorescences* axillary and terminal, inflorescence paniculate, 30–100 cm long. *Spatheoles* glabrous, lanceolate, 2.1–4.9 cm long. *Rachis internodes* fragile, pilose with yellow hairs, linear, 0.10–0.15 cm long. *Racemes* solitary, drooping, 7–8 sterile spikelets rarely 6 or 9, 2–3 fertile spikelets, 1.0–4.4 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male or barren, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 0.75–1.65 cm long, 0.15–0.20 cm wide; callus cuneate, slightly pubescent, attached obliquely, < 0.10 cm long; lower glume surface slightly hirsute with yellow non-tuberculate hair, chartaceous, lanceolate, margins fringe and winged keels, apex acute, 1 spikelet long and wide; upper glume surface glabrous, chartaceous, lanceolate, margin fringe, apex acute, shorter than the lower glume, 0.55, 0.8, 1.2, 1.3 cm long, < 0.1 cm wide; lower lemma glabrous, membranous, oblong, margin fringe, apex obtuse, 0.45─1.20 mm long, 0.1 cm wide; upper lemma glabrous, membranous, oblong, margins entire, apex obtuse, 0.46 –1.10 cm long, < 0.1 cm wide; palea linear lanceolate, 0.3 cm long; lodicules 3, cuneate, coriaceous, < 0.1─0.1 cm long. *Fertile pairs* bisexual and barren, deciduous entirely, 2─3 fertile pairs rarely 1 or 4, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, 0.55─0.90 cm long, 0.15─0.20 cm wide; callus cuneate, pilose with tawny hairs, attach obliquely, 0.10─0.15 cm long; lower glume pilose with tawny hairs throughout, coriaceous, elliptic, margins partly enclosed upper glume, apex obtuse, 1 spikelet long and wide; upper glume pilose with tawny hairs, coriaceous, oblong, margins entire, apex acute, slightly shorter than the lower glume, 0.55–0.82 cm long, < 0.1 cm wide; lower lemma glabrous, membranous, lanceolate, margin ciliate at the top, apex acuminate, 0.40─0.80 cm long, < 0.10 cm wide; upper lemma attached to the awn, glabrous, membranous, ovate, margins entire, apex acuminate, 0.40─0.65 cm long, < 0.10 cm wide; palea absent, if present, ovate, 0.20 cm long; lodicules 3, cuneate, coriaceous, < 0.1─0.15 cm long, companion spikelets, pedicelled, well developed, male, lanceolate, 0.85─1.90 cm long, < 0.10─0.15 cm wide; callus linear, pilose with yellow hairs, 0.15─1.20 cm long; lower glume glabrous or slightly puberulous, chartaceous, lanceolate, margins fringe, apex acute, 1 spikelet long and wide; upper glume glabrous, chartaceous, lanceolate, margin fringe, apex acute, 1.0─1.2 cm long, < 0.10─0.10 cm wide; lower lemma glabrous, membranous, lanceolate, margins ciliate, apex acute, 0.60─1.15 cm long, < 0.1 cm wide; upper lemma glabrous, membranous, lanceolate, margin entire, apex acute, 0.60─1.10 cm long, < 0.1 cm wide; palea absent or present, 0.15–0.35 cm long, < 0.1 cm wide, membranous; lodicules 3, cuneate, coriaceous, < 0.10─0.15 cm long. *Awn* present, straight, column twisted and hispidulous, 0.2─3.2 cm long, 0.07─0.23 mm thick. *Anthers* 3, 0.2─0.5 cm long. *Ovary and Stigma* ovary 1, 0.1─0.2 cm long, stigmas 2, plumose. *Caryopsis* 0.25─0.55 cm long, 0.49─1.35 mm thick.

Etymology. – The specific epithet ‘*villosa*’, combining two Latin words *villi* (long soft hairs) and *-osa* (abundance), describes hairy nature of stem, leaf, and spikelet of this species.

Vernacular names. – Jian (菅; Chinese name), Loei sanggar (Sumatra), Pi-li (Tibet)

Geographic distribution. – *Themeda villosa* is distributed in South Central China and Southeast Asia such as Indonesia, Malaysia, the Philippines, and Thailand.

Phenology. – Themeda villosa flowers throughout the year, but main flowering season span from September to December and from February to April.

Habitat & Ecology. – Main habitats of *Themeda villosa* are wetland with tall C_4 grasses (e.g., *Imperata*, *Phragmites*, *Saccharum*, and *Thysanolaena*) and semi-aquatic grasses in genus *Microstegium* or occasionally found in tropical moist deciduous savannas, especially in microhabitats near alluvium.

Phylogenetic position and morphological evolution. – *Themeda villosa* is grouped in the subclade of wetland species (Arthan et al., 2022).

Cytogenetics. – Only tetraploid populations (2n = 40) were reported for Themeda villosa (Birari, 1980, 1981).

Uses and ethnology. – *Themeda villosa* is used for thatching by Monpa people in Tibet as their leaves are wide and long (Li et al., 2020).

Specimens examined. – Please see full list of specimens examined in Appendix XIV U.

Themeda yunnanensis S.L. Chen & T.D.Zhuang in Bulletin of Botanical Research, Harbin 9(2): 58. 1989 — **Lectotype (designated here)**: China, Yunnan, Pingbian Xian, 1400 m. alt., 14 September 1934, *H. T. Tsai 61976* (HUH barcode A00105302!).

Description. – *Habit* perennial. *Rhizomes* absent. *Stilt roots* absent. *Culms* erect, unbranched, glabrous, 50-100 cm long, ca. 3.80 cm thick. *Leaf sheaths* glabrous, 7─10 cm long. *Ligule* truncate, jagged, 0.1 cm long. *Leaf blades* non-plicate, abaxial and adaxial surfaces glabrous, lanceolate, margin scabrid, apex acuminate, 15-30 cm long, 0.3-0.5 cm wide. *Inflorescences* axillary and terminal, inflorescence paniculate. *Spatheoles* wrapped around peduncle, surfaces glabrous, ovate, 3-6 cm long. *Rachis internodes* fragile, oblique at the apex, sparsely pilose, straight, 0.1─0.2 cm long. *Racemes* solitary, 7 sterile spikelets, 2 fertile spikelets, 2.5-3.5 cm long (excluding awns). *Triad* present. *Homogamous pairs* spikelets 4 in number, male, a pair arranging at different levels, persistent, sessile spikelets similar to the pedicelled ones, well developed, lanceolate, 1.5 cm long, xx mm wide; callus squared, glabrous, ca 0.1 cm long; lower glume pilose with white tuberculate hairs, chartaceous, lanceolate, margins partly enclose upper glume, apex obtuse, 1.45‒1.85 cm long, 0.15‒0.25 cm wide; upper glume glabrous, coriaceous, oblong, margin fringed and membranous, apex acute, shorter than the lower glume, 1.10‒1.35 cm long, 0.10‒0.15 cm wide; lower lemma glabrous, membranous, oblong, margin entire and fringed, apex acuminate, 1.00‒1.25 cm long, ca 1.0 mm wide; upper lemma absent; palea absent; lodicules 3, cuneate, coriaceous, < 0.1 cm long. *Fertile pairs* bisexual and barren, deciduous entirely, 1 spikelet pair, fertile spikelets different from pedicelled ones, sessile spikelets, well developed, bisexual, elliptic, 0.70‒0.85 cm long, 1.5 mm wide; callus cuneate, densely hairy, attached obliquely, 2.5 mm long; lower glume densely pubescent with ivory hairs, deep grove in the middle, coriaceous, ovate, margins partly enclosed upper glume, apex obtuse, median groove on the back, 1 spikelet long and wide; upper glume densely pubescent with ivory hairs, coriaceous, oblong, entire, apex obtuse, shorter and narrower than the lower glume, 0.75 cm long, 0.1 cm wide; lower lemma glabrous, membranous, oblong, margin entire, apex acuminate, 0.5 cm long, < 1.0 mm wide; upper lemma absent; palea absent or minute; lodicules 3, cuneate, coriaceous, < 0.1 am long, companion spikelets, pedicelled, well developed, male or barren, lanceolate, 1.50‒1.90, 3.0 cm long, 0.10‒0.20 cm wide; callus glabrous or sparsely pilose with white non tuberculate hairs, linear, 0.15‒0.25 cm long; lower glume pilose with white tuberculate hairs, chartaceous, narrowly lanceolate, margins partly enclose upper glume, apex acute, 1 spikelet long and wide; upper glume glabrous, coriaceous, shape lanceolate, margin entire, apex slightly aristate, shorter than the lower glume, 1.10‒1.30 cm long, 0.10‒0.15 cm wide; lower lemma glabrous, membranous, linear, margin entire, apex acuminate, 0.90‒0.95 cm long, 1.0 mm wide; upper lemma glabrous, membranous, linear, margin entire, apex acuminate, 0.80‒0.90 cm long, 1.0 mm wide; palea absent; lodicules 3, cuneate, coriaceous, < 0.1 cm long. *Awn* present, geniculate or bigeniculate, column twisted and hispidulous, 3‒6 cm long, 0.42‒0.49 mm thick. *Anthers* 3, 0.30‒0.65 cm long. *Ovary and Stigma* ovary 1, < 1.0 mm long; stigmas 2, plumose. *Caryopsis* 4.53-5.50 mm long, 1.30-1.41 mm thick.

Etymology. – The specific epithet '*yunnanensis*' refers to Yunnan, China where the species was first discovered.

Vernacular names. – Yun nan jian (云南菅; Chinese name)

Geographic distribution. – Yunnan, South central China.

Phenology. – September to October.

Habitat & Ecology. – Poaceae account in Flora of China (Shouliang & Philips, 2006) documented that *T. yunnanensis* exists in dry mountain slopes, which implies that this species exists in open habitats. Tian et al. (2007) described that *T. yunnanensis* is dominant species in natural habitat of temperate region at high altitude with latosol (red earth) and precipitation ranging from 1600-1650 mm/year.

Phylogenetic position and morphological evolution. – Although phylogenetic position of *T. yunnanensis* remains unknown, its inflorescence and spikelet structures resemble the wetland species. Phylogenetic and morphological evidence suggest that phylogenetic position of *T. yunnanensis* might belong to the wetland group.

Cytogenetics. – No cytogenetic data provided for *T. yunnanensis.*

Uses and ethnology. – No use data provided for *T. yunnenensis*.

Specimens examined. – **CHINA. Yunnan Province:** Pingbian Xian, 1400 m, 14 September 1934, *H. T. Tsai 61976* (HUH). **Guangdong Province:** Zhongxing Town, Zhongxing Village, National Highway 206, 50-100 m, 23 October 2011, *Z. Shouzhou et al. 4766* (SZG).

Note. – Holotype from JSBI(NAS) has not been found in the database, thus, lectotypification was performed with specimen with the same number deposited in A.

EXCLUDED TAXA

Themeda polycephala Velk. in Blumea 61: 29–40. 1989 — Holotype: Laos, Champassak Province, 55 km from Paksong, at Tateng, Boloven Plateau, 1000–1200 m. alt., 13 November 1938, *Poilane 28428* (L barcode L1344970!; isotypes: K barcode K000607925!).

Note: This species possesses *Hyparrhenia* characteristics of paired racemes. This species needs further investigation if it is a new *Hyparrhenia* species.

5.5 CONCLUSIONS

Ecological, morphological, and phylogenetic data facilitate species delimitation in the complex *Heteropogon-Themeda* group. Phylogenetic results provide a guide to setting morphological boundaries. Inflorescence branching orders, the number of homogamous spikelets, and the number of spikelet pairs are shown to be the main useful distinguishing characters. Other characters such as awn type, glume hairiness, and caryopsis shape can also be used as fine-scale classifications. Ecological data is additionally helpful when ambiguous cases exist in species with overlapping distributions. Although *Heteropogon* and *Themeda* form a monophyletic group under many analyses and shared morphological characters are documented, both genera are recognized as distinct in this study. This perspective benefits the stability of names as these genera contain well-known species such as *Heteropogon contortus* and *Themeda triandra*. Retaining both genera supports consistent name use by ecologists, evolutionists, and taxonomic systematists.

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CHAPTER 6

GENERAL DISCUSSION AND CONCLUSION

6.1 OVERALL DISCUSSION

This thesis has worked towards an integrative multidisciplinary understanding of the biodiversity of the *Heteropogon-Themeda* group by investigating the evolutionary history, macroecological patterns, climatic characteristics, functional ecology, and the systematics of the *Heteropogon-Themeda* group based on ecological, morphological, and phylogenetic evidence. In chapter 3, phylogenetic reconstructions, based on finer taxon samplings and plastome and nuclear data, revealed new findings in evolutionary processes, origin, and phylogenetic relationships between *Heteropogon* and *Themeda*. In chapter 4, macroecological patterns of *Heteropogon* and *Themeda* were investigated by using climatic characteristics and functional traits. Climate and functional trait data were analyzed with phylogenetic comparative methods to explain climatic niche history and functional trait evolution. Major events in climatic niche history were biome shifts from savannas into wetlands, which was supported by differences in precipitation regimes and adaptive traits between the two groups. In Chapter 5, phylogenetic evidence, climatic data, and morphological traits were applied to update the systematics of *Heteropogon* and *Themeda*. The revision yielded updated criteria for generic and species delimitations, updated morphological descriptions, new taxonomic combinations, and exemplified how to use integrative approaches in the taxonomy of Poaceae. Here, key findings from each chapter are discussed and future research questions are proposed, based on what have been discovered from this thesis.

6.1.1 Phylogenomic Study Reveals Evolutionary Processes, Origin, and Biogeographic Patterns of *Heteropogon* and *Themeda* (Chapter 3)

Incongruence in phylogenetic positions observed in plastome- and nuclear gene-based phylogenomic reconstructions suggested polyploidization and intergeneric hybridization are involved in the evolution of *Heteropogon -Themeda* lineages. For example, *Heteropogon triticeus* formed a clade with *Cymbopogon* spp. in the plastome tree but it was placed with *H. contortus* in the coalescent tree. Cytogenetic study by Tothill & Hacker (1976) documented that *H. triticeus* is a hexaploid plant (6X = 60). It could be hypothesized that this species acquired a maternal genome from *Cymbopogon* and paternal ones from conspecific individuals. Morphological resemblance of *H. triticeus* to *H. contortus* rather than to *Cymbopogon* species is possibly from asymmetric genome allocation from the paternal side

(Rensing, 2014). Such a phenomenon commonly happens in Andropogoneae as exemplified by *Bothriochloa-Capillipedium-Dichanthium* complex (Estep et al., 2014). Coalescent methods revealed that there exists genetic variation in nuclear composition among *H. contortus* and *T. triandra* populations since equal proportions of nuclear genes produce alternative topologies. Such conditions implied sets of genes might derive from different progenitors through polyploidizations or introgression (Wendel et al., 2016). These phenomena occur not only in widespread species but were also observed in narrower-ranging species (Brittingham et al., 2018). These findings from *Heteropogon* and *Themeda* emphasized that complex evolutionary relationships of Andropogoneae cannot always be interpreted as bifurcating patterns, but rather be viewed as the result of many processes.

Origin and divergence patterns of the *Heteropogon-Themeda* group highlighted the ecological significance of the group. *Heteropogon* and *Themeda* were estimated to originate during the Miocene C_4 grassland expansion and shown to diversify in the last 8–10 million years.

Current distributions of most *Heteropogon* and *Themeda* species cover Indomalayan regions encompassing savanna environments with unique climatic regimes (Ratnam et al., 2016). Both ecological history and geographical distribution bring about hypotheses that the evolutionary history and macroecological patterns of *Heteropogon* and *Themeda* might be associated with savannas and their climatic regimes. Two wide-ranging species, *H. contortus* and *T. triandra*, did not spread between continents and diversify until the Pleistocene. One possible explanation is that *H. contortus* and *T. triandra* could be more tolerant to drought than other plants and filled the empty niche during severe desiccation in the Pleistocene. What exact abiotic and biotic factors contribute transcontinental migration and establishment has not been investigated. Plastome and nuclear trees support geographic clustering of *Themeda triandra*. African and Middle Eastern populations formed a cluster while Asian and Australian populations are more closely related than the former group. Underlying causes are not yet investigated but could be that populations from two clades occupy different climatic spaces and developed sets of traits to respond to the environment differently. In contrast, no such patterns were observed among *H. contortus* populations. These contrasting situations implied different modes of dispersal, habitat suitability, climatic preferences, functional traits, and demographic structures.

6.1.2 Ecological Diversity of *Heteropogon-Themeda* Lineage (Chapter 4)

The analyses of climatic variables and habitat classification demonstrated that current geographic distributions of *Heteropogon-Themeda* species are determined by the existence of savannas and wetlands. Climatic analyses showed by the climatic envelope of wetland species occupy higher annual precipitation and precipitation of the driest quarter and less precipitation seasonality than that of savanna species. The Indomalayan region is considered the geographic area comprising the majority of wetlands in the world. Why the wetland species were only found in this region could be explained by some ecological barriers such as limited habitat connectivity, competitive abilities of species, or lack of genetic diversity. According to phylogenetic comparative methods, climatic niche analyses showed niche divergence between savanna and wetland species. Savanna is the ancestral habitat of the group and adaptations to wetland evolved later in the lineage. Presence of seasonality in savannas might provide a pre-adaptive condition to occupy wetlands. Niche divergence might be caused by ecological sympatric speciation that might happen due to the geographic orientation of savannas and wetlands in intermittent fashion. Adapting to wetlands occurred at least two times in the lineages, one with most wetland species being an early-diverged lineage and the other is *Themeda novoguineensis* belonging to more recent subclade. Repeated ecological adaptations marked the lability in adaptation to wetland environments, especially to the availability of precipitation.

Precipitation and temperature niche only broadly explain distribution ranges at the species level. General trends are that climatic spaces of widespread species mostly cover the ones of smaller-ranging species. For example, a floristic survey recorded co-occurrence of *H. contortus* and *T. triandra* with endemic *T. anathera*. In another case, niche equivalency and similarity indicated *H. triticeus* and *T. arguens* do not share a climatic niche with most species and reflect being Southeast Asian natives. Climatic data have not yet explained the local separation between *Heteropogon-Themeda* species sharing geographic distribution such as endemic species. Why narrow-ranging species co-occur or do not expand beyond their current distribution relies not only on climate but also competition, adaptability in populations, and disturbances.

6.1.3 Functional Traits

Climatic changes and habitat preferences between savanna and wetland groups suggested adaptation through different functional traits. Wetland species are taller than savanna species, have greater leaf area, and develop stilt roots. Greater height benefits wetland species to compete for light with other plant species under inundated conditions. Greater leaf area complements the requirement of high photosynthesis for growth in wetland species. In contrast, resources in savannas might be more limited than in wetlands, especially because of limited water availability in longer dry seasons than the wetlands. In the drier conditions in savannas, slower plant growth and narrower leaf blade prevent loss of water from desiccation. Stilt roots prop up wetland plant stature due to unstable soil surface in mesic or flooded conditions and in some cases function as a respiratory organ in anoxic environments. In addition, awn types differ between savanna and wetland species. Geniculate awns in savanna species are thought to facilitate diaspore burial in the soil or suitable microhabitats to escape fire. Straight awns or absence of awns are more suitable in inundation as soil penetration might not be necessary for the wetland species in flooded conditions.

Transitions in plant height, leaf area and different awn types stemmed from pre-adapted traits and were under selective pressure. Capabilities for increased heights in wetland species was likely be facilitated by preadaptation from an Andropogoneae ancestor. Comparative analyses predicted that the strength of selection and trait optimum values are higher in the wetland species than in the savanna species. Differences in both values indicated more constraints in the wetland species to enlarge plant size and leaf area rather than decreasing them as seen in the savanna species. Possible causes for the constraints might be extra resource acquisition, trade-offs between traits (e.g., height and hydraulic functions), or competition. Changes towards shorter or smaller sizes are less contingent on extrinsic than intrinsic factors. The geniculate awn was ancestral in the *Heteropogon-Themeda* lineage. The change of awn types has no intermediate states; awn types were altered from geniculate to either straight awn or awnless state. This implies directional change, high lability of this trait, and different levels of evolutionary pressure determine awn state in the lineage. Trait lability was supported by molecular work identifying that only a few genes regulate the expression of awn. However, exact evolutionary pressure on awn characteristics (e.g., awn type and awn length) and functions of the *Heteropogon-Themeda* clade and Andropogoneae as a whole is still in doubt (Petersen & Kellogg, 2022).

6.1.4 Ecology, Morphology, and Phylogenetics: Three Musketeers of Plant Systematics (Chapter 5)

Investigation of ecological, morphological, and phylogenetic diversity from chapter 3 and 4 benefit taxonomic revision of the *Heteropogon-Themeda* group. Here, both *Heteropogon* and *Themeda* are recognized as genera, and three *Heteropogon* and 26 *Themeda* species and 2 varieties are accepted. The nuclear gene tree indicates that *Heteropogon* and *Themeda* are paraphyletic groups as traditionally defined. Morphologically, *Heteropogon* species shared numerous homogamous spikelets and spikelet pairs, and first-order branching inflorescence. Although *H. contortus* and *H. triticeus* are not sister species in the plastome tree, the nuclear tree and morphology indicate that they can still be placed in the same genus. Three species are accepted in the genus *Heteropogon*. *Heteropogon contortus* and *H. triticeus* are both accepted, supported by different phylogenetic positions, spikelet morphology, and wetter climatic occupation of *H. triticeus*. *H. polystachyos* is still accepted despite lack of ecological and phylogenetic evidence because it possesses strictly terminally inflorescence which represents a meaningful morphological character. Within *Themeda*, six wetland species comprising *T. arundinacea*, *T. caudata*, *T. idjenensis*, *T. intermedia*, *T. novoguineensis*, *T. villosa*, are accepted. *Themeda gigantea* was treated as a synonym of *Themeda intermedia* due to overlapping climatic spaces and distribution range, and minor differences in quantitative traits. Most Chinese and Indian endemic *Themeda* species are accepted and mainly distinguished by morphology and phylogenetic relationships. For instance, early diverged positions, unique morphology of possessing a few spikelet pairs and absence of awn, and climatic occupancy confirmed *Themeda anathera* as a species. *Themeda helferi*, *Themeda laxa*, *T. quadrivalvis*, and *T. unica* were merged in *Themeda triandra* as they intermix in a single clade and represent continuous climatic and morphological variations. Concordant phylogenetic results based on plastomes and nuclear genes suggested *H. melanocarpus* and *H. ritchiei* should be in genus *Themeda*. Intermediate morphology of *H. melanocarpus* and *H. ritchiei* back up this classification. Rare Chinese and Indian endemics *T. minor, T. odishae, T. palakkadensis, T. saxicola*, and *T. yunnanensis* are all accepted, but only based on inflorescence branching patterns and spikelet characteristics. This was due to limited availability of DNA resources and occurrence data.

We encountered some limitations in using each dataset for species delimitation. Not all DNA data from *Heteropogon* and *Themeda* species were included in the phylogenetic analyses due to poor quality leaf materials and rare occurrence in natural habitats, but more than 80% of species were included in phylogenetic analyses, which meet the acceptable criteria to decrease phylogenetic error and cover phylogenetic diversity (Folk et al., 2018; Heath et al., 2008). A few morphological characters (e.g., plant height, awn, and caryopses) could be missing due to collecting method and low number of specimens available for morphological examinations. Ecological data depend on primary data source (e.g., occurrence data and satellite data) and require careful interpretation. Using inappropriate or insufficient primary data can cause misinterpretation or statistical unreliability. In this study, ecological analyses performed with rare species were affected by small sample sizes of less than five occurrence points, which render ecological niche modelling or climatic niche overlap untestable. One way to compensate these drawbacks is to use descriptive data in the literature, but this should be considered case by case.

6.2 FUTURE RESEARCH

Here, I propose potential long-term research and applications based on new findings and knowledge gaps remained unanswered from this thesis. This research plan makes use of existing data resources and generating new data (e.g., DNA data), and holds collaborative effort in grass biodiversity research communities. I begin with small-scale applications within *Heteropogon* and *Themeda* and other lineages and end with how to build large-scale framework from the smaller ones.

6.2.1 Extended research within *Heteropogon-Themeda* lineage.

Evidence of reticulate phylogenetic history and relationships of *Heteropogon* and *Themeda* (Chapter 3) prompts questions about the roles of hybridization and polyploidization in evolutionary history and ecology. Previous local-scale studies showed tetraploid *Themeda triandra* populations were more tolerant to drought than the diploid ones, which resulted in distinct distribution ranges in Australia (Godfree et al., 2017). Geographic clustering of *Themeda triandra* populations in Chapter 3 raises the question if ploidy levels have an influence on different adaptations to climate or functional traits (e.g., awn length and leaf traits). Providing that there are correlations between ploidy levels and climatic regimes, might there have been genetic components responsible for adapting in different climate? However, such geographic patterns are less obvious in *Heteropogon contortus* populations. This scenario might imply different adaptation strategies that shape geographic distributions of *Heteropogon contortus* or random processes.

Findings from Chapter 4 provides fundamental knowledge about climatic niche and functional traits to further explore their ecological roles in C_4 grassy biomes. In Chapter 4, habitat preferences of *Heteropogon* and *Themeda* species were broadly categorized into two groups, savanna, and wetland. However, both savanna and wetland include several habitat subgroups defined by distinct vegetation types, disturbances, and soils. Testing relationships between functional traits and abiotic and biotic variables could lead to more understanding in vegetation dynamics in C_4 grassy biomes and its ecological history. For example, leaf anatomical traits explain leaf structures (Harrison et al., 2021) or overlooked underground traits deliver resprouting strategies, root biomass, and root branching could explain response to fire, soil properties, and fungal interactions (Pausas & Keeley, 2014; Tavşanoğlu & Pausas, 2018).

6.2.2 Applications with other tropical grasses

Knowledge gaps in evolutionary history, functional ecology, and systematics of most C_4 grasses remain incomplete. Genus *Hyparrhenia* is another dominant savanna grasses in African savanna, but only taxonomic work from Clayton (1969) and phylogenetic work from McAllister et al. (2019) investigated biodiversity of *Hyparrhenia*. Hence, systematics of the genus should be updated with in-depth morphological, phylogenetic, and ecological data. Adaptability to African savanna environments (e.g., specific fire regimes) of *Hyparrhenia* urges questions about functional traits and how the traits can predict distribution of the genus in the Anthropocene. Likewise, Asian savanna systems and associated grass lineages are understudied (Ratnam et al., 2016). For example, genera *Dimeria*, *Eremochloa*, *Ischaemum*, and *Mnesithea* have no solid biodiversity information due to insufficient morphological description and lack of molecular data, which impede understanding in phylogenetic history and relationships. This thesis provide framework for following biodiversity research for other grass groups.

6.2.3 Crosstalk between disciplines and lineages

Biodiversity research is tightly linked with conservation science and scientific public engagement. Biodiversity of C_4 grassy biomes is threatened by misconception about tropical grasslands and savannas as degraded habitats, inappropriate management, invasive species, and climate change. Taxonomic investigation of C_4 grasses is the initial step in estimating species number and recognizing species characteristics. Phylogenetic frameworks support classifications and comparative studies. Ecological studies reveal functional roles and responses to the environments. Then, creating integrative taxonomy or monograph yields basic information for proper conservation and habitat management plans, predictions of environmental scenarios, and correlation analyses, and also distribution of accurate knowledge, and emphasis on the importance of C_4 grassy biomes to the public. Future work requires fast actions in revising systematics of grasses to secure biodiversity in C_4 grassy biomes.

Increase in evolutionary backgrounds and data generation in multiple lineages enable large-scale comparative studies. Combining different datasets from grass lineages expand perspectives from ecoregions to biomes scale (Luebert & Weigend, 2014) and from generic to tribal and subfamilial scale (Welker et al., 2020), produce mega phylogenetic reconstructions that with more accurate estimations of speciation events, diversification rates, and time of origin (Smith et al., 2009), and yield biodiversity information for large-scale conservation (Fisher & Owens, 2004). For instance, comprehensive taxon sampling in phylogenetic reconstruction of C_4 lineages (e.g., Andropogoneae, Aristida, core Chloridoideae; Sage et al., 2011) facilitates comparative studies shedding light on when and how C_4 grass lineages assemble in the grassy biomes and how functional traits and climatic histories evolved in the lineages and lead to understanding in how past climatic histories project on future distribution of C_4 grasses under climate changes.

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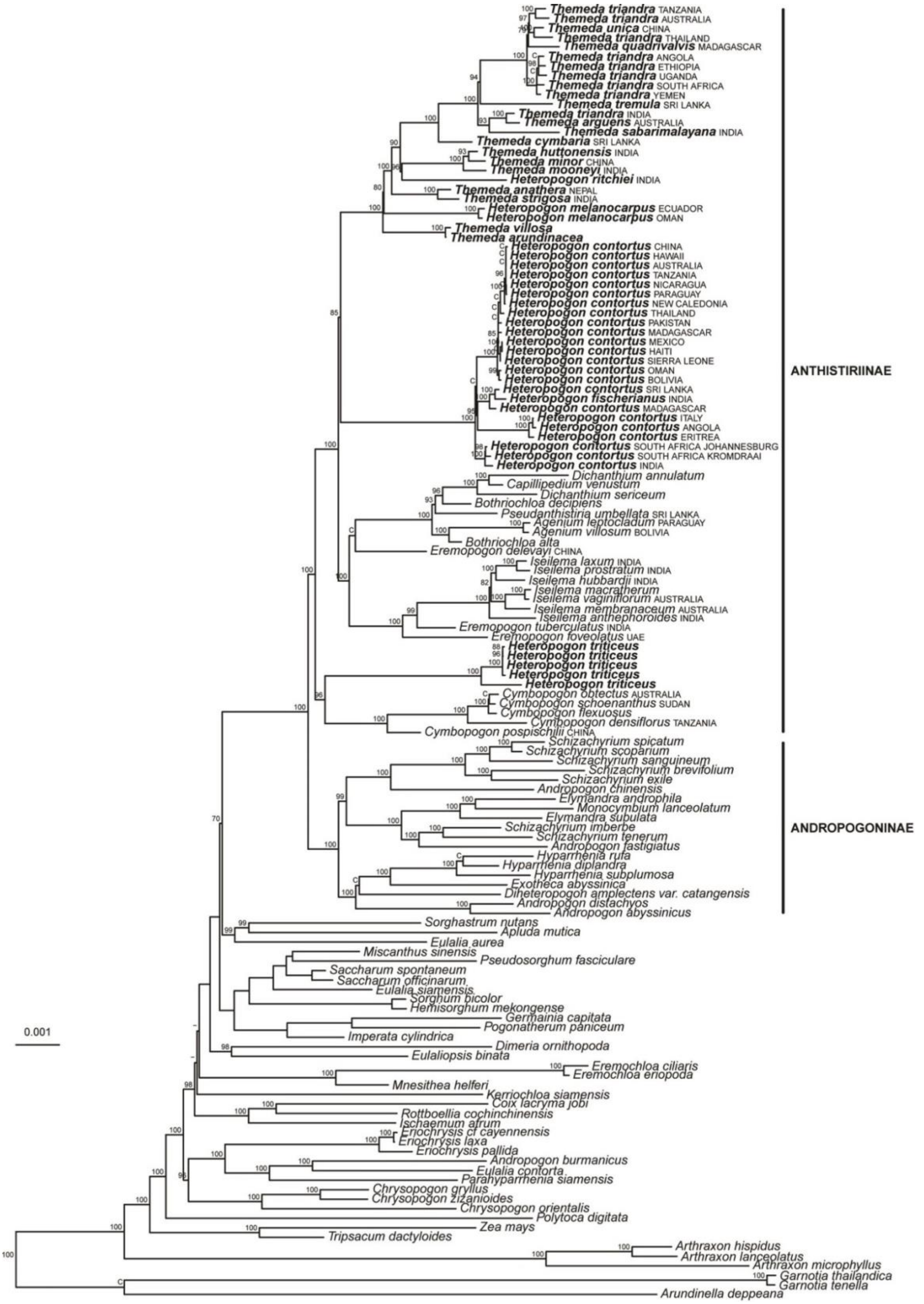
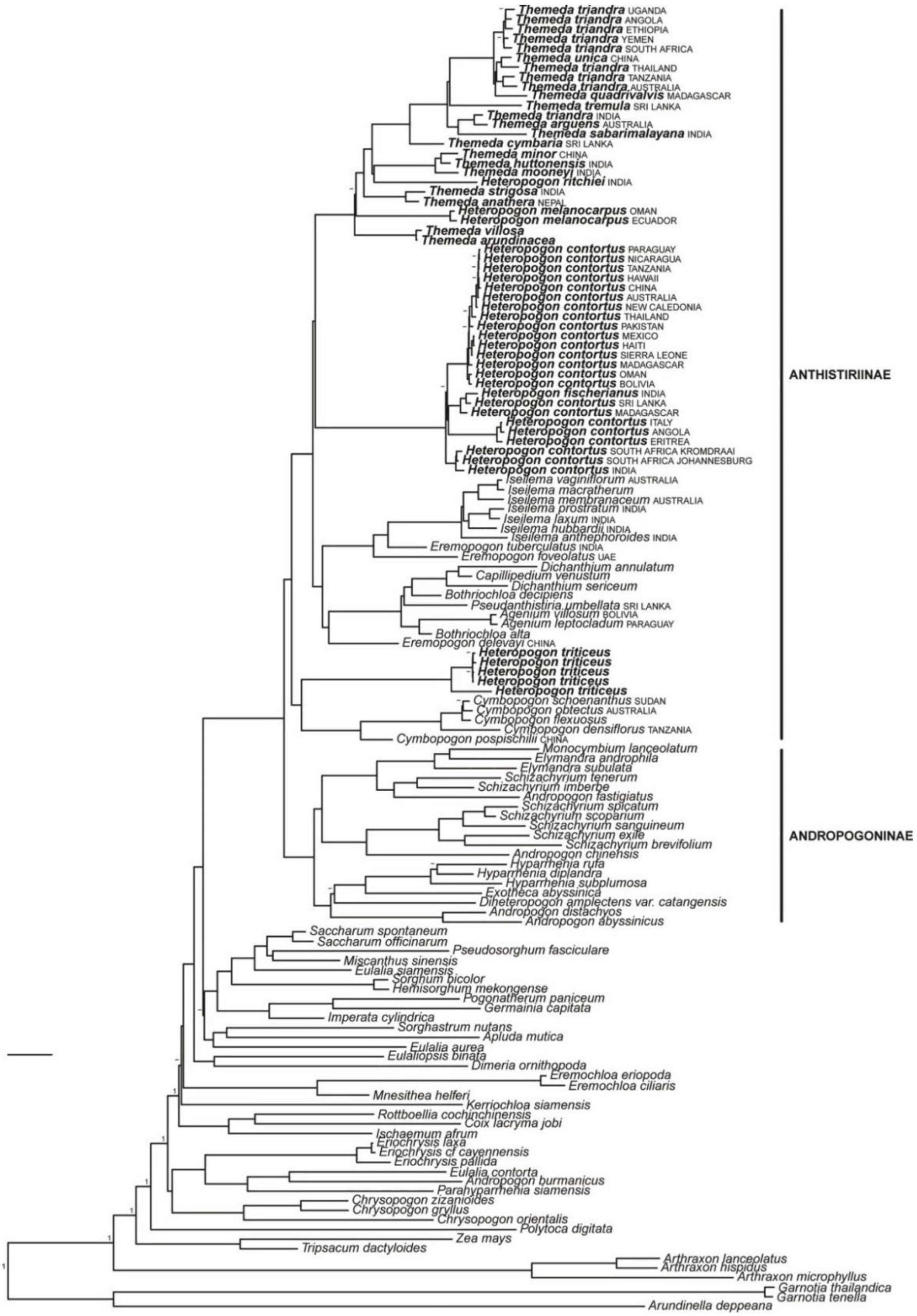
APPENDICES

Appendix I. Plastome tree for 136 taxa of Andropogoneae analysed with maximum likelihood under the GTR+Γ+I model. Phylogenetic tree showing relationships of major clades, the subtribe



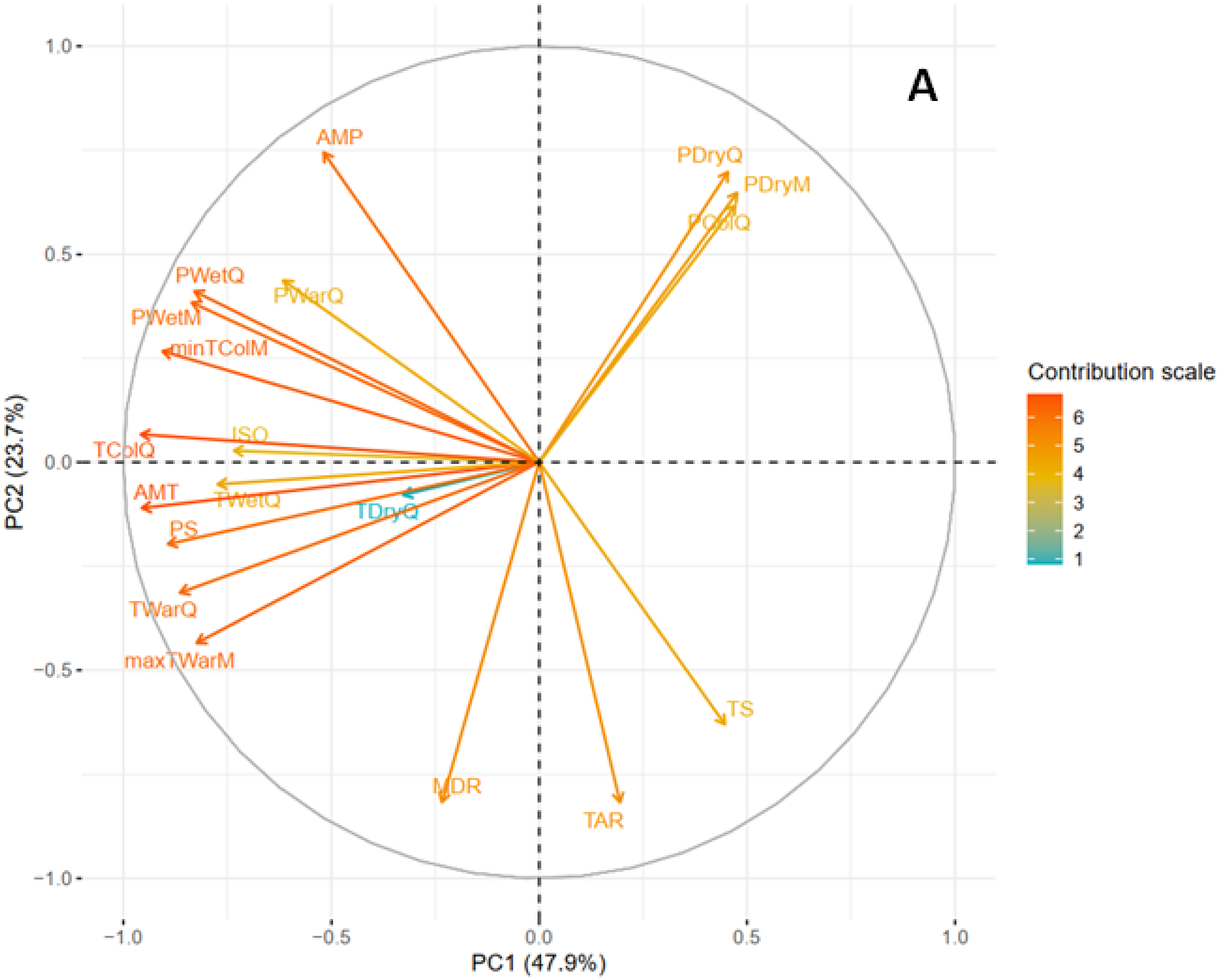
Andropogoninae (DASH clade) and Anthistiriinae, respectively. Only nodes supported by ML bootstrap > 70% are labelled in the tree.

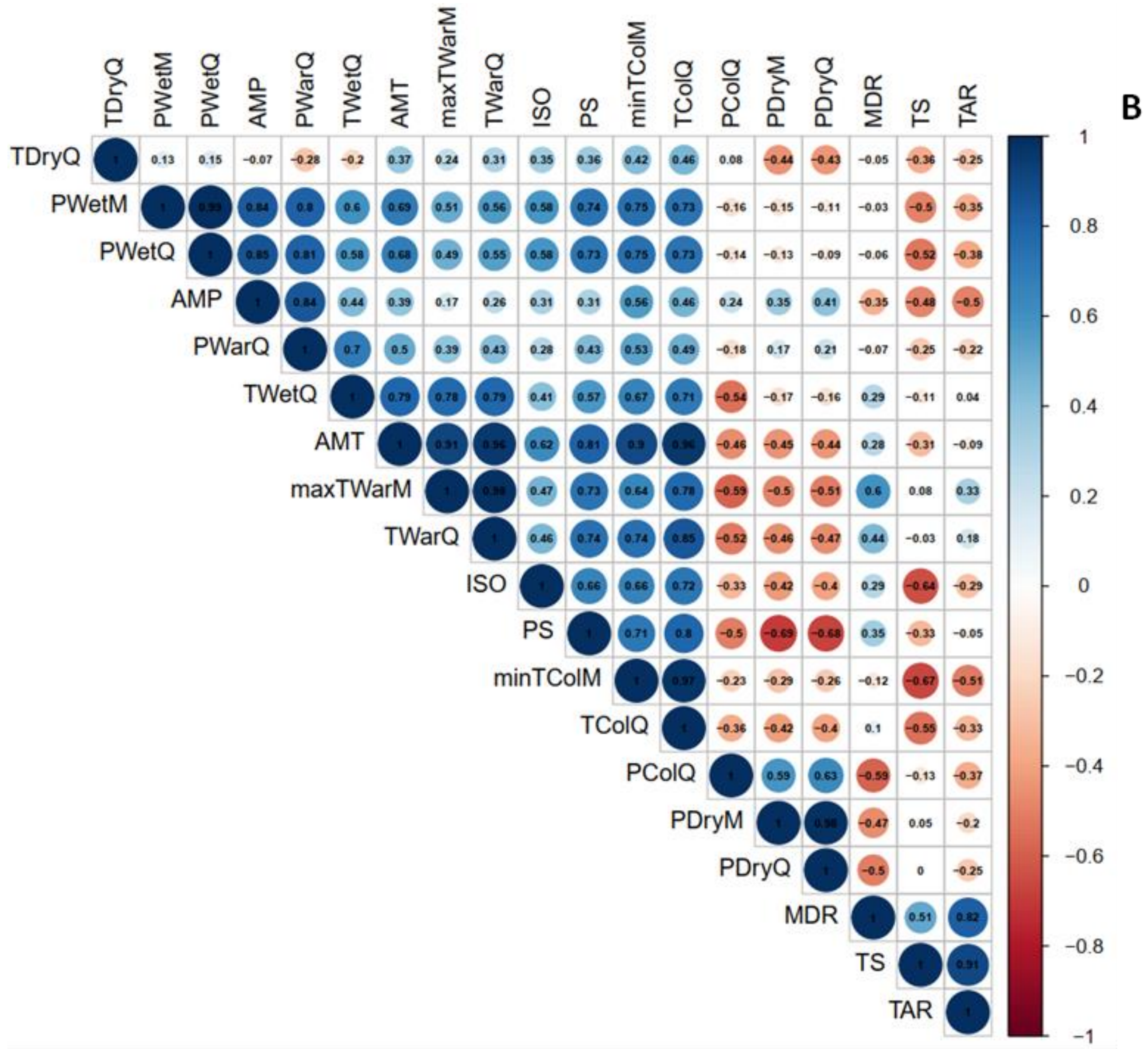
Appendix II. Plastome tree for 136 taxa of Andropogoneae analysed with Bayesian inference analysis under the GTR+Γ+I model. Phylogenetic tree showing relationships of major clades, the subtribe

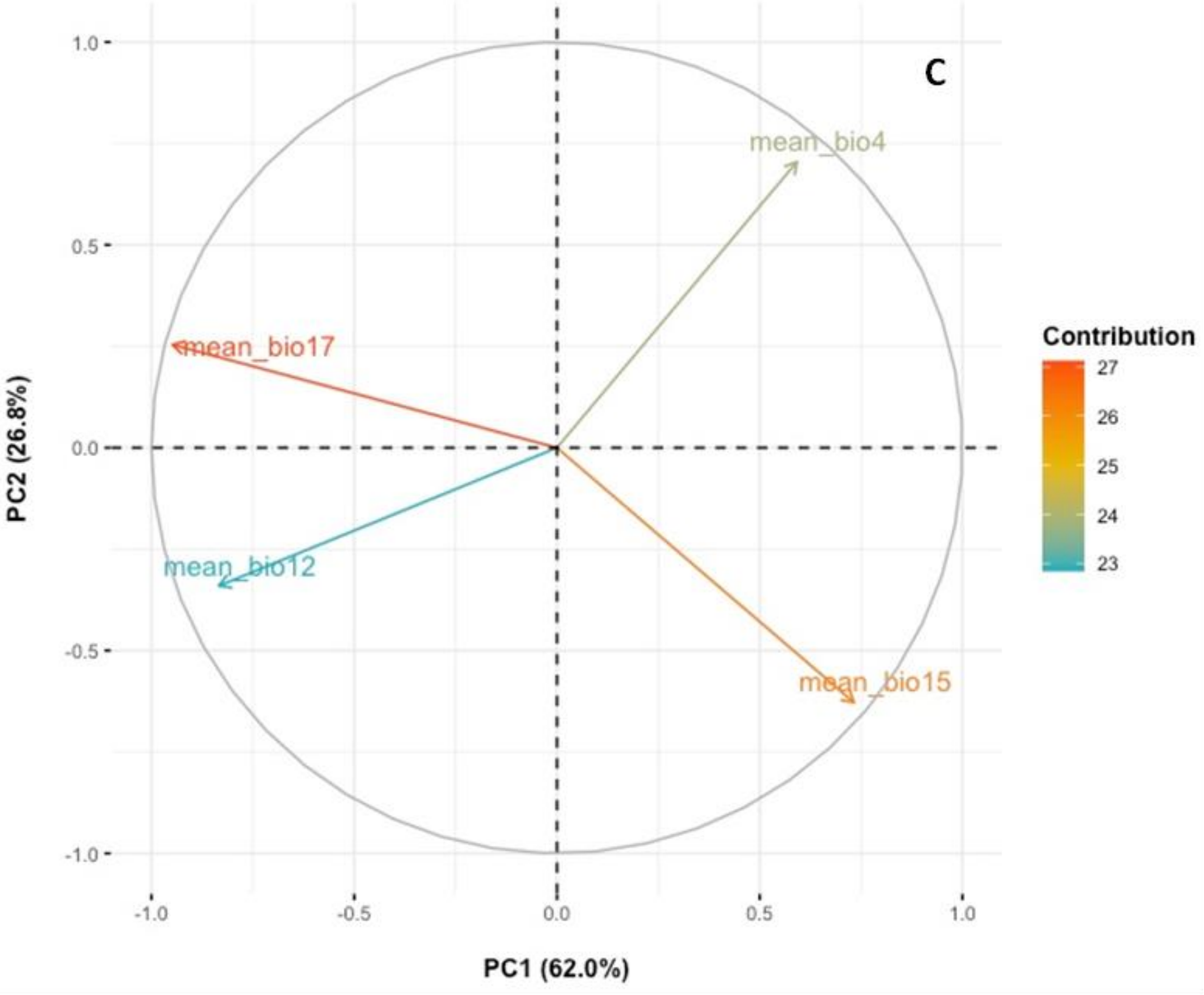


Andropogoninae (DASH clade) and Anthistiriinae, respectively. Only nodes supported by posterior probability > 0.95 are labelled in the tree.

Appendix III. Principal component analysis (PCA) of 19 bioclimatic variables complied from all *Heteropogon* and *Themeda* species showing the first two axes which represent accumulated percentage of 71.60% of all variation **(A)** Pearson's coefficient matrix among 19 bioclimatic variables **(B)** Principal component analysis of 4 selected bioclimatic variables showing the first two axes explaining 88.80% of variation **(C)**.




B
TDryQ
PWetM
PWetQ
AMP
PWarQ
TWetQ
AMT
maxTWarM
TWarQ
ISO
PS
minTColM
TColQ
PColQ
PDryM
PDryQ
MDR
TS
TAR
TDryQ 1 0.13 0.15 −0.07 −0.28 −0.2 0.37 0.24 0.31 0.35 0.36 0.42 0.46 0.08 −0.44 −0.43 −0.05 −0.36 −0.25
PWetM 1 0.93 0.84 0.8 0.6 0.69 0.51 0.56 0.58 0.74 0.75 0.73 −0.16 −0.15 −0.11 −0.03 −0.5 −0.35
PWetQ 1 0.85 0.81 0.58 0.68 0.49 0.55 0.58 0.73 0.75 0.73 −0.14 −0.13 −0.09 −0.06 −0.52 −0.38
AMP 1 0.84 0.44 0.39 0.17 0.26 0.31 0.31 0.56 0.46 0.24 0.35 0.41 −0.35 −0.48 −0.5
PWarQ 1 0.7 0.5 0.39 0.43 0.28 0.43 0.53 0.49 −0.18 0.17 0.21 −0.07 −0.25 −0.22
TWetQ 1 0.79 0.78 0.79 0.41 0.57 0.67 0.71 −0.54 −0.17 −0.16 0.29 −0.11 0.04
AMT 1 0.91 0.96 0.62 0.81 0.9 0.96 −0.46 −0.45 −0.44 0.28 −0.31 −0.09
maxTWarM 1 0.98 0.47 0.73 0.64 0.78 −0.59 −0.5 −0.51 0.6 0.08 0.33
TWarQ 1 0.46 0.74 0.74 0.85 −0.52 −0.46 −0.47 0.44 −0.03 0.18
ISO 1 0.66 0.66 0.72 −0.33 −0.42 −0.4 0.29 −0.64 −0.29
PS 1 0.71 0.8 −0.5 −0.69 −0.68 0.35 −0.33 −0.05
minTColM 1 0.97 −0.23 −0.29 −0.26 −0.12 −0.67 −0.51
TColQ 1 −0.36 −0.42 −0.4 0.1 −0.55 −0.33
PColQ 1 0.59 0.63 −0.59 −0.13 −0.37
PDryM 1 0.98 −0.47 0.05 −0.2
PDryQ 1 −0.5 0 −0.25
MDR 1 0.51 0.82
TS 1 0.91
TAR 1
1
0.8
0.6
0.4
0.2
0
−0.2
−0.4
−0.6
−0.8
−1


C
mean_bio4
mean_bio17
mean_bio12
mean_bio15
Contribution
27
26
25
24
23
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
PC2 (26.8%)
PC1 (62.0%)

Appendix IV. List of quantitative vegetative and reproductive traits of *Heteropogon* and *Themeda* species used in this study.

Species	Plant Height (cm)			Leaf length (cm)			Leaf width (cm)			Maximum Leaf area (cm^2)	Leaf width -to-length ratio	Sessile spikelet length (cm)			Pedicelled spikelet length (cm)		
	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean			Max	Min	Mean	Max	Min	Mean
HC	100	30	64.87	30	3	14.11	0.80	0.20	0.47	24.0	0.036	1.00	0.55	0.71	1.50	0.50	0.86
HF	40	30	35.00	7	2.5	4.75	0.40	0.20	0.30	2.8	0.069	0.90	0.75	0.83	0.90	0.70	0.80
HM	250	50	198.67	50	10	32.50	1.20	0.30	0.80	60	0.031	1.15	0.80	0.91	2.50	1.00	1.74
HR	120	90	105.00	45	15	30.00	1.00	0.80	0.90	45	0.038	0.60	0.45	0.53	1.30	1.00	1.15
HT	300	100	211.76	80	20	48.33	1.80	0.30	0.88	144	0.02	1.50	0.80	1.10	2.50	1.50	1.89
TA	120	20	88.76	45	5	23.39	0.70	0.35	0.43	31.5	0.03	1.00	0.70	0.92	0.90	0.60	0.78
TAN	120	30	78.82	30	15	23.26	0.40	0.20	0.24	12	0.015	0.70	0.50	0.60	0.80	0.50	0.59
TAR	600	100	317.51	100	40	72.92	2.50	0.50	1.28	250	0.016	1.15	0.90	0.94	1.70	1.00	1.47
TAV	200	100	145.61	100	15	34.19	0.15	0.10	0.13	15	0.007	1.70	1.30	1.50	3.00	2.00	2.06
TC	600	100	220.39	150	15	83.14	1.60	0.25	0.94	240	0.013	1.15	0.60	0.83	1.90	0.85	1.43
TCY	250	150	220.48	60	30	45.00	0.80	0.40	0.60	48	0.013	0.60	0.40	0.50	0.80	0.45	0.63
TG	400	100	250.00	100	30	56.00	2.50	0.45	1.15	250	0.015	0.78	0.65	0.72	0.90	0.40	0.74
THE	30	15	22.50	20	5	12.50	0.40	0.20	0.36	4	0.048	0.40	NA	NA	0.60	0.40	0.51
THO	90	20	56.85	20	3	15.22	0.60	0.20	0.29	12	0.028	0.85	0.45	0.60	1.20	0.80	1.02
THU	100	60	80.00	20	10	15.35	0.80	0.40	0.47	16	0.035	0.55	NA	NA	1.20	1.10	1.15
TID	500	300	400.00	100	50	66.67	1.20	0.40	0.80	120	0.011	1.10	0.80	0.98	1.60	1.00	1.34
TIN	500	200	315.94	100	50	83.33	1.50	0.30	1.17	150	0.015	1.15	0.70	0.85	1.40	1.00	1.19
TMI	40	30	35.00	8	3	5.50	0.20	0.10	0.15	1.6	0.029	0.40	NA	NA	0.50	0.30	0.40
TMO	40	20	36.00	30	15	19.73	0.40	0.20	0.25	12	0.013	0.65	NA	NA	0.85	NA	NA
TNO	400	150	253.25	100	30	61.50	2.50	0.20	0.90	250	0.014	0.90	0.70	0.71	0.90	0.60	0.79
TPSEU	200	80	140.00	60	30	45.00	1.20	0.50	0.85	72	0.018	0.30	0.25	0.28	0.60	0.50	0.55
TQ	200	10	101.79	30	7	22.33	0.60	0.20	0.47	18	0.024	0.60	0.40	0.49	0.70	0.40	0.53
TSAB	200	50	125.00	40	15	27.50	1.00	0.50	0.75	40	0.027	0.60	0.50	0.55	0.60	0.40	0.5
TSAX	35	20	27.50	6	3	4.50	0.30	0.25	0.28	1.8	0.046	0.80	0.75	0.78	1.00	NA	NA
TSTR	150	100	125.00	35.5	15	22.68	0.40	0.30	0.35	12	0.015	0.35	NA	NA	0.35	NA	NA
TT	200	30	91.62	65	8	19.42	1.00	0.10	0.38	65	0.023	1.10	0.50	0.84	1.40	0.60	0.99
TTR	120	15	83.76	30	8	13.99	0.80	0.30	0.44	24	0.047	0.35	0.30	0.33	0.65	0.40	0.57
TTRI	195	150	172.50	80	40	54.17	0.60	0.40	0.57	48	0.011	1.00	0.70	0.85	1.50	1.20	1.35
TUN	250	100	175.00	60	30	45.00	1.00	0.40	0.70	60	0.015	1.00	0.70	0.85	2.00	NA	NA
TVI	350	150	294.41	250	50	117.00	2.00	0.60	1.39	500	0.013	0.80	0.70	0.79	1.90	1.00	1.28
TYUN	100	50	75.00	30	15	22.50	0.50	0.30	0.40	15	0.018	1.00	NA	NA	1.50	NA	NA

[†] Abbreviations: HC = *Heteropogon contortus*, HF = *Heteropogon fischerianus*, HM = *Heteropogon melanocarpus*, HR = *Heteropogon ritchiei*, HT = *Heteropogon triticeus*, TA = *Themeda arguens*, TAN = *Themeda anathera*, TAR = *Themeda arundinacea*, TAV = *Themeda avenacea*, TC = *Themeda caudata*, TCY = *Themeda cymbaria*, TG = *Themeda gigantea*, THE = *Themeda helferi*, THO = *Themeda hookeri*, THU = *Themeda huttonensis*, TID = *Themeda idjenensis*, TIN = *Themeda intermedia*, TMI = *Themeda minor*, TMO = *Themeda mooneyi*, TNO = *Themeda novoguineensis*, TPSEU = *Themeda pseudotremula*, TQ = *Themeda quadrivalvis*, TSAB = *Themeda sabarimalayana*, TSAX = *Themeda saxicola*, TSTR = *Themeda strigosa*, TT = *Themeda triandra*, TTR = *Themeda tremula*, *TTRI* = *Themeda trichiata*, TUN = *Themeda unica*, TVI = *Themeda villosa*, TYUN = *Themeda yunnanensis*.

Appendix IV. List of quantitative vegetative and reproductive traits of *Heteropogon* and *Themeda* species used in this study.

Species	Caryopsis length (mm)			Caryopses width (mm)			Callus length (cm)			Awn length (cm)		
	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean
HC	4.78	3.58	4.07	0.74	0.59	0.63	0.30	0.20	0.22	8.00	5.00	7.57
HF	NA	NA	NA	NA	NA	NA	0.35	0.25	0.30	7.00	4.00	5.50
HM	NA	NA	NA	NA	NA	NA	0.40	0.30	0.34	15.00	7.00	9.25
HR	NA	NA	NA	NA	NA	NA	0.20	NA	NA	4.00	3.00	3.50
HT	NA	NA	NA	NA	NA	NA	0.60	0.45	0.56	18.00	10.00	11.75
TA	3.18	2.89	3.04	0.76	0.57	0.67	0.30	0.08	0.13	12.00	3.50	7.25
TAN	3.27	3.03	3.16	1.04	0.88	0.95	0.10	NA	NA	0.00	0.00	0.00
TAR	4.93	3.48	4.34	1.06	0.95	1.05	0.35	0.20	0.26	11.00	2.00	6.08
TAV	7.38	3.42	5.43	1.46	0.98	1.27	0.70	0.50	0.62	10.00	4.00	7.00
TC	5.58	4.39	5.14	1.52	1.08	1.34	0.30	0.10	0.22	6.00	2.30	3.43
TCY	2.15	1.90	2.03	0.64	0.62	0.63	0.10	0.05	0.08	2.00	1.00	1.50
TG	4.32	1.81	3.33	1.19	0.35	0.89	1.50	NA	NA	0.00	0.00	0.00
THE	3.37	2.52	2.90	0.89	0.58	0.78	0.10	0.05	0.08	5.50	3.80	4.33
THO	4.49	3.20	4.04	1.21	0.95	1.08	0.20	0.10	0.15	4.00	2.00	3.08
THU	NA	NA	NA	NA	NA	NA	0.10	NA	NA	2.50	2.00	2.25
TID	NA	NA	NA	NA	NA	NA	0.30	0.10	0.20	5.80	1.50	3.13
TIN	4.40	2.27	3.08	1.31	0.50	0.79	0.25	0.15	0.18	3.00	0.00	NA
TMI	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.40	NA	NA
TMO	NA	NA	NA	NA	NA	NA	0.15	NA	NA	4.50	2.50	3.50
TNO	NA	NA	NA	NA	NA	NA	0.30	0.10	0.21	5.00	0.85	2.59
TPSEU	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.00	2.00	2.50
TQ	4.53	3.18	3.84	1.29	0.81	1.00	0.10	0.05	0.08	5.00	1.00	3.75
TSAB	NA	NA	NA	NA	NA	NA	0.30	0.10	0.20	3.00	1.50	2.25
TSAX	NA	NA	NA	NA	NA	NA	0.20	NA	NA	3.00	NA	NA
TSTR	NA	NA	NA	NA	NA	NA	0.05	NA	NA	1.00	NA	NA
TT	5.71	3.68	4.74	1.35	0.70	1.19	0.40	0.07	0.25	7.00	2.50	4.84
TTR	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.50	1.50	2.50
TTRI	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.00	2.00	3.50
TUN	5.18	NA	NA	2.42	NA	NA	NA	NA	NA	4.00	2.00	3.00
TVI	4.71	3.78	4.20	1.23	1.08	1.14	0.30	0.15	0.19	3.20	NA	NA
TYUN	5.50	4.53	5.02	1.41	1.30	1.35	NA	NA	NA	6.00	3.00	4.50

[†] Abbreviations: HC = *Heteropogon contortus*, HF = *Heteropogon fischerianus*, HM = *Heteropogon melanocarpus*, HR = *Heteropogon ritchiei*, HT = *Heteropogon triticeus*, TA = *Themeda arguens*, TAN = *Themeda anathera*, TAR = *Themeda arundinacea*, TAV = *Themeda avenacea*, TC = *Themeda caudata*, TCY = *Themeda cymbaria*, TG = *Themeda gigantea*, THE = *Themeda helferi*, THO = *Themeda hookeri*, THU = *Themeda huttonensis*, TID = *Themeda idjenensis*, TIN = *Themeda intermedia*, TMI = *Themeda minor*, TMO = *Themeda mooneyi*, TNO = *Themeda novoguineensis*, TPSEU = *Themeda pseudotremula*, TQ = *Themeda quadrivalvis*, TSAB = *Themeda sabarimalayana*, TSAX = *Themeda saxicola*, TSTR = *Themeda strigosa*, TT = *Themeda triandra*, TTR = *Themeda tremula*, *TTRI* = *Themeda trichiata*, TUN = *Themeda unica*, TVI = *Themeda villosa*, TYUN = *Themeda yunnanensis*.

Appendix V. List of qualitative vegetative and reproductive traits of *Heteropogon* and *Themeda* species used in this study.

Species	Presence of stilt root	Presence of awn	Awn type
HC	Absent	Present	Geniculate
HF	Absent	Present	Geniculate
HM	Present	Present	Geniculate
HR	Absent	Present	Geniculate
HT	Present	Present	Geniculate
TAN	Absent	Absent	Awnless
TA	Present	Present	Geniculate
TAR	Present	Present	Straight
TAV	Present	Present	Geniculate
TC	Present	Present	Straight
TCY	Present	Present	Geniculate
TG	Present	Absent	Awnless
THE	Absent	Present	Geniculate
THO	Absent	Present	Geniculate
THU	Absent	Present	Geniculate
TID	Present	Present	Straight
TIN	Present	Present	Straight
TMI	Absent	Present	Straight
TMO	Absent	Present	Geniculate
TNO	Present	Present	Straight
TPSEU	Absent	Present	Geniculate
TQ	Absent	Present	Geniculate
TSAB	Absent	Present	Geniculate
TSAX	Absent	Present	Geniculate
TSTR	Absent	Present	Geniculate
TTR	Absent	Present	Geniculate
TT	Absent	Present	Geniculate
TTRI	Absent	Present	Geniculate
TUN	Present	Present	Geniculate
TVI	Present	Present	Straight
TYUN	Absent	Present	Geniculate

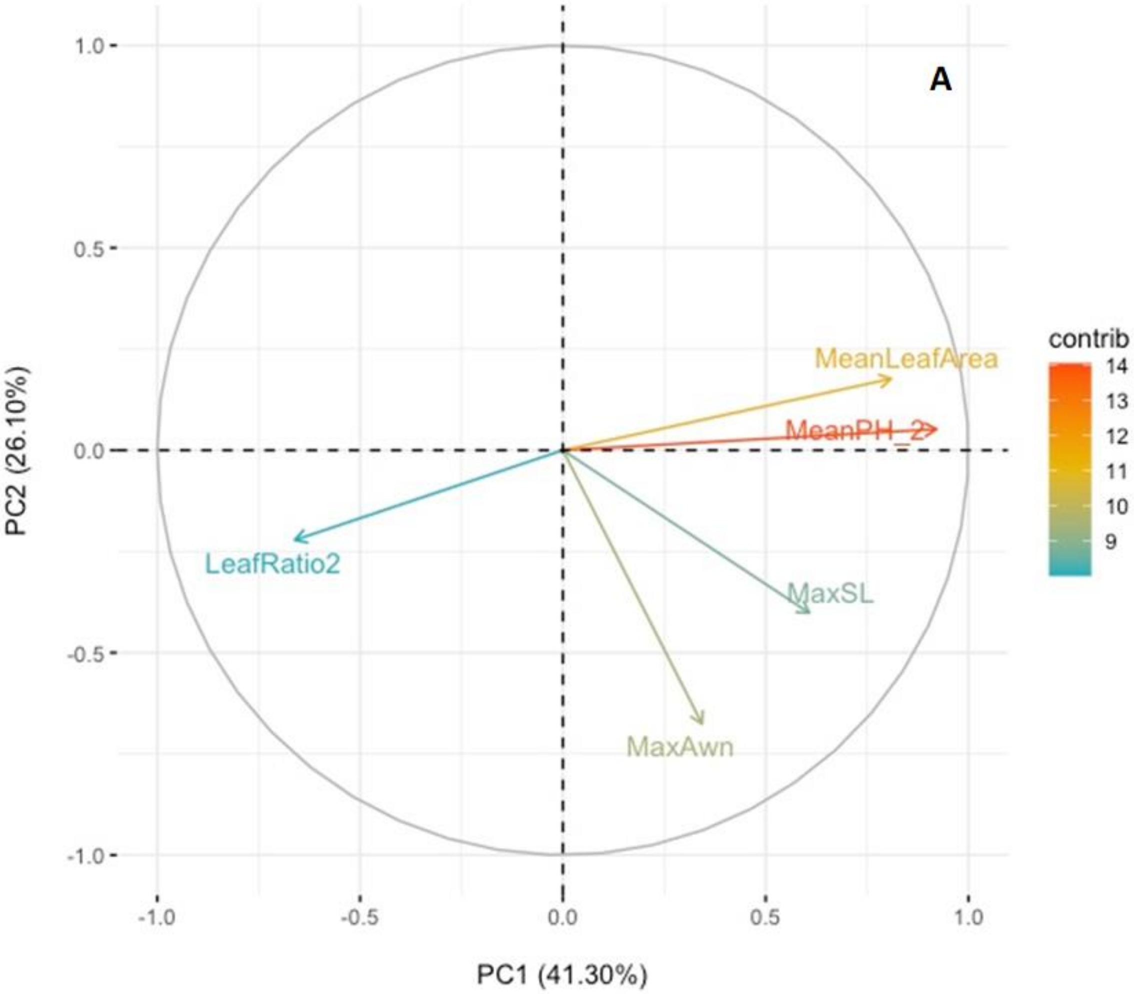
† Abbreviations: HC = *Heteropogon contortus*, HF = *Heteropogon fischerianus*, HM = *Heteropogon melanocarpus*, HR = *Heteropogon ritchiei*, HT = *Heteropogon triticeus*, TA = *Themeda arguens*, TAN = *Themeda anathera*, TAR = *Themeda arundinacea*, TAV = *Themeda avenacea*, TC = *Themeda caudata*, TCY = *Themeda cymbaria*, TG = *Themeda gigantea*, THE = *Themeda helferi*, THO = *Themeda hookeri*, THU = *Themeda huttonensis*, TID = *Themeda idjenensis*, TIN = *Themeda intermedia*, TMI = *Themeda minor*, TMO = *Themeda mooneyi*, TNO = *Themeda novoguineensis*, TPSEU = *Themeda pseudotremula*, TQ = *Themeda quadrivalvis*, TSAB = *Themeda sabarimalayana*, TSAX = *Themeda saxicola*, TSTR = *Themeda strigosa*, TT = *Themeda triandra*, TTR = *Themeda tremula*, *TTRI* = *Themeda trichiata*, TUN = *Themeda unica*, TVI = *Themeda villosa*, TYUN = *Themeda yunnanensis*.

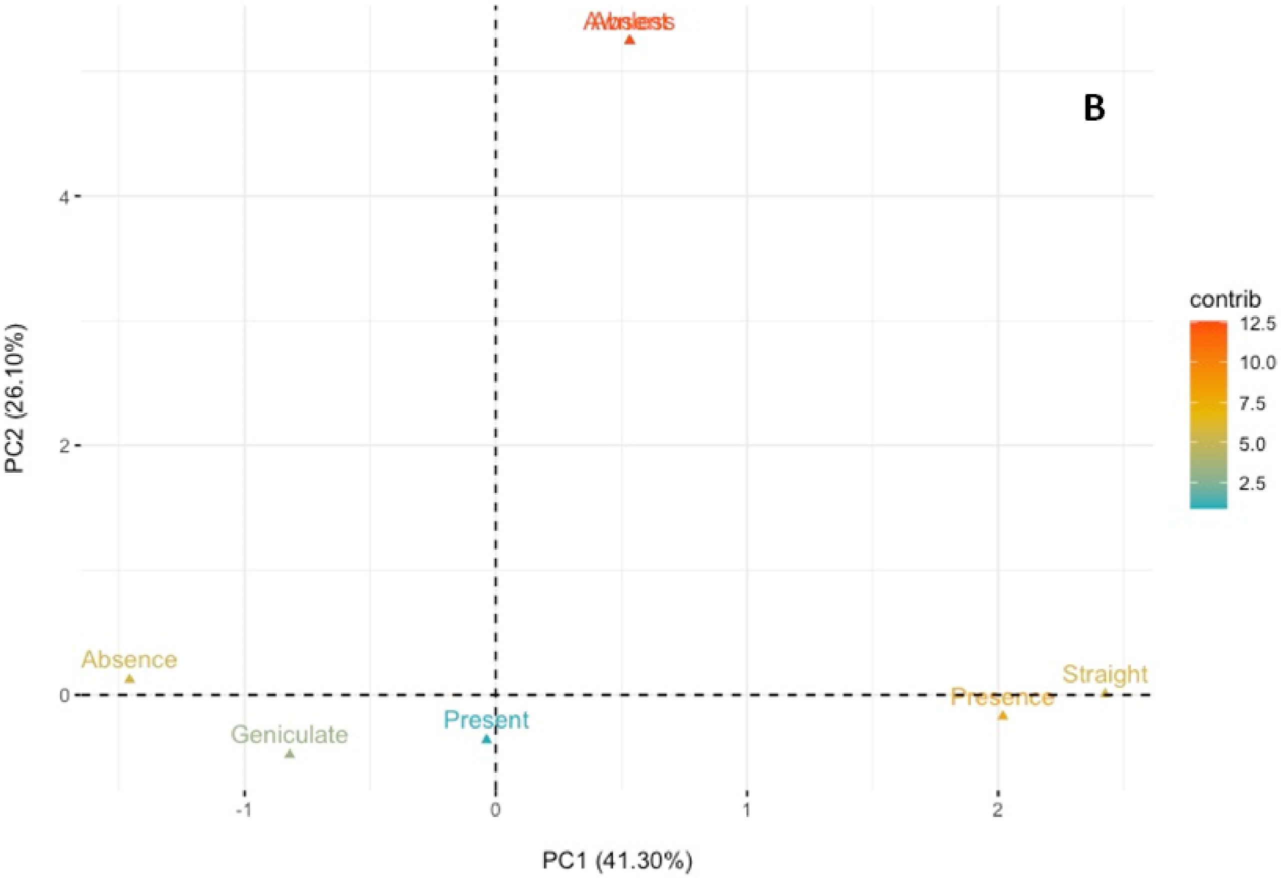
Appendix VI. PCA and FAMD results of bioclimatic data and functional traits.

Bioclimatic variables	**PC1**	**PC2**	**PC3**
	Eigenvalue	**Eigenvalue**	**Eigenvalue**
Temperature seasonality	-0.376	-0.680	0.629
Mean annual precipitation	0.529	0.329	0.681
Precipitation seasonality	-0.465	0.607	0.367
Precipitation of driest quarter	0.602	-0.245	0.077
Percent contribution	62.00	26.80	9.70

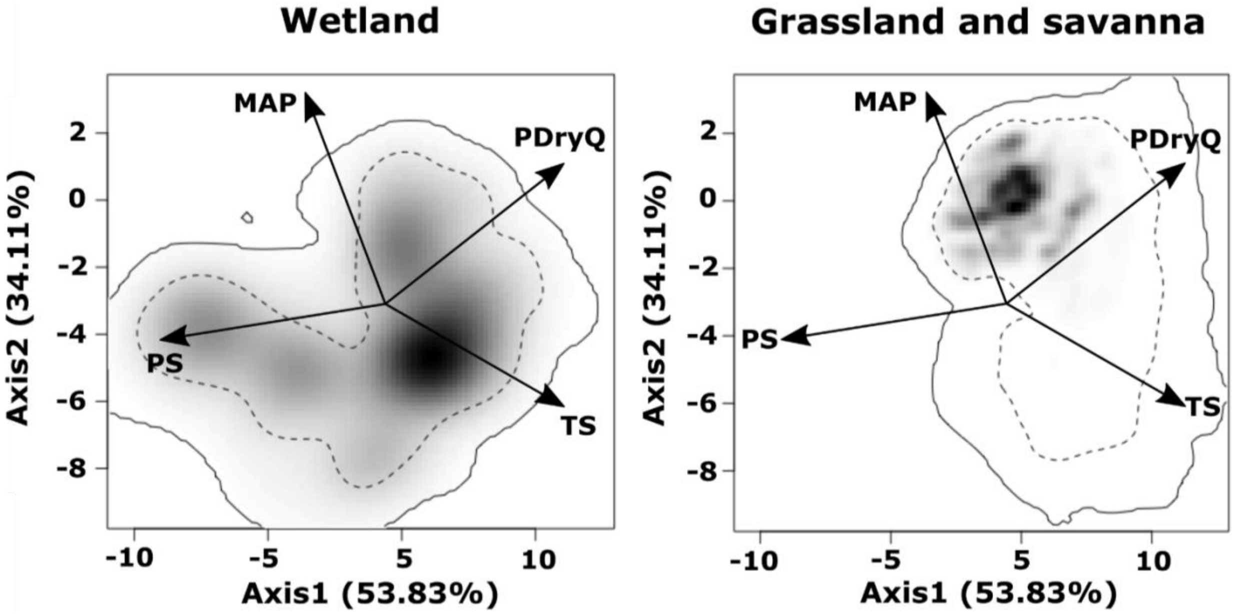
Functional traits	**PC1**	**PC2**	**PC3**
	Eigenvalue	**Eigenvalue**	**Eigenvalue**
Maximum plant height	0.849	0.003	0.023
Leaf area	0.655	0.031	0.093
Leaf ratio	0.437	0.049	1.055e-06
Maximum sessile spikelet length	0.369	0.162	0.328
Maximum awn length	0.118	0.457	0.308
Presence of awn	0.005	0.809	0.173
Awn type	0.491	0.826	0.421
Presence of stilt root	0.792	0.009	0.024
Percent contribution	41.29	26.05	15.22

Appendix VII. Quantitative functional traits contribution plot with the first two axes explaining 67.40% of variation (A) Qualitative traits contribution plot with the first two axes explaining 67.40% of variation (B) The positions and directions of eigenvectors in both plots indicate the relationships among bioclimatic variables.




Absent
Awnless
B
PC2 (26.10%)
4
2
0
Absence
Geniculate
Present
Presence
Straight
-1
0
1
2
PC1 (41.30%)
contrib
12.5
10.0
7.5
5.0
2.5

Appendix VIII. Niche overlap analysis among grassland/savanna and wetland species by PCA-env methods using four bioclimatic variables illustrating niche separation between two groups. Schoener's D and Warren's I metrices representing degree of niche overlap (D = 0.190, I = 0.410) between the two groups with statistical significance from both niche equivalency and similarity tests indicating that the two groups are not identical in occupying climatic niche spaces.



Appendix IX. Matrix of background or similarity tests between species pairs of 21 *Heteropogon-Themeda* clade in two directions. White and grey boxes indicate that the species pairs are significantly similar ($p > 0.05$) or dissimilar ($p < 0.05$), respectively. Non-parametric tests were performed with 1000 pseudoreplicates (Warren et al, 2021). Schoener's D (upper diagonal) and Warren's I (lower diagonal) matrix from niche equivalency tests indicating how niche between species pair is identical (interchangeable).

	HC	HM	HR	HT	TAN	TA	TAR	TAV	TC	TCY	TG	THE	THO	TID	TIN	TMO	TNO	TQ	TT	TTR	TVI
HC		0.61	0.14	0.22	0.34	0.19	0.14	0.53	0.40	0.05	0.23	0.16	0.11	0.17	0.29	0.07	0.16	0.27	0.29	0.05	0.36
HM	0.79		0.00	0.18	0.05	0.16	0.25	0.37	0.21	0.25	0.10	0.21	0.12	0.15	0.12	0.03	0.00	0.27	0.32	0.03	0.27
HR	0.34	0.00		0.22	0.01	0.30	0.18	0.17	0.06	0.00	0.01	0.18	0.04	0.00	0.05	0.08	0.00	0.37	0.03	0.01	0.07
HT	0.40	0.39	0.38		0.15	0.31	0.21	0.01	0.11	0.02	0.00	0.16	0.00	0.00	0.06	0.24	0.09	0.36	0.05	0.00	0.16
TAN	0.55	0.12	0.01	0.27		0.00	0.04	0.42	0.14	0.17	0.08	0.03	0.00	0.01	0.00	0.02	0.12	0.00	0.23	0.00	0.15
TA	0.42	0.37	0.45	0.54	0.00		0.19	0.07	0.15	0.11	0.02	0.28	0.00	0.12	0.08	0.07	0.00	0.54	0.07	0.02	0.33
TAR	0.37	0.41	0.20	0.42	0.05	0.25		0.09	0.15	0.30	0.12	0.29	0.12	0.28	0.39	0.21	0.04	0.21	0.07	0.03	0.06
TAV	0.70	0.48	0.24	0.04	0.58	0.12	0.15		0.25	0.22	0.19	0.06	0.29	0.00	0.02	0.05	0.00	0.11	0.31	0.00	0.32
TC	0.54	0.34	0.15	0.29	0.28	0.33	0.36	0.41		0.27	0.39	0.14	0.05	0.19	0.20	0.03	0.02	0.20	0.15	0.24	0.65
TCY	0.19	0.36	0.00	0.05	0.25	0.19	0.50	0.30	0.45		0.26	0.15	0.09	0.39	0.13	0.01	0.08	0.22	0.04	0.15	0.17
TG	0.30	0.14	0.01	0.00	0.11	0.08	0.23	0.22	0.51	0.41		0.26	0.00	0.20	0.48	0.01	0.06	0.03	0.26	0.45	0.33
THE	0.37	0.43	0.27	0.29	0.10	0.51	0.50	0.14	0.33	0.23	0.49		0.26	0.15	0.15	0.15	0.00	0.34	0.02	0.00	0.12
THO	0.32	0.34	0.07	0.00	0.00	0.00	0.15	0.51	0.22	0.19	0.00	0.36		0.00	0.00	0.12	0.00	0.05	0.01	0.00	0.06
TID	0.34	0.22	0.00	0.00	0.03	0.33	0.35	0.00	0.31	0.55	0.44	0.17	0.00		0.00	0.00	0.23	0.08	0.01	0.15	0.07
TIN	0.44	0.15	0.08	0.14	0.00	0.13	0.52	0.02	0.30	0.19	0.60	0.17	0.00	0.00		0.07	0.32	0.37	0.15	0.50	0.39
TMO			0.10	0.43	0.09	0.24	0.44	0.22	0.19	0.05	0.03	0.37	0.27	0.00	0.23		0.01	0.16	0.02	0.00	0.02
TNO	0.31	0.00	0.00	0.18	0.18	0.00	0.07	0.00	0.06	0.29	0.24	0.00	0.00	0.46	0.55	0.02		0.00	0.03	0.02	0.03
TQ	0.50	0.49	0.53	0.62	0.00	0.74	0.33	0.17	0.41	0.31	0.06	0.51	0.13	0.13	0.52	0.38	0.00		0.06	0.01	0.33
TT	0.39	0.52	0.12	0.20	0.45	0.18	0.20	0.59	0.34	0.17	0.42	0.13	0.11	0.07	0.29	0.11	0.12	0.16		0.12	0.23
TTR	0.11	0.07	0.07	0.00	0.00	0.07	0.10	0.00	0.35	0.37	0.70	0.02	0.00	0.34	0.71	0.03	0.14	0.04	0.22		0.27
TVI	0.53	0.41	0.18	0.35	0.34	0.48	0.24	0.46	0.79	0.40	0.54	0.33	0.24	0.26	0.59	0.14	0.18	0.53	0.49	0.47	

[†] Asterisks above figures represent that bioclimatic niche between species pairs are significantly not identical (not interchangeable). The niche equivalency test with p-value < 0.05, analyzed by non-parametric tests with 1000 pseudoreplicates (Warren et al, 2021).

[‡] Some species are discarded from the analyses as they provide less than five presence records which ENMTools package does not allow in the analyses.

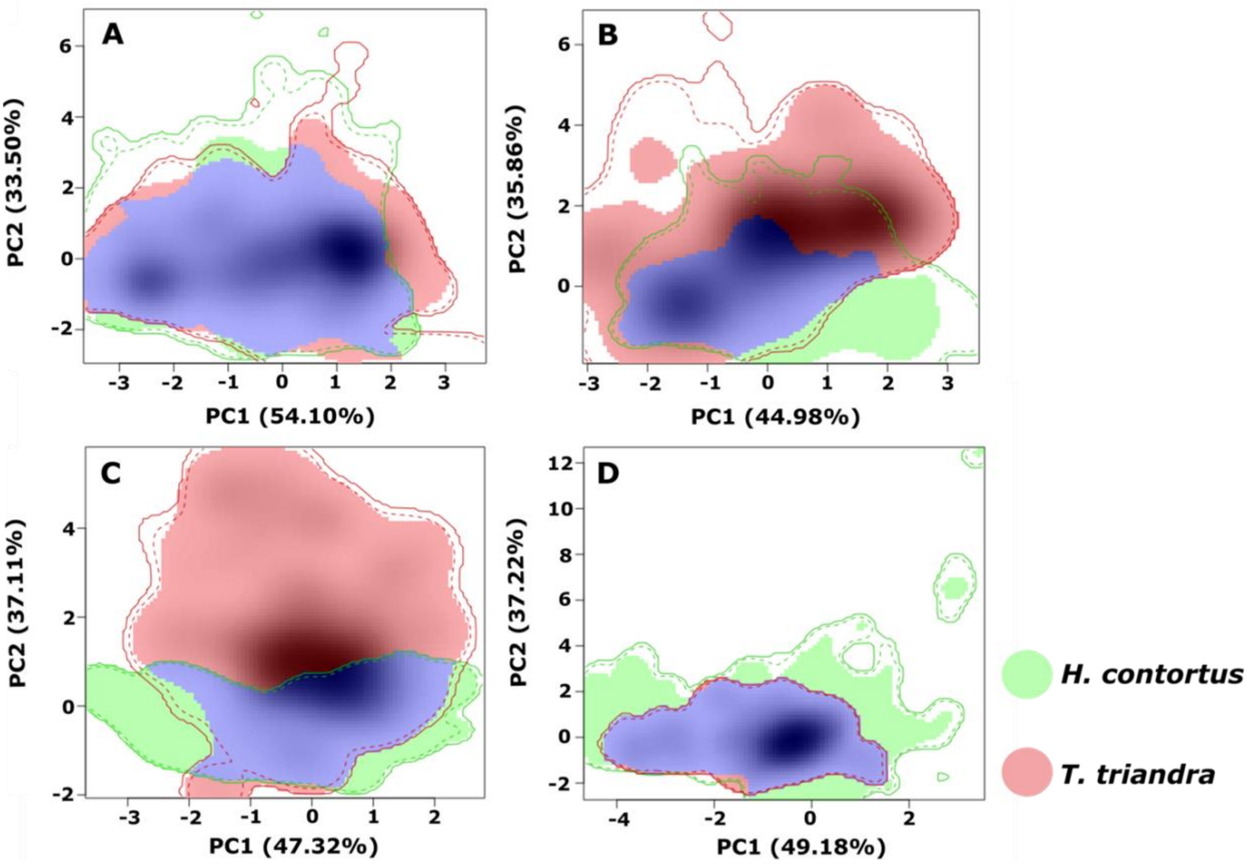
[§] Abbreviations: HC = *Heteropogon contortus*, HM = *Heteropogon melanocarpus*, HR = *Heteropogon ritchiei*, HT = *Heteropogon triticeus*, TAN = *Themeda anathera*, TA = *Themeda arguens*, TAR = *Themeda arundinacea*, TAV = *Themeda avenacea*, TC = *Themeda caudata*, TCY = *Themeda cymbaria*, TG = *Themeda gigantea*, THE = *Themeda helferi*, THO = *Themeda hookeri*, TID = *Themeda idjenensis*, TIN = *Themeda intermedia*, TNO = *Themeda novoguineensis*, TQ = *Themeda quadrivalvis*, TT = *Themeda triandra*, TTR = *Themeda tremula*, TVI = *Themeda villosa*

Appendix X. Schoener' s D (upper diagonal) and Warren' s I (lower diagonal) matrix from niche equivalency and similarity tests assessing how bioclimatic niches between *Heteropogon contortus* (HC) and *Themeda triandra* (TT) populations among continents in the Tropics are distinct.

	HC_AF	**HC_AM**	**HC_AS**	**HC_AUS**	**HC_ME**	**TT_AF**	**TT_AS**	**TT_AUS**	**TQ_ME**
HC_Africa		0.468	0.326	0.413	0.048*	0.529*	0.368	0.246	0.012*
HC_America	0.607		0.410	0.229*	0.183	0.665	0.380*	0.333*	0.045*
HC_Asia	0.467	0.558		0.271	0.030*	0.286	0.651	0.312	0.013*
HC_Australia	0.555	0.453	0.485		0.107	0.261*	0.197	0.733	0.008
HC_MiddleEast	0.194*	0.323	0.082*	0.302		0.019*	0.011*	0.016	0.351
TT_Africa	0.708*	0.789	0.442	0.449*	0.302*		0.433	0.287	0.003
TT_Asia	0.501	0.607*	0.812	0.331	0.052*	0.568		0.227*	0.002*
TT_Australia	0.385*	0.480*	0.501	0.861	0.066	0.451	0.427*		0.012
TQ_MiddleEast	0.087*	0.201*	0.075*	0.040	0.5	0.055	0.015*	0.079	

[†] Asterisk indicates that climatic niches are significantly different, tested by niche equivalency and similarity.
[‡] Abbreviations: AF = Africa, AM = America, AS = Asia, AUS = Australia, ME = the Middle East.

Appendix XI. Climatic niche overlap comparisons between American *H. contortus* and Asian **(A)**, African **(B)**, Australian **(C)**, and overall tropical **(D)** *T. triandra* populations. Green and red areas represent bioclimatic envelopes of *H. contortus* and *T. triandra*, respectively. Solid and dash lines cover 100% and 50% of background or available environments.



Appendix XII. Schoener's D (upper diagonal) and Warren's I (lower diagonal) matrix from niche equivalency and similarity tests assessing how bioclimatic niches between *Heteropogon contortus* (HC) and *Themeda triandra* (TT) populations in tropical and temperate regions are not significantly different.

	HC_Temperate	**HC_Tropical**	**TT_Temperate**	**TT_Tropical**
HC_Temperate		0.430	0.400	0.464
HC_Tropical	0.547		0.194	0.609
TT_Temperate	0.617	0.282		0.182
TT_Tropical	0.584	0.751	0.259	

[†] Asterisk indicates that niches are significantly different, tested by niche equivalency and similarity.

Appendix XIII. Alternative model comparisons showing log likelihood values, probabilities at root nodes (R1, R2, R3), and transition rates among states.

Model	q01	q02	q10	q12	q20	q21	R1	R2	R3	-InL
ARD	3.881	2.065	12.156	5.505	17.033	14.630	0.333	0.333	0.333	-17.487
ER	1.309	1.309	1.309	1.309	1.309	1.309	0.719	0.142	0.139	-21.344
Reversible equal + no 12/21 changes	8.066	1.875	8.066	0	1.875	0	0.444	0.423	0.133	-22.920
Reversible unequal + no 12/21 changes	4.114	1.820	11.919	0	17.315	0	0.334	0.333	0.333	-17.218
Reversible equal	7.477	6.318	7.477	6.881	6.318	6.881	0.377	0.326	0.297	-25.804
Reversible equal (01/10 and 02/20) + Unequal (12/21)	14.170	1.650	14.170	2.708	1.650	17.942	0.338	0.331	0.331	-21.806
Reversible unequal (High-low order)	3.991	0	13.026	4.243	0	15.331	0.334	0.334	0.333	-17.223
Reversible unequal (Low-high order)	0.265	0.081	0	1.148	0	0	1	0	0	-21.284
Reversible equal (Low- high order)	0.072	0.072	0	0.072	0	0	1	0	0	-19.933

Appendix XIV. Specimen examinations

A. *Heteropogon contortus*

FRANCE. Pyrénées-Orientalis: Banyuls-sur-Mer, August 1851, *unknown 876* (WAG). **Alpes-Maritimes:** Cannes, July 1937, *J. Calle s.n.* (L). **ITALY. Lazio:** Latina province, Gaeta, Monte Vannelamare, side of 'Flacca' road, 40-70 m, 27 November 1991, *P. Marchi & M. Iberite 15808* (WAG). **Trentino-Alto Adige/Südtirol:** Trentino province, near Riva, Mountain Brione, August 1900, *P. Porta 67* (L, WAG); South Tyrol province, Bolzano, *s.d.*, unknown 8020 (L). **Veneto:** Verona province, Torri del Benaco, 100-130 m, August 1882, *B. Breslau s.n.* (L). **Sicily:** Palermo, October 1901, *H. Ross 962* (WAG); Palermo, *s.d.*, *H. Rap s.n.* (L); Palermo, at Mountain Peregrino, *s.d.*, *Todaro s.n.* (L). **SPAIN. Valencian Community:** Castellón province, Baix Maestrat, Benicarló, October 1908, *F. Sennen 619* (L). **SWITZERLAND. Ticino:** Bellinzona, July 1841, anonymous (L); Lugano, Castagnola, Gandria, 17 July 1922, Danser 5014 (L). **ISRAEL. Jelusalem:** Wad-el-Kelt, J. 13 July 1904, *J. E. Dinsmore 5355* (L); Kulonieh, 640 m, 08 May 1903, *J. E. Dinsmore 777* (L). **OMAN. Dhofar:** Tawi Atiar, 17 April 1993, *I. McLeish s.n.* (K); Taqah, Madinat al Happ, 830 m, 22 September 1993, *T. A. Cope s.n.* (K); Jabal Samhan, 1200 m, 27 September 1991, *T. A. Cope s.n.* (K); Raysut, September 1987, P. N. Allison s.n. (K); Jabal Qara, 400 m, 30 September 1979, *A. G. Miller s.n.* (K). **Ad Dakhiliyah:** Saiq, 12 June 1993, *I. McLeish s.n.* (K); Tapah, Jabal Shams, north of Al Hamra, 1900 m, 11 June 1992, *M. D. Gallaher s.n.* (K); Jabal Akhdar, 1900 m, 11 June 1992, *M. D. Gallaher s.n.* (K). **SAUDI ARABIA. Jizan region:** Jazan**,** Wadi Baysh, 30 March 1991, *J. S. Collenette s.n.* (K)**;** South province**,** Faifa', Jabal Fayfa**,** 20 November 1981, *S. Chaudhary s.n.* (K). **YEMEN. Ibb Governorate:** Ba'dan district, Bani Mansour, 1500 m, 26 September 1977, *J. R. I. Wood s.n.* (K)**. Amran Governorate:** Huth district, north of Sanaa, 1900 m, 26 August 1977, *A. Radcliffe-Smith & S. J. Henchie s.n.* (K). **Al Mahwit Governorate:** Milhan district, Wolledje, 20 January 1889, *G. Schweinfurth s.n.* (K). **Al Mahrah Governorate:** Hawf district, Hawf Mountains, Shah'rut, 650-700 m, 02 October 1901, N. Kilian & M. A. Hubaishan YP702 (K). **Socotra Governorate:** Jebel Rughid, 1000 m, 23 May 1967, *A. R. Smith & J. Lavranos s.n.* (K); Hagghiher Mountains (Hajhir), Arundo Pass, 775 m, 06 March 1989, *A. G. Miller & al. s.n.* (K). **ALGERIA. M'Sila:** Bou Saâda, Jabal Kerdada, Jan 1865, S. Reboud s.n. (L). **Oran:** Plage, slopes on the coast near Chenoua, 10 April 1960, *A. Dubuis & L. Faurel 4184* (L). **MOROCCO. Marrakesh-Safi:** Essaouira (Mogador), Ter Mountain, Summit of Djebel-Hadid, *s.d.*, *B. Balansa s.n.* (L). **TUNISIA. Kairouan Governorate:** Cherichira, west of Kairouan, 20 June 1883, *M. M. E. Cosson & al. s.n.* (P)**. CHINA. Sichuan Province:** Garzê, Luding, 1000 m, 18 October 1997, *R. J. Soreng, P. M. Peterson & Sun Hang s.n.* (K); Panzhihua, 1250 m, 19 October 1997, *R. J. Soreng, P. M. Peterson & Sun Hang s.n.* (K)**. Yunnan Province:** Baoshan, Nu Shan, Xiahewang village, 1525 m, 07 September 1997, *R. J. Soreng, P. M. Peterson & Sun Hang s.n.* (K); Old Town of Lijiang, Black Dragon Pool, 1950 m, 05 September 1997, R. J. Soreng & P. M. Peterson s.n. (K). **Hong Kong:** Luk Keng, Nam Chung, Yeung UK village, 07 July 1924, To & Ts'ang s.n. (K); Victoria Island, Pokfulan reservoir, 31 May 1969, Shiu Ying Hu s.n. (K); Yau Tsim Mong, Yau Ma Tei, King's Park, 22 October 1971, *Paul But s.n.* (K); New Territories, Tsun Wan, Tai Mo Shan, 12 May 1940, Y. W. Taam 1312 (L). **Hubei Province:** Yichang, March 1886, *Dr. Henry s.n.* (K). **Macau:** Taipa, Taipa Grande, 07 September 1961, *F. A. Soares s.n.* (K). **Guizhou:** Yingkiang Hsien, 600 m, 12 December 1931, *A. N. Steward, C. Y. Chiao & H. C. Cheo 899* (L). **TAIWAN. Taichung:** Xitun, Dadu Shan, 22 October 1985, *C. S. Kuoh 10119* (L). **PAKISTAN. Punjab:** Soon valley, Sakesar, 4,000 ft, 24 August 1902, *J. R. Drummond s.n.* (K); Sargodha, Shahpur, 5,000 ft, 10 September 1902, *Kaber* (K). **Khyber Pakhtunkhwa:** Hazara, 02 September 1999, *J. F. Duthie s.n.* (K). **Sindh:** Nagarparkar, 25 October 1970, *M. Oarser & al.* (K). **INDIA. Tamil Nadu:** Kongu Nadu, Erode, Sathyamangalam, March 1902, *A. G. Sady Bourne s.n.* (K); Kongu Nadu, Coimbatore, Kalapatti, 2000 ft, 23 January 1931, *S. R.*

Raju & Naganatham s.n. (K); Pulney hills, 6000 m, 22 February 1922, *S. J. Auglade s.n.* (K); Nilgiris, 6000 m, August 1883, *J. S. Gamble s.n.* (K); Dindigul, Kodaikanal, Thandikudi, 4000 m, 02 January 1886, K. M. Matthew s.n. (K); Dindigul, Fairy falls, 27 April 1898, *Bourne 1207* (K); Tiruchi, Thuraiyur, Pacchaimalais, Sobanapuram, Forest rest house, 500 m, 10 November 1977, *W. Punt 783* (K); Dindigul, Kodaikanal, Pulney Hills, 01 July 1901, *A. G. Bourne 2026* (CAL, K, MH); Coimbatore, Valpari (Poonachimalai), Anaimalai Hills, 10 October 1901, *C. A. Barber 3719* (MH, K). **Kerala:** Kannur, 150 m, 23 November 1981, D. V. Sreekumar s.n. (K); Idukki district, Mattapetty, 1500 m, *s.d.*, *Dr. H. Guyer s.n.* (K); Madras, Salem, Sanyasimalai Reserved Forest, 17 September 1965, *K. N. Surramanian 1987* (K). **Karnataka:** Kodachadri, 17 November 1978, *anonymous* (K); Hassan, Arsikere, 08 October 1969, *C. J. Saldanha 15179* (K). **Maharashtra:** Pune, Khandala, 17 September 1951, *H. Santapau s.n.* (K); Mumbai, Sanjay Gandhi National Park, 08 November 1952, *R. R. s.n.* (K); Gadchiroli, near Ashti, Wainganga Riverbank, 163 m, 27 February 1915, F. M. S. A. Kirkels, *C. R. T. Martes & F. Peterse G38-1* (K). **Andhra Pradesh:** Rayalaseema, Mayor-Council, Kadapa, 1,800 m, February 1883, *J. S. Gamble s.n.* (K); Godavari River, Srivaka, 03 January 1902, *Bourne 3394* (K); Godavari, Polavaram, 08 January 1902, *Bourne 3569* (K). **Telangana:** Hyderabad, Patancheru, 600 m, 04 October 1977, *J. G. van der Maesen s.n.* (K). **Himachai Pradesh:** Chamba, 4000 ft, 04 September 1896, *G. A. Gammie s.n.* (K); Shimla, 7,500 m, 09 September 1918, *H. H. Rich s.n.* (K). **Rajasthan:** Sirohi, Mount Abu, 1,120 m, 06 October 1916, *Father E. Blatter s.n.* (K). **Gujarat:** Junagadh, Girnar hills, 02 October 1953, *M. B. Raizada s.n.* (K). **Kashmir and Jammu:** Jammu, Garhi, 2,500 ft, September 1928, *R. R. Stewart s.n.* (K); Poonch, Haveli, Poonch valley, 22 November 1847, *J. E. Winterbottom s.n.* (K). **Meghalaya:** East Khasi Hills, Shillong, 4,500 ft, 03 September 1885, *C. B. Clark s.n.* (K); West Khasi, Khasi hills, 3000 ft, 19 September 1954, *Thakur Rup Chand 8238* (K). **Jharkhand:** Hazaribagh, 2,000 ft, 10 October 1893, *C. B. Clark 21203* (K). **Manipur:** Karong, 3,500 ft, 27 October 1950, *Thakur Rup Chand 3910* (K). **Uttar Pradesh:** Allahabad, Sallahpur, along railways tracks, 23 October 1978, *B. K. Misra 837* (K). **ANDAMAN AND NICOBAR ISLANDS. South Andamans:** Port Blair, Corbyn’s cove, sea level, 31 October 1973, *N. P. Balakrishnan 561* (K). **SRI LANKA. Northwestern province:** Puttalam, road between Puttalam and Anuradhapura, 30 m, 24 November 1969, *T. R. Soderstorm & S. Kulatunge s.n.* (K); Anuradhapuram Sadpuda Kallu, 30 m, 29 Dec 1968, *F. R. Fosberg 50811* (K). **Central Province:** Nuwara Eliya, Bulugahapitiya, 12 March 1970, *F. W. Gould 13058* (K); Matale, Dambulla, 200 m, 06 January 1970, *D. Clayton 5051* (K); Matale, Sigiriya Fortress, 700 ft, 11 October 1974, *G. Davidse 7441* (L). **North Central Province:** Polonnaruwa district, Polonnaruwa, 60 m, 08 January 1970, *D. Clayton 5120* (K); Anuradhapura, Wilpattu National Park, 30 m, 01 February 1970, *D. Clayton 5579* (K). **Northern province:** Jaffna, Vallipuram, sea level, 13 January 1970, *D. Clayton 5217* (K). **UVA:** Monaragala, 11 miles west of Tanamalwila, 125 m, 24 November 1974, *G. Davidse & D. B. Sumithraarachchi 8805* (K); Badulla, Welimada, 2,000 ft, 24 January 1964, *J. Carrick 1292* (K); Ruhuna National Park, 24 June 1968, *D. Mueller-Dombois & R. G. Cooray s.n.* (K); Moneragala, Gal Oya National Park, Senanayake Samudra Dam, 17 March 1970, *F. W. Gould 13109* (K). **Southern Province:** Hambantota, Karaugas Wala, Block 1, Ruhuna National Park, 10 m, 02 March 1970, *D. Clayton 5936* (K). **BHUTAN. Paro:** Paro, 7,200 ft, 17 September 1987, *D. J. Miller s.n.* (K). **Kauchaupur:** Royal Shuklaphanta Wildlife Reserve, 600 ft, 10 November 1975, *D. Schaal s.n.* (K). **NEPAL. Madhesh province:** Dhanusha district, Janakpur, Dolakha, Kabhre, 4,500 ft, 17 September 1964, *Dr. Baner and Parly s.n.* (K). **Gandaki province:** Myagdi, 3,000 ft, 05 September 1954, *Stainton, Sykes & Williams 4182* (K). **Lumbini province:** Palpa, near Tansing, 4,000 ft, 10 October 1954, *Stainton, Sykes & Williams s.n.* (K). **MYAMMAR. Sagaing:** Shwebo, Swedo, 375 ft, 14 October 1928, *anonymous* (K). **Mandalay:** Mandalay, Pyin Oo Lwin, 3,500 ft, 17 July 1908, *J. H. Lace 3292* (K); Nyaung-U, Popa hill, Taung Kalat, 1,500 ft, 15 November 1941, *D. Chatterjee s.n.* (K). **Yangon:** Insein, Myaukhlaing Reserve, 100 ft, 21 September 1948, *Dr.*

Po Khant 855 (K); Mingaladon Township, Hlawga Lake, 25 June 1947, *U. Thein Lwin 103* (K). **Kachin:** Myitkyina, 25 November 1948, *U. Thein Lwin 645* (K). **THAILAND. Lampang:** Ngao, Mae Huat, 350 m, 26 May 1954, *T. Smitinand 1613* (BKF, K); Wang Nua, Doi Luang National Park, west side of and below Doi Nawk, 08 November 1998, *O. Petrmitr 354* (L). **Lampoon:** Pa Sang, Nam Dip, Cham Chompu village, 350 m, 29 November 1904, *J. F. Maxwell 04-750* (K). **Loei:** Phu Kradueng, Sam Haek, 400 m, 16 October 1954, *T. Smitinand 2032* (K); Wang Saphung, Sithan, 300 m, 17 October 1955, *T. Smitinand 3063* (K); Phu Ruea, Phu Ruea National Park, 30 September 1990, *P. Chantaranothai, J. Parnell & D. Simpson 90/478* (K). **Chiang Mai:** Payap, Mae Klang waterfall, 350 m, 15 December 1965, *M. Tagawa & al. 2203* (K); Chom Thong, Yang Kram, Ban Huai Namkhao, 350 m, 03 December 1991, *J. F. Maxwell 91-1085* (L); Mae Soi, Mae Soi Valley, 450 m, 10 November 1990, *J. F. Maxwell 90-1254* (K). **Chiang Rai:** Doi Tung, 150-600 m, 18 November 1920, *A. F. G. Kerr 4610* (K). **Sukhothai:** Sawankhalok, 200 m, 19 December 1969, *D. E. Parry s.n.* (K). **Ratchaburi:** Huai Yang, July-August 1966, *Kai Larsen & al. 1596* (K); Suan Phueng, Ta Nao Si, 11 November 1904, *K. Pruesapan & al. KP40* (K). **Nakhon Ratchasima:** Lat Bua Kao, October 1916, *C. Boden Kloss s.n.* (K). **Sa Kaeo:** Aranyaprathet, 16 October 1928, *Put 1967* (K). **Chon Buri:** Banglamung, Koh Pai, 0.5 m, 24 February 1928, *A. Marcau 2313* (K); Siracha, Khao Kiew, 250 m, 10 April 1975, *J. F. Maxwell 75-408* (K). **Prachuap Kiri Khan:** Hua Hin, 2 m, 05 November 1927, *A. Marcau 2229* (K); Pran Buri, Sam Roi Yod National Park, trail from Sai cave to Phraya Nakhon cave, 40 m, July 2000, *M. F. Newman & al. 1180* (K). **Tak:** Ma Bon, 05 December 1957, *J. V. Santos 6689* (L); Ban Tak, Tak Ok, Forest Park, 255 m, 07 November 1910, *R. Pooma & al. 7627* (BKF, E, K, L, QBG). **Kanchanaburi:** Chong Sadao, Pu Prom meditation center, Gaeng Blah Gote village, 50 m, 28 October 1908, *J. F. Maxwell 08-188* (L). Saraburi: Muang, Sam Lan Forest, 125 m, 15 June 1974, *J. F. Maxwell 74-598* (L); Srisawat, along track from Huai Bankou, 150-750 m, 15 November 1971, *C. F. van Beusekom & al. 3789* (K). **Si Saket:** near Cambodian border, about 20 km south of Kantharalak, 210 m, 08 October 1984, *G. Murata & al. 49676* (K). **Prae:** Song, Sahiab, Mae Yom National Park, west side of Yom river, 225 m, 14 November 1991, *J. F. Maxwell 91-1049* (K). **Lop Buri:** Chai Badan, Lam Narai, 170 m, 29 August 1901, *R. Pooma & al. 2980* (K). **Sakhon Nakhon:** Phu Phan National Park, 380-450 m, 12 November 1984, *G. Murata & al. 51319* (K). **Petchaburi:** Cha-am, Huai Sai, 19 August 1903, *P. Puudja 1220* (K). **Udon Thani:** Phu Luang, from Ban Na Luang to north ridge, 500 m, 03 December 1965, *M. Tagawa & al. T1036* (K). **Phitsanulok:** Thung Salaeng Luang National Park, Poi waterfall, 210 m, 22 October 1984, *G. Murata & al. T38496* (K). **Phuket:** Muang, Laem Promthep, 25 m, 01 December 1986, *J. F. Maxwell 86-1025* (K). **VIETNAM. Ninh Thuận:** Phanrang, east side of Kromphra station, 25 November 1941, *M. Poilane 30632* (L). **Khánh Hòa:** Nha Trang, Cauta, 28 February 1922, *M. Poilane s.n.* (E, K, L). **Đắk Lắk:** Buôn Ma Thuột, 350-400 m, s.d., *M. Schmid 455* (P). Danang: Bank to Hue divide, 03 August 1927, *J. & M. S. Clemens 4127* (P). **LAOS. Savannakhet:** Savannakhet, 0.6 m, 18 October 1938, *E. Poilane 28099* (K, L). **Champasak:** between Pakse and Pakson, 23 November 1938, *E. Poilane 28516* (K, L). **CAMBODIA. Kratié:** Sambour, Mekong River, Rohng Ngiew island, east side at Wae Wah, 30 m, 15 November 1906, *J. F. Maxwell 06-877* (L). **Takéo:** Samraŏng, Phnom Chisor, about 50 km south of Phnom Penh, 09 January 1910, *H. Schaefer 2010* (P). **INDONESIA. Aceh:** southern part of Gunung Leuser Nature Reserve, Alas River Valley, near the mouth of the Renun river, about 50 km south of Kutacane, 50-125 m, 21 July 1979, *W. J. J. O. de Wilde & B. E. E. de Wilde-Duyfjes 18955* (L). **Bali:** 42 km east of Singaraja, 14 June 1976, *W. Meuer 10310* (L). **Banten:** Toppershoedje, 05 April 1934, *Shoedijn 2900* (L). **Central Sulawesi:** 25 km south of Palu, 100 m, 21 April 1979, *van Balgooy 2952* (K, L). **East Java:** Pasuruan, Gunung Semonkrong, 09 April 1931, *Dr. van Hoolen 2436* (K); Pasuruan, Probolinggo, Gugung Bentar, 30 m, 10 June 1918, *C. A. Backer 24322* (L); Asembagus, Port Lading, Besuki, 100 m, 02 March 1922, *Begnin 186* (L); Pasuruan, Wangon, 15 m, 06 May 1913, *C. A. Backer 7530* (L); Kangean Island, 01 January

1954, *A. Hoogerwerf s.n.* (L); Madura Island, north from Pamekasan, 200 m, 18 March 1915, *C. A. Backer 20351* (L); Baluran National Park, 21 May 1949, *F. W. Rappard Jr. 39* (L); Mediun, Babadan, 70 m, 05 May 1921, *C. A. Wisse 446* (L); Surabaya, 14 April 1905, *anonymous 45265* (L); Panarukan, Petjaron, 10 m, 15 June 1918, *C. A. Backer 24692* (L); Bondowoso, Ringgit, 16 August 1929, *E. W. Clason 23* (L). **East Nusa Tenggara:** Sumba, Waingapu, 06 April 1965, *anonymous 400* (K, L); East Sumba, north of Baing, about 4-5 km northwest of Gunung Laipupu, 300 m, 05 December 1994, *McDonald & Sunaryo 4433* (K, L); West Flores, south part near Mborong, 11 April 1965, *A. J. G. H. Kostermans 22035* (K, L); Alor Island, Taramana, Pisigomo, 200 m, 11 May 1938, *O. Jaag 923* (L); Kupang, vicinity of Aerodrome, 10 m, 12 December 1953, *C. G. G. J. van Steenis 17977* (L); Flores, about 13 km northwest of Maumere, about 1 km south of Waturia, 200 m, 10 August 1993, *J. J. Wieringa 1825* (L); Komodo Island, 01 June 1982, *Father J. A. J. Verheijen 4890* (L); West Timor, Amarassi, east of Baun, 200 m, 03 May 1950, *Monod de Froideville 1461* (L); Manggarai, Lembor, West Lori, 01 January 1982, *Fr. E. Schmutz 4952* (L); Amanuban Barat, Mnelalete, 500 m, 20 March 1969, *C. W. Kooy 690* (L); Fatumnasi, 1000 m, 15 January 1975, *H. Wiriadinata 450* (K, L); Ruteng, Kedang, Lembata Island, 150 m, 07 April 1987, *Father J. A. J. Verheijen 5533* (L); Kefamenanu, 400 m, 24 July 1949, *Monod de Froideville 1127* (L); Endeh, Mount Kingo, 50 m, 22 February 1939, *S. Bloemberg 3228* (L). **Maluku:** Tanimbar Islands, Palau Selaru, Adaut, 15 March 1956, *D. R. Pleyte 126* (K, L, SING); Tanimbar Islands, Yamdena Island, road from Saumlahi to Olili, 08 March 1938, *P. Buwalda 4032* (K, L). **North Sulawesi:** Manado, 450 m, 01 March 1934, *Neth. Ind. For. Service s.n.* (L). **North Sumatra:** Toba, Balige, s.d., *H. S. Yates 2193* (L). **West Nusa Tenggara:** West Sumbawa, Semongkat Atas, Olat Sekampil, 700 m, 13 May 1961, *Kuswata 159* (K, L); West Sumbawa, Mount Batulanteh, Batudulang and Sampar Olat Ridges, north of Batudulang, 500-700 m, 02 May 1961, *A. J. G. H. Kostermans 18633* (K, L). **West Sumatra:** Lake Singkarak, near Umbilin, 05 August 1957, *W. Meijer 7185* (L); Indarung, near Padang, 150 m, 14 July 1956, *W. Meijer 6006* (L). **Papua:** Sentani, Cyclops Mountains, 15 December 1985, *E. A. Widjaja & Hamzah 2973* (K, L); Okaba, gorund Okaba, 14 September 1907, *B. Branderharst 68* (K, L). **South Sulawesi:** Sidenreng Rapang, south of Rapang, near bridge over the Putjuk, 20 m, 13 June 1937, *P. J. 301* (L); Selayar Islands, Palau Bonerate, 07 May 1913, *anonymous s.n.* (L). **Riau Islands:** Gunung Bungsu, 22 November 1955, *W. Meijer 4544* (L). **Southeast Sulawesi:** Buton Island, Baoe, 10 February 1929, *anonymous 115* (L). **THE PHILIPPINES. National Capital region:** Caloocan, November 1903, *E. D. Merrill 3677* (K, P); Lone, Muntinglupa, May 1963, *Jose vera Santos 7372* (L). **Llocos region:** La Union, Bauang, February 1904, *A. D. E. Elmer 5699* (K, P); Llocos Sur, Quirino, Barrio Lamag, May 1953, Jose Vera Santos 5733 (L). **Calabarzon:** Rizal, Antipolo, October 1914, *E. D. Merrill 501* (K, L, P); Rizal, Bosoboso, October 1909, E. Fenix 115 (K, P); Cavite, Molino neighbourhood, October 1940, *Jose Vera Santos 500* (L); Rizal, Rodriguez, January 1912, *A. Loher 12727* (P). **Northern Mindanao:** Misamis Oriental, Cagayan de Oro, October 1957, *Jose Vera Santos 6660* (L). **Mimaropa:** Occidental Mindoro, Lone, Mamburao, Tangkalan, Barrio Malibago, Jan 1954, *Jose Vera Santos 6494* (L). **Soccsksargen:** South Cotabato, General Santos, Barrio San Jose, April 1960, *Jose Vera Santos 6886* (L). **Central Visayas:** Negros Oriental, Siaton, Barrio Bundo, August 1980, *Jose Vera Santos 8256* (L). **Western Visayas:** Iloilo, Guinaras island, Nueva Valencia, Salvacion, October 1977, *Jose Vera Santos 8153* (L). **Cordillera Administrative region:** Abra, Lone, Lagangilang, Ojas-Igat reforestation project, October 1979, *Jose Vera Santos 8187* (L). **Central Luzon:** Zambales, Santa Cruz 10 km off the coast, Hermana Mayor Island, December 1954, *Jose Vera Santos 6180* (L). **TIMOR-LESTE. Manatuto:** Manatuto, Laclo, Metinaro-Manatuto, road in Beheda, February 1905, *J. Paiva, P. Silveira & J. Pratas T703* (L). **PAPUA NEW GUINEA: Milne Bay:** Cape Vogel, between Dabora and Wabubu, 30 m, 08 April 1953, *L. J. Brass 21880* (K, L); Cape Vogel, Tapio, 200 m, 15 July 1954, *R. D. Hoogland 4300* (K, L); Moi Biri Bay, Baiawa, 30 m, 7-10 May 1953, *L. J. Brass 22136* (K, L). **Morobe:** Lae, road to and around Nadzab airport, 22 June 1989, *L. Raulerson 18897* (K); Lae, Wawin, 400 ft, 12 February 1973, *M. Pirkis NGF49449* (K, L, US); Leron, Leron Plain, January 1953, *E. E. Henty 178* (L). **Central Province:** Kairuku-Hiri, about 8 miles west of Kanosia plantation, Rogers airstrip, 30 ft, 13 July 1962, *P. J. Darbyshire 661* (K, L); Rigo, south coast near Hood Bay, 60 ft, 18 June 1969, *K. Pajimans 845* (L). **National Capital District:** Port Moresby, Moitaka, 250 ft, 14 December 1964, *A. N. Gillison 22053* (K, L, US). **AUSTRALIA. Queensland:** 2.3 km southwest of Kyong homestead, 340 m, 02 April 1992, *E. J. Thompson & B. K. Simon BUC665* (K, NSW); Shire of Mareeba, Mareeba, 400 m, 15 April 1962, *H. S. McKee 9081* (K); Howick island, 3 m, 22 October 1973, *D. R. Stoddart 4841* (K, L); Cape York Peninsula, 10 miles west southwest of Somerset, Lockerbie, 30 m, 23 April 1948, *L. J. Brass 18367* (K, L); Burke district, Cloncurry area, 19 July 1962, *T. F. Warman s.n.* (K); Leichhardt district, north of Springsure, Minerva, 800-1000 ft, 13 March 1935, *S. T. Blake 8039* (K); Wide Bay, Bundaberg, 25 April 1936, *S. T. Blake 11294* (K); between Normanton and Croydon, Blackbull, 169 ft, 23 May 1935, *S. T. Blake 9144* (K); Port Curtis, Rockhampton, 25 ft, 02 March 1935, *S. T. Blake 7776* (K); Cook district, Torres Strait Islands, Thursday Island, April 1931, *F. Hockings s.n.* (K); Cook district, Boigu Island, 20 October 1981, *J. R. Clarkson 3865* (K); Mount Coot-tha, near Brisbane, Taylor Range, 600 ft, 05 April 1930, *C. E. Hubbard 2023* (K); 40 miles southwest of Brisbane, between Calvert and Lanefield, 160 ft, 12 April 1930, *C. E. Hubbard 2106* (K); Brisbane, Kangaroo Point, 27 April 1930, *C. E. Hubbard 2407* (K); Stradbroke Island, Amity Point, 10 ft, 21 April 1930, *C. E. Hubbard 2322* (K); Townsville, Castle Hill, 200-800 ft, 17 January 1931, *C. E. Hubbard & C. W. Winders 6616* (K); North Kennedy, Bowen, Queens Beach, 3 m, 20 April 1975, *T. J. McDonald & G. N. Batianoff* 1692 (K). **Northern Territory:** between Borroloola and Tanumbirini, 26 March 1912, *G. F. Hill 813* (K); Nitmiluk National Park, 12 March 1991, *M. Evans 3705* (K); Victoria Daly Region, Timber Creek, 10 April 1990, M. Evans 3075 (K); Barkly Tableland, Nicholson River area, near fish river gorge in China Wall, 200 m, 09 June 1974, A. Kanis 1775 (K, L, US); Elcho Island, Warangaiyu, 02 July 1975, *P. K. Latz 6058* (L); Kakadu National Park, near Garnamarr on road to Jim Jim Falls, 28 September 1907, *B. K. Simon 4351* (L); Darwin, Nightcliff, about 8 km southeast Darwin, 24 May 1958, *G. Chippendale NT4396* (L); East Arnhem Region, Gulf of Carpentaria, Bickerton Island, 17 June 1948, *R. L. Specht 586* (L). **Western Australia:** Leopold Ranges, 30 km on Millewinde road from Gibb River road, 19 April 1988, *B. K. Simon 4003* (K); North Kimberly, Governor Island, Napier Broome Bay, 19 May 1984, *E. A. Chesterfield 252* (L). **New South Wales:** Clarence River, Copmanhurst, May 1916, *J. L. Boorman 12801* (K). **NEW CALEDONIA. South Province:** Nouméa, Magenta, 02 May 1983, *H. S. McKee 41421* (K, P); Nouméa, Anse Vata, 28 December 1960, *H. S. McKee 7820* (K, L); Nouméa, Montravel, 50-100 m, 20 March 1969, *H. S. McKee 20306* (K, P); Nouméa, Ouen Toro Mount, 22 September 1950, *M. G. Baumann-Bodenheim 6140* (L, P); L'Île-des-Pins, Central Plateau, 100 m, 01 April 1971, *H. S. McKee 23504* (K); L'Île-des-Pins, Kuto, 30 May 1951, *Guillaumin 763* (P); L'Île-des-Pins, Plateau de Moué, 80 m, 20 December 1965, *H. S. McKee 14101* (P); Tontouta, Mount N'dui, 100 m, 18 February 1976, *H. S. McKee 30760* (K, P); Boulouparis, L'île Léprédour, Southeats plateau, 100-200 m, 23 April 1969, H. S. McKee 20591 (P). **North Province:** Koumac, Kokondo, 10 m, 09 January 1983, *H. S. McKee 41171* (K, P); Voh, base of Mount Katepahie, 50 m, 19 January 1963, *H. S. McKee 10059* (K, L, P); Gomen, Toela, 400 m, 13 April 1978, *H. S. McKee 34979* (K, P); Pouembout, Devillers in Goyetta, 10 May 1983, *Ph. Morat 7369* (P); Pangou, Haute Ouaième, 300 m, 14 April 1978, H. S. McKee 35034 (P). **Loyalty Islands Province:** Lifou, Chepenehe, 5 m, 23 February 1974, *H. S. McKee 28310* (K, P). **FIJI. Western Division:** Ra province, Vaileka, Gout station, 29 June 1954, *J. W. Parham 8105* (K); Ba province, Lautoka, 25 September 1980, W. Greenwood 97 (K); Ba province, Viti Levu, Tholo North, vicinity of Tavua, 30-150 m, 02 April 1941, *O. Degener 14961* (K, L). **Eastern Division:** Lau Islands, Matuku Island, 02 August 1929, *J. D. Tothill 310* (K). **Northern Division:** Vanua Levu, Mathuata, Southern base of Mathuata range, North of Natua, 100-250 m, 1-4 December 1947, *A. C. Smith 6809* (K). **TONGA. Ha'api:** Nomuka, sea level, 28 April 1959, *E. Soakai 653* (K). **Vava'u:** along the northern side of the island above Leimatu'a, 150 m, 20 May 1953, *T. G. Yucker 16064* (L). **GUAM. Northern Mariana Islands:** Tinian, Mount Alutom, 900 ft, 01 July 1946, *E. Y. Hosaka 3057* (L); Tinian, terrace on southeast coast of island, northeast of Carolinas Point, 60-80 m, 11 June 1946, *F. R. Fosberg 24823* (L); Saipan, sea cliffs in Tsukimi bay, east of Mount Petosukara, 75 m, 28 June 1946, *F. R. Fosberg 25202* (L); Pagan Island, Isthmus, 6 m, 26 September 1949, *D. Anderson 561* (L). **Malesso:** Merizo Annex, 90 m, 05 March 1963, *F. R. Fosberg 43509* (L). **IVORY COAST. Zanzan:** Bounkani, Téhini, about 40 km east of Ouangofetini, north side of Parc National de Bouna, 26 August 1963, W. J. J. O. de Wilde 811 (K, L, P, WAG). **Savanes:** Poro, Korhogo, 06 October 1974, *Bésar 102* (K, L, P, WAG). **BURKINA FASO. Centre-Sud region:** Nahouri, near bridge over Nazinon river, at 35 km north of Po coming from Ouagadougou, 277 m, 28 September 2000, *A. Diallo & M. van Slageren MSAD1055* (K). **Est region:** Fada N'gourma, 26-29 July 1910, *anonymous 24574* (K); Tapoa, Piste, from Namounou-Yobri, 30 October 1990, *K. Hahn 289* (L). **Centre-Est region:** Boulgou, southeast of Tenkodogo, 300 m, 04 September 96, *Jens Elgaard Madsen 5543* (L). **Cascades region:** Comoe, Sindou, 09 July 1958, *E. J. Adjanohoun 114A* (P). **CAPE VERDE. São Vicente:** Monte Verde, September 1934, *Aug. Chevalier 45733* (K, P). **São Nicolau:** Pertela, Ribeira, Babosa, 21 April 1956, *L. A. Grandvaux Barbosa 7272* (L). **Santiago:** village of Pensamento, 22 November 1955, L. A. Grandvaux Barbosa 5586 (L). **Santo Antão:** Santa Cruz, 25 September 1934, *Aug. Chevalier 45619* (P); Covão, 16-17 September 1934, *Aug. Chevalier 45386* (P). **Fogo:** Chupadeiro, 25-26 July 1934, *Aug. Chevalier 44903* (P); Achada Furna, 27 July 1934, *Aug. Chevalier 44972* (P). **SIERRA LEONE. Western Area:** Western Area Urban, Freetown, Mount Aureol, 26 January 1965, *D. Gledhill 150* (BM, K, WAG); Freetown, Fourah Bay college, near Kennedy building, 11 December 1967, *E. A. Cole EAC17* (K, L, WAG). **GHANA. Greater Accra Region:** Accra, Accra plains, 02 October 1949, *Jr. J. T. Baldwin 13440* (K); Accra, Legon, Legon hill, southwest facing grassland slope, 120 m, 27-29 November 1993, *R. D. Noyes & C. C. H. Jongkind 1130* (L); Ningo Prampram, Prampram, 04 October 1953, *J. K. Morton s.n.* (K); Shai hills, along road on flood plain, 63 m, 31 July 1909, *A. P. M. van der Zon 5644D* (L). **Northern region:** Bunkpurugu-Yunyoo, outskirts of Nakpanduri village, 17 September 1963, *R. Rose Innes 32144* (K); Nanton, Nanton village, Kanvile-Yamalkaraga road, 01 August 1963, *R. Rose Innes 31855* (K); Yendi Municipal, Yendi town, resthouse compound, 19 September 1963, *R. Rose Innes 32173* (K); Tamale Metropolitan district, 08 October 1949, *J. T. Baldwin, Jr. 13552* (K); Savelugu-Nanton district, Pong-Tamale, 05 July 1932, *T. Lloyd Williams 834* (K). **Upper West region:** Wa Municipal, Wa town, 17 October 1963, *R. Rose Innes 32368* (K). Upper East region: Bolgatanga East district, Zuarungu, *s.d., C. W. Lynn 1077* (K). Central region: Effutu Municipal district, Winneba, Winneba plains, 27 February 1927, *Dr. J. M. Dalziel 8425* (K, P). **Ashanti region:** Mampong Municipal, Mampong, 06 October 1949, *J. T. Baldwin, Jr. 13530* (K); Bobiri Forest Reserve, near guest house, 22 April 1909, *A. P. M. van der Zon 5354* (L). **Savannah region:** Mole National Park, 1 km west of Brugbani, 157 m, 04 July 1911, A. P. M. van der Zon 6528 (L). **Brong-Ahafo region:** Wenchai-Bamboi road, 250 m, 06 October 1995, *C. C. H. Jongkind 2363* (L). Volta region: Tegbi, 2 km north of Keta, 10 April 1909, *A. P. M. van der Zon 5323* (L). **TOGO. Savanes:** Nagouangou, 6 km north of Dapaong, 29 July 1979, *U. Scholz & al. 221* (L). **BENIN. Litterol department:** Cotonou, 14 July 1902, *anonymous 4464* (K). **Mono department:** Avégodo, 13 October 1994, *L. Pauwels 7654* (L); Athiémè, 14 October 1994, *L. Pauwels 7669* (L). **Borgou department:** Monastère, north of Parakou, 27 September 1994, *L. Pauwels 7507* (L). **Collines department:** Dassa-Zoumé, 9-10 May 1910, *Aug. Chevalier 23630* (L); Glazoué, 01 October 1994, *Houinato 220* (L). **Atlantique department:** Ouidah, 21 km from Ouidah to Comé, 20 m, 11 November 2000, *L. J. G. van der Maesen 7415* (L). **Zou department:** Bohicon, 05 August 1998, *J. P. Essou, P. Agbani & H. Yédomonhan* 783 (L); Abomey, Davougou, 17 October 2000, *A.*

Akoegninou, H. Yédomonhan & P. Agbani 3953 (L); Dassa, Bétèkoukou, 29 September 1994, *L. Pauwels 7547* (L); Covè, Toue Jachère, 62 m, 23 August 1901, A. Akoegninou 5252 (L). **Ouémé department:** Zagnanado, Don, 06 October 1994, *L. Pauwels 7612* (L). **SENEGAL. Kédougou region:** Kenéméré, 15 November 1965, *Fotius K769* (P). **Diourbel region:** Bambey, 22 October 1965, *J. Audru 3002* (P). **Dakar region:** Dakar, Bargny, November 1955, *R. P. Berhaut 1883* (P). **EQUITORIAL GUINEA. Annobón:** Annobón Island, San Antonio de Palé, 03 September 1987, *Carvalho 3054* (L). **NIGER. Dosso region:** Gaya department, 3 km north of Bengou, 710 m, 26 October 1968, *G. Boudet 5248* (P). **MALI. Kayes region:** Nioro du Sahel Cercle, *s.d.*, *de Tarra 42* (P). **NIGERIA. Kwara state:** Ilorin, Lokoja, 19 September 1971, *Gbile, Wit & Daramola 64138* (K); Jebba, 31 December 1963, *R. Wheeler Haines 102* (K); Ilorin, 900 ft, October 1948, *J. F. Ward 78* (K). **Plateau State:** Langtang, Langtang North, 4000 ft, 20 September 1947, *W. E. Freeman 5110* (K). **Kano State:** Kano, Kano experiment station, November 1932, *C. B. Taylor 2* (K). Kaduna State: Kaduna, Zaria, 1975, *S. O. Magaji MG607* (K). **Niger State:** Borgu Game Reserve, Oli River, 13 August 1971, C. Geerling 3976 (K, L, P, WAG). **North-East State:** Adamawa, Yola, Government reservation area, 23 October 1971, *M. G. Latilo 63496* (K, L). **Kogi State:** Kabba, Lokoja, 07 November 1950, *R. W. J. Keay FHI28094* (K): Okene, March 1947, *D. H. Maggs 34* (P). **Borno State:** Biu, September 1944, *J. D. Kennedy FHI8003* (L); Samaru, *s.d.*, *P. N. de Leeuw 322* (L). Lagos State: Dawodu, August 1907, *anonymous 204* (P). **CAMEROON. North region:** Garoua, Campus Ecole de Faune, 04 November 1979, *P. Wit 3236* (K, L); Bénoué department, Garoua, Mount Tinguelin, 11 km north of the village, 400 m, 12 December 1964, *A. Raynal 12421* (K, P); Bénoué department, Garoua, Figuole, 450 m, 18 September 1968, *A. Muerillon 1384* (K); Mayo-Tsanaga department, Mogodé, 1000 m, 08 October 1972, *A. J. M. Leeuwenberg 10422* (L, P). **Far North region:** Moutouroua, Hills of Moutouroua, 45 km from south southwest of Marous-Garoua route, 22 August 1964, *Ed. Bounougou 38* (K, P); Diamaré department, Maroua, Kaele, August 1969, *Staff of college national 1502* (K, L). **CENTRAL AFRICAN REPUBLIC. Nana-Mambéré:** Bouar, 01 September 1960, *J. Koechlin 6308* (P). **CHAD. Chari-Baguirmi:** Loug Chari, Ba Ili, 28 October 1966, *P. Audry 859* (K). **Tibesti:** Zouarké, through Natron Mountain, 19 September 1958, *C. Rossetti 58/81* (L, P). **Mayo-Kebbi Ouest:** Lac Léré, Léré, 16 November 1974, *D. Klein 137* (P); Lac Léré, Léré, Mombaroua, 16 November 1974, *D. Klein 128* (P). **SÃO TOMÉ AND PRÍNCIPE. São Tomé:** Lobata, Praia das Conchas, about 1 km from the ocean shore, 30-50 m, 26 January 1980, *J. J. F. E. de Wilde, J. C. Arends & L. Groenendijk 299* (L). **RWANADA. Eastern province:** Kibungo, Kagera National Park, environments of Lake Ihema, 1350 m, 24 January 1958, *G. Troupin 5783* (K, L); Akagera National Park, Kalenga, about 8 km from Rulama, 1300 m, 14 January 1972, *P. Auquier 2237* (L). **Western province:** Rusizi, Bugarama, Kibangira, 1200 m, 13 June 1975, *Runyinya 130* (L). **Kigali province:** Bugesera, between Nemba and Karama, 1450 m, 23 January 1970, *Bouxin & Radoux 1443* (L). **BURUNDI. Bujumbura Mairie province:** Bujumbura, Uvira road, 780 m, 05 February 1972, *J. Lewalle 6518* (K, L). **Bururi province:** between Minago and Resha, Castle Akh-En-Atin, Lake Tanganyika, 780 m, 16 September 1974, *P. van der Veken 11279* (L). **Bubanza province:** Bubanza, Ruzizi plain, 800 m, 06 June 1971, *J. Lewalle 5894* (L). **CONGO. Haut-Lomami province:** near Bukama, 23 March 1971, *M. Lukuesa 1045* (K). **Ituri province:** Kasenyi, Bunia road, 2060 ft, 21 August 1935, *H. B. Johnston 1084* (K); Kasenyi, Petros Village, *H. B. Jonhston 1056* (K); Mahagi, plaine of Ishwah, *Froment 60* (K); Mahagi, Mahagi Port, 700-1160 m, 01 September 1931, *J. Lebrun 3771* (P). **Nord-Kivu province:** plain of Lake Edward, Nyamushengero, 1000 m, 19 March 1945, *R. Germain 3928* (K, P); Albert National Park, May-Ya-Moto, 950 m, 01 July 1937, *J. Lebrun 6901* (P) **Haut-Katanga province:** Mitwaba territory, Upemba National Park, 07 March 1949, *G. F. de Witte 5760* (L); Pweto, 930 m, 17 April 1926, *W. Robyns 1970* (P). **Kongo Central province:** between Songololo and Matadi, 29 March 1974, *L. Pauwels 5193* (L); Boma, Mateba Island, 01 May 1959, *Wagemans 2284* (L). **Kinshasa:** Lemba, campus of Kinshasa, 05 February

1979, *L. Pauwels 6188* (L). **SUDAN. Red Sea state:** Read Sea Hills, 3000 ft, 28 December 1962, *A. Pettet E22* (K); Read Sea Hills, Diris Pass, 10 April 1953, *anonymous J2864* (K). **South Kordofan state:** Jebel Nubah, 08 November 1960, *G. E. Wickens s.n.* (K); Idris, Jebel Korongo, Nuba Mountains, 14 April 1930, *N. D. Simpson 7768* (K, P); Nuba Mountains, North side of Gebel Talodi, 12 April 1930, *N. D. Simpson 7749* (K). **Blue Nile state:** Fung, Jebel Maiak, 1948, *D. F. Ferguson 352* (K). West Darfur state: Jebel Marra, 5800 ft, 15 July 1964, *G. E. Wickens 1939* (K). West Darfur: Jebel Marra, Gollol, 4900 ft, 21 June 1963, *I. J. Blair 61* (K); Jebel Marra, Gallabat, 3300 ft, 25 July 1964, *G. E. Wickens 2004* (K). **SOUTH SUDAN. Eastern Equatoria state:** Torit County, Torit, 620 m, 24 June 1949, *J. K. Jackson 826* (K); Loronya, Lafit Mountains, 26 June 1940, *J. G. Myers 13348* (K). **Central Equatoria state:** Juba County, Juba, 09 July 1929, *N. D. Simpson 7305* (K, P); Juba County, Mongalla, 450 m, 14 October 1948, *J. K. Jackson 367* (K); Juba County, Lado, Yei River, 10 November 1919, *F. Sillitoe 43* (K). **Western Equatorial state:** Zande, Sue River, near mouth of Bo, 21 July 1937, *J. G. Myers 7263* (K). **Lakes state:** Rumbek, 15 February 1949, *M. N. Harrison 694* (K). **Jonglei state:** Bor county, Bor, 06 July 1929, *N. D. Simpson 7237* (K). **ERITREA. Northern Red Sea region:** Imbatikala, 39 km from Asmera, first bend after village, 1300 m, 08 Jan 1987, *S. Edwards & G. E. Tewolderberhan 3888* (K); Ghinda, 1000 m, 09 February 1891, *G. Schweinfurth 170* (K). **Central region:** Asmera, Asmera town, Bet Giorgis, between the War Cementary and the Zoological Garden, 2400 m, 14 August 1988, *O. Ryding 1387* (K). **ETHIOPIA. Somali region:** Degahabur Segef, Dega Hedo, 07 December 1972, *Boudet 8151* (K, L, WAG); Shinile, Erer, Erer Valley, 22 km southeast of Harar, highway to Jijiga, 1350 m, 21 July 1961, *W. Burger & A. Getahun 336* (K); Liben zone, Filtu, 12 November 1972, *G. Rippstein 819* (P). **Oromia region:** East Shewa Zone, Awash National Park, Fantale track, 15 April 1969, *M. G. & S. B. Gilbert 1252* (K); 15 km east of Curfacelli, road to Gara Mullata Mount, 5800 ft, 23 September 1961, *W. Burger 990* (K); East Hararghe zone, Haro Maya district, Haramaya, Awalla Valley, 12 km from College of Agriculture, 1930 m, 07 July 1975, *P. C. M. Jansen 1976* (L). **Sothern Nations region:** south of Sodo, Sodo-Arba Minch road, 19 October 1975, *Jago 19* (K); Mago National Park, about 30 km northwest of the Mago National Park headquarter, road to the Mursi Hills, 550 m, 22 December 1998, *I. Friis, S. Bidgood, M. Wonderfrash & Getu Terefa 9588* (K). **Sidama region:** Awasa, 3 km west of Awasa town, 1650 m, 25 September 1973, *Ash 2160* (K); about 80 km from Arba Minch, along road from Arba Minch to Soddo, 1210 m, 30 September 1975, *P. C. M. Jansen 3864* (L). **Harari region:** East Hararghe zone, Uadendeo plateau, 36 km east southeast of Harar on road to Jijiga, 1520 m, 12 October 1961, *W. Burger 1123* (K). **DJIBOUTI. Tadjourah region:** Day Forest National Park, 12 April 1983, *J. Blot 3* (P). **Ali Sabieh region:** Gourroumo Plain, 17 March 1983, *J. Blot 79* (P). **SOMALIA. Maroodi Jeex region:** Ga'an Libah Forest station, 5400 ft, 21 September 1957, *Bally B11728* (K); Hargeisa, 4600 ft, 13 October 1932, *J. B. Gilbert 4252* (K, P); Gabiley, Tog Wajaale, 5100 ft, 26 August 1938, *A. S. McKinnon S.9* (K). **Togdheer region:** Sheikh, 4600 ft, 05 November 1924, *J. R. Inmide Wood s.n.* (K); Golis range, 26 February 1906, *Dr. Drake Brockman 88* (K). **Sanaag region:** Sugli, Al Hills, 5000 ft, November 1929, *C. N. Collenette 333* (K); Daallo forest, 07 July 1945, *P. E. Glover and Gilliland 1140* (K). **Galguduud region:** El Dher, November 1986, *D. Herlocker 460* (K); **Mudug region:** 46 km on road between Gal Hareeri and Xarardheere, 340 m, 26 May 1989, *M. Thulin & A. M. Dahir 6565* (K). **Lower Juba:** Balahaji, 22 June 1978, *S. M. A. Kasmi, Elmi & Rodol 650* (K, L). **UGANDA. Northern region:** Agago, path leading to Oliri Konyanga Hill, 1225 m, 1 August 1913, *S. Santini 919* (K); Atumatak, near Moroto Kaeamoja, 26 July 1959, *O. Kerfoot 1202* (K). **Western region:** Kasese district, Kikorongo, 3700 ft, December 1925, *T. D. Maitland 955A* (K); Mohokya, 19 March 1936, *L. George 1379* (K); Lake George, Lake George Flats, 3000 ft, 10 December 1952, *N. R. Brockingtou 29* (K); Queen Elizabeth National Park, Toro U2, East side of Lake Kitagata, 1000 m, 01 June 1970, *K. A. Lye & A. B. Katende 5496* (K). **Eastern region:** Kumi district, 3400 ft, July 1926, *T. D. Maitland 1250* (K); Serere district, Serere, 3700 ft, July 1926, *T. D. Maitland 1431* (K); Bugisu, Buwalasi, Mount Elgon, 5000 ft, 13 December 1927, *anonymous 1247* (K). **Northern region:** Karamoja, southwest plain of Karamoja, Morunyagai, 4000 ft, 03 July 1957, *Dyson-Hudson 270* (K); Acholi, Nwoya, Pakuba, top of Emoruagaberru, near Nabilatuk, 4300 ft, 22 May 1956, *Dyson-Hudson 11* (K); Acholi, Nwoya, Pakuba, Murchison Falls National Park, 11 November 1957, *H. K. Buechner 123* (K); Acholi, Nwoya, Murchinson Falls National Park, Butiaba escarpment, 2500 ft, May 1935, *H. B. Johnston 951* (K); Karamoja, Kokumongole, 4000 ft, 28 May 1939, *A. S. Thomas 2840* (K); Karamoja, Moroto, 5000 ft, 21 May 1940, *A. S. Thomas 3410* (K). **Central region:** Kampala Capital City Authority, Rubaga, Mengo, Lwampanga, 3450 ft, 11 September 1954, *L. Brown 1240* (K). **KENYA. Mombosa County:** Mombosa, sea level, July 1934, *N. B. Johnston 1004* (K); **Makueni County:** Simba, West Simba Mount, 1500 ft, 18 March 1902, *Kässner 379* (K); Kibwezi, 3000 ft, January 1922, *R. A. Dummer 5090* (K); Chyulu Hills, 27 December 1910, *W. R. Q. Luke & P. A. Luke 15009* (K). **Nakuru County:** Mount Longonot, 8000 ft, March 1922, *R. A. Dummer 5328* (K); Great Rift Valley, near Eburru, 2000 m, 01 August 1929, *H. Humbert 9104* (P). **Marsabit County:** Mount Kulal, 6000 ft, March 1959, *J. Adamson 6* (K); Songa, Marsabit forest, 5 km from Songa to Karare,980 m, 29 July 1905, *J. M. Muasya GBK12* (K); Moyale, Bila, 3600 ft, 12 July 1952, *J. B. Gilbert 13578* (K). **Embu County:** Embu, Kirathange, 3200 ft, 08 December 1925, *F. B. Butler 105* (K). Kwale County: Kwale, Shimba Hills, Longomwagandi area, 1400 ft, 29 March 1973, G. W. Sangai 15791 (K); Mwea, Riakanau, Kitthunguthya Village, Dr. Muasya's farm, 1020 m, 30 January 1902, *A. M. Muasya. P. Muthoka & P. Kirika NMK297* (K). **West Pokot County:** above Turkwell Gorge, near Nakhang camp, 1100 m, 13 August 1978, *K. A. Lye 9092* (K); Nairobi County: Kahawa Sukari estate, opposite Kenyatta University, 1700 m, 26 July 1901, *M. K. Wakaneme 872* (K). **Taita-Taveta County:** Tsavo East National Park, Northern Yatta Plain, 4160 ft, 28 January 1938, *D. C. Edwards 88* (K); Tsavo National Park, east of Lugards Falls, 32.9 miles from Voi Gate, Galana River, 900 ft, 01 January 1967, *P. J. Greenway and Kanuri 12925* (K); Msau River Valley, 800-950 m, 18 May 1985, *C. H. S. Kabuye & al.* 729 (K); Taita Hills, Bura-Bura, 1 km from the mission, 08 March 1998, *G. Mwachala & al. EW1243* (K). **Kilifi County:** Sabaki, 4 miles north of Malindi, 20 ft, 12 November 1961, *Polhill & Paulo 749* (K); Kwale, Gongoni forest, less than 100 m, 26 February 1972, *I. Backéus & L. Jonsson 263a* (L). **Machokos County:** 2 miles north of Masii, 4000 ft, 18 January 1954, *D. Clayton DC33* (K). **Kajiado County:** Eastern Rift Valley, Olorgesailie Plains, 3400 ft, 03 August 1943, *Bally 2648* (K). **Lamu County:** Kiunga, 55 miles northeast of Lamu, 20 ft, 06 August 1961, *J. B. Gillespie 154* (K). **Narok County:** Kipleleo massif, along the track at the base of and north of the mount, 6000 ft, 24 May 1962, *P. E. Glover and Samuel 2872* (K); Mara, Aitong Hill, 5700 ft, 05 June 1961, *Glover, Gwynne and Samuel 1541* (K). **Kwale County:** between Samburu and Mackinnon Road, near Taru, 350 m, 08 September 1953, *R. B. Drummond & H. Hemsley 4196* (K); Kwale, some km north northeast of Lungalunga, 14 January 1971, *O. Vitikainen 9603* (L). **Tana River County:** Kora National Reserve, 6 miles west from Kora Reserve Camp, 300 m, 24 August 1983, *Mr. J. G. Mutangah 89* (K). **TANZANIA. Iringa region:** Msembe-Mbagi-Kimiramatonge track junction, Tanganyika River, 2800 ft, 02 March 1970, *P. J. Greenway and Kanuri 14004* (K); Ruaha National Park, west of park headquarters at Msembe, 2600 ft, 16 May 1968, *S. A. Renvoize 2177* (K). **Manyara region:** Mbulu, Lake Manyara National Park, Mbagayo River, 3200 ft, 14 November 1963, *P. J. Greenway and Kanuri 11017* (K); Tarangire National Park, Tarangire Ridge, 4550 ft, 26 January 1959, *D. Vesey-Fitsgerald 2183* (K). **Kilimanjaro region:** Kilimanjaro National Park, Sanya Plains, 3500 ft, 15 June 1952, *anonymous* (K). **Mara region:** Serengeti National Park, Seronera, 5100 ft, 20 March 1961, *P. J. Greenway 9857* (K). **Tanga region:** Korogwe, Mombo, s.d., *Dr. A. Eichinger 5889* (K); Serengeti National Park, Nyaruswiga Hills, 27 April 1958, *S. Paulo 394* (K). **Mbeya region:** Nyassa Hochland, Kyimbila Station, 1200 m, May 1912, *A. Stolz 1243* (L); Rungwe, 5000 ft, 22 February 1932, *R. M. Davies 322* (K); Mbozi, near Songwe Hot Springs, 1200 m, 07 May 1991, *P. Lovett &*

C. Kayombo 187 (L). **Tanga region:** Korogwe, 5 km west of Tonibombo, 505 m, 13 June 1912, *P. Peterson & al. 24215* (K); Lushoto, West Usambara Mountains, above Mzinga Village, below Baga II F. R., between Mgwashi and Mtai, 1350-1600 m, 31 January 1985, *A. Borhidi, S. T. Iversen & W. R. Mziray 85390* (K); Handeni, Kwa Rhono, 1700 ft, 27 June 1966, *N. E. Archbold 761* (K); Handeni, Kideleko, 2080 ft, 01 July 1965, *N. E. Archbold 466* (K); Steinbruch Forest Reserve, near Maweni, 80 m, 31 December 1969, *Botany Students DSM1414* (L); Kumburu, Ngomeni, 100 m, 01 May 1951, *B. Kemp 31* (P); Usambara, Amboni, June 1893, *C. Holst 2767* (P). **Morogoro region:** eastern Mahenge, between Mahenge Plateau and confluence of Kilombero and Luwegu to Rufiji, 400 m, 08 June 1932, *H. J. Schlieben 2276* (K); Kilosa, Mkata River Valley, 1600 ft, 13 June 1973, *P. J. Greenway and Kanuri 15113* (K); Mikumi National Park, hills east of road, 01 May 1984, *G. de Nevars & S. Charnley 3385* (L); Bondwa, Bondwa Peak, 04 July 1970, *C. H. S. Kabuye 261* (L); Uluguru Mountains, 500 m, 21 February 1933, *H. J. Schlieben 4013* (P). **Shinyanga region:** Old Shinyanga, 3800 ft, 08 March 1950, *J. R. Welch 29* (K). **Rukwa region:** Ufipa Plateau, Mpui Escarpment, 6000 ft, 10 March 1959, *M. McCallum Webster T5* (K). **Dodoma region:** Kondoa, Kolo, 5000 ft, 29 January 1928, *B. D. Burtt 1264* (K). **Ruvuma region:** Songea, about 2.5 km east of Johannabruck, 930 m, 18 April 1956, *E. Milne-Readhead & P. Taylor 9761* (K); Songea, Lumecha Bridge, 21 km north of Songea, 03 January 1956, *E. Milne-Rehead & P. Taylor 8037* (K). Lindi Region: Kilwa, at Rushungi, 0-9 m, 17 May 1912, *P. Peterson & al. 23819* (K). **Kagera region:** Muleba, Rubya mission, about 90 km south of Bukoba, 1200 m, 01 February 1978, *E. P. W. Zuidgeest s.n.* (L). **Pwani region:** Kisarawe, Soga, 09 January 1964, *T. Tateoka 3311* (P). **MOZAMBIQUE. Zambezia province:** Mbobo, Massingire, 27 April 1943, *A. R. Torre 5211* (K); Mocuba, Namagao Plantation, June 1947, *H. Faulkner 148* (K). **Sofala province:** Beira, February 1912, *Rev. F. A. Rogers 5940* (K). **Niassa province:** Mossuril, Lumbo, 05 May 1948, *Pedro and Pedrogão 3112* (K). **Inhambane province:** Inhassoro, Santa Carolina Island, 1-15 m, 04 November 1958, *A. O. D. Mogg 28799* (K); Cobro, 11 km from Mabote and Lake Banamana, 20 March 1974, *M. F. Correia and A. Marques 4117* (L). **Tete province:** Angónia, Ulongue, near Livelange River, 17 December 1980, *L. Macuácua 1468* (K, L); between Estima and Inhacapirire, 23.8 km from Estima, 19 February 1972, *J. M. de Aguiar Macèdo 4863* (K); Cabora Bassa, Post of Repetition, near Geodésico, 30 March 1983, *A. Nuvunga 1309* (L); Cabora Bassa, Zambezi River, from Dam to upstream south slope, rectangular rang, 818 m, 03 May 1972, *A. Pereira & M. F. Correis 2357* (L). **Maputo province:** Boane, between Boane and Porto Henrique, 19 February 1981, *J. de Koning & C. Boane 8668* (K); near Marracuene district, 33 km north of Lourenço Marques, 27 February 1946, *A. Jones and Sansa 3372* (K); Namaacha, Mount Penduine, near the radar post, 800 m, 26 March 1969, *M. F. Correia and A. Marques 635* (L). **Nampula province:** Mossuril, between Crusse Forest and the coast, 18 February 1984, *J. de Koning, E. H. C. Greenendijk & J. Dungo 9688 (L).* **Gaza province:** Guijá, Caniçado, 30 km from Massingir to the sides of the border, Mechapane River, 13 November 1970, *M. F. Correia 1981* (L). **Cabo Delgado province:** Montepuez, Chipembe Dam, 30 November 1983, *A. Nuvunga 1309* (L). **MALAWI. Northern region:** Rumphi, Livingstonia escarpment, 3500 ft, 14 June 1971, *J. Pawek 4916* (K); Rumphi, St. Patrick Mission, 1 mile east of Rumphi, 3500 ft, 02 April 1977, *J. Pawek 12574* (K, L); Chitipa, Kaseye Mission, 4100 ft, 05 April 1969, *anonymous 1929* (K); Mzimba, Kasitu valley, 3400 ft, 26 January 1938, *J. E. L. Fennes 214* (K); Mzimba, 20 miles west of Mzuzu, Lunyangwa River Bridge, 4000 ft, 18 April 1974, *J. Pawek 8348* (L); Karonga, Vintukhutu Forest, 2 miles north of Chilumba, 550 m, 26 April 1975, *J. Pawek 9583* (K). **Southern region:** Zomba, near Makwapala, 2350 ft, 15 March 1937, *E. Lawrence 324* (K); Chikwawa, Lengwe Game Reserve, 100 m, 09 March 1970, *R. K. Brummit and A. J. Hall-Martin 8988* (K); Chikwawa, Medalamu Village, 05 May 1969, *E. A. Banda 1080* (K); Mulanje, Lukulezi Swamps, 650 m, 20 June 1962, *E. A. Robinson 5396* (K); Nsanje, between Thangadzi and Lilanje River, 300 ft, 25 March 1960, *J. B. Phipps 2685* (K); Ngwezi, Mazabubu, 4000 ft, 30 January 1964, *W. L.*

Astle 2900 (K). **Central region:** Kasungu, 8 km north of Kasungu by quarry, 1060 m, 07 May 1970, *R. K. Brummit 10429* (K); Dedza, Chongoni Forest, near Kanjoli, 12 January 1967, *A. J. Salabeni 485* (K). **ZAMBIA: Lukasa province:** Chilanga, Luieu Lake, 3600 ft, September 1929, *C. Sandwich 46* (K); Kafue, Muvuma Hills, on the road to Mahabuka-Munali Pass, 1200 m, 25 March 1972, *J. Kornaś 1455* (K); west end of Lazy J Ranch, 20 km southeast of Lukasa, 1300 m, 12 March 1996, *M. G. Bingham 10985* (K). **Eastern province:** Chipata, Fort Jameson, 1100 m, 04 January 1959, *N. K. B. Robson 1029* (K); Luangwa Valley Game Reserve, 3 km south of Lubi, 2000 ft, 12 April 1967, *S. D. Prince 466* (K). Southern province: Mazabuka, Ross's Farm, 12 miles north of Choma, 01 February 1960, *F. White 6674* (K); Jumbe, Machinje Hills, Luangwe Valley, 2500 ft, 04 March 1966, *W. L. Astle 4625* (K); South Luangwe National Park, Mfuwe, Mushilashi River, 2000 ft, 16 February 1966, *W. L. Astle 4562* (K). **Western province:** Sesheke, Sichinga Forest, *29 December 1952*, A. Angus 1068 (K). **Muchinga province:** Luangwa Game Reserve, 2 miles upstream of Mfuwe, 28 April 1965, *B. L. Mitchell 2730* (K). **Northern province:** Mbala, Kasaba Camp, Lake Tanganyika, 2500 ft, 17 February 1959, *M. McCallum Webster A68* (K). **ZIMBABWE. Mashonoland:** Hartley-Norton, 28 miles west of Salisbury, 10 February 1946, *O. Weber 203* (K). **Mashanoland Central:** Mount Darwin, southeast corner of Chiswiti Reserve, 2260 ft, 22 January 1960, *J. B. Phipps 2372* (K); Bindura, Kerry Farm, 3200 ft, 16 July 1969, *A. O. D. Mogg 34207* (K). **Mashonaland East:** Marondera, Digglefold, from Joplando, 05 January 1949, *H. D. L. Corby 345* (K). **Matabeleland North:** Binga, Chizarira Game Reserve, Bimba Vlei, Vlei Verges, 3350 ft, 16 January 1968, *W. R. Thomsom 54* (K); Hwange, Hwange National Park, 0.6 miles west of main camp, along Shapi Road, 3500 ft, 25 January 1969, *J. E. Rushworth 1454* (K); Hwange, Victoria Falls, Zambezi Camp, 3010 ft, 16 January 1974, *P. Gonde 42/73* (K); Zambezi National Park, Leshomo Valley, near Victoria Falls, *s.d., Dr. E. Holub s.n.* (K); Nyamandhlovu, Pasture Research Station, 01 April 1956, *D. C. H. Plowes 1939* (P). **Matabeleland South:** Matobo, Matopos Research Station, 4500 ft, 12 February 1954, *J. M. Rattray 1599* (K); Matobo, Matobo Hills, Rhodes Estate, 1250 m, 15 April 1934, *H. Humbert 15412* (K, P); Bulalimamangwe, Dombodema Mission Station, Dombodema Secondary School, about 100 m north of the gate, 1300 m, 03 April 1972, *G. Norrgrann 124* (L); Shangani, Lupsani Valley, 3500 m, 01 March 1954, *R. Davis 49038* (L). **Masvingo:** Masara Village, Makokoli Experiment Station, 10 February 1977, *E. Senderayi 69* (K); Chiredzi, Gonarezhou National Park, Chipinda Pools, 06 January 1978, *J. R. Peek 109/78* (K); Chiredzi, Bangala Dam, 10 February 1972, *G. E. Gibbs Russell 1466* (K). **Bulawayo:** Waterford, south of Waterford School, 1400 m, 06 February 1974, *G. Norrgrann 504* (K). **Harare:** Cleveland Dam, 10 km southeast of Harare, 1500 m, 08 January 1991, *S. Laegaard 16181* (K). **Manicaland:** Mutare, Fairbridge Farm, on Inyanga Main Road, 1200 m, 06 March 1969, *A. O. Crook 858* (K); Chimanimani, Nyanyadzi Farm, 3000 ft, 16 February 1954, *A. O. Crook 523* (K). **Midlands:** Gwelo, Teacher's Training College, 4600 ft, 11 January 1967, *H. M. Biegel 1821* (K). **BOTSWANA. North-West District:** Maun, Thamalakane River, 26 February 1974, *P. Smith 873* (K); Okavanga Delta, Chief's Island, southeast Chief's Camp, 20 February 1910, *A. & R. Heath 1913* (K). **South-East District:** Lobatse, *s.d., C. Sandwich 98* (K); Gaborone, Gaborone Campus, 3250 ft, 04 December 1973, *P. J. Mett 36* (K). **Ghanzi District:** Groote Laagte, Fossil River Valley, 15 March 1980, *P. A. Smith 3199* (K). **Ngamiland District:** Aha Hills, 22 April 1980, *P. A. Smith 3395* (K). **Central District:** northeast corner of Makgadikgadi Pan, Simonware River, 900 m, 23 April 1957, *R. B. Drummond & S. C. Seagrief 5205* (K); Mahalapye, Mahalapye-Shoshong Road, 3200 ft, 15 February 1958, *I. S. de Beer 584* (K). **Kgalagadi District:** 12 km northwest of Lephepe Village, near Kalahari Sandveld Pasture Research Station, March 1969, *E. T. Kelaole 524* (K). **ANGOLA. Benguella Province:** country of the Ganguellas and Ambuellas, s.d., *Mr. J. Gossweiler 1671* (K). **Huíla Province:** Gambos, about 50 km of Cahama to Chibemba, 06 April 1970, *A. Menezes, Barroso & Sousa 3349* (K, P); Gambos, 2.7 km of Areia to Quihita River, 13 November 1970, *A. Menezes 3534* (K); Chibia, Km 15 of Chibia-

Hungueria Road, from Munher River, 06 May 1971, *A. Borges 181* (K, P); Lubango, Km 20 of path to Chibia, 24 March 1965, *A. Menezes 1641* (K, P). **Cuando Cubango Province:** Rápidos M'Pupo, Cuito River, between Dingo and Lumeta, 16 April 1913, *T. Harris & F. Murray-Hudson 781* (K). **SAINT HELENA, ASCENSION AND TRISTAN DA CUNHA. Ascension Island:** Green Mountain, Mountain Red Hill, 309.7 m, 03 July 1915, *M. R. Corocan MARC221* (K); North slope of Middleton's Ridge, 376 m, 13 September 1908, *P. W. Lambdon, A016* (K). **MADAGASCAR. Diana Region:** Anstiranana, Ambanja, base of Galoko Mountain chian, 0.5 km northeast of Antanamalandy, on path to Ambatoharanana, 20 m, 23 March 1909, *M. Briggs MB280* (K, P); Nosy Be Island, 11 September 1912, *R. Viguier and H. Humbert 102* (P). **Atsimo-Andrefana Region:** Tulear, Beza Mahafaly Reserve, near Befioky, Parcelle No.1, 130 m, 31 April 1987, *P. Phillipson 1752* (K, L, MO, P); Sakahara, Analafanja Forest, north of Fiherenana, 950-1000 m, 01 March 1934, *H. Humbert 14283* (P); Toliara, Middle Valley of Mandrare, near Anadabolava, Vohitrotsy Mountain, 700-800 m, 01 December 1933, *H. Humbert 12701* (P). **Menabe Region:** Morondava, Bemanonga, Fokontany, Marofandilia, Kirindy Forest, About 60 km northest of Morondava, 59 m, 21 April 1913, *R. Razalamalala & al. 7490* (P); Miandrivazo, plateau of Isalo Valley, west of Ranohira, 800-1250 m, *s.d.*, *H. Humbert 29859* (P). **Sava Region:** Vohemar, Daraina, Ambilondomba forest, west of Antsahaba, 1.5 km southeast of Point Cote, 300 m, 08 March 1903, *L. Gautier, S. Wohlhauser & L. Nusbaumer LG4283* (K, P); Darina, Solaniampilana-Moroadabo forest, 360 m from point 214, 165 m, 10 March 1904, *L. Gautier, S. Wohlhauser, L. P. G. Nusbaumer & P. Ranirison LG4536* (G). **Haute-Matsiatra Region:** Fianarantsoa Province, vicinity of Zazafotzy, on route number 7, between Ambalavao and Ihotsy, 710 m, 02 February 1975, *T. B. Croat 30394* (L). **Anosy Region:** Taolanaro, Ampasimena, Manampanihy Valley, 20-100 m, 18-23 March 1947, *H. Humbert 20637* (P); Fort Dauphin, 20 May 1890, *G. F. Scott Elliott 2606* (P). **Analamanga Region:** Antananarivo, Nanisana, 25 June 1906, *anonymous* (P). **Boeny Region:** Majunga, Pointe du Caïman, 06 September 1912, *B. N. & H. H. 19* (P). **Analanjirofo Region:** Maroantsetra, northwest of Maroaomby, Manambolo Valley, 300-400 m, 01 December 1933, *H. Humbert 12803* (P). **Androy Region:** Ampandrandava, between Bekily and Tsivory, 28 April 1905, *M. S. Seyrig 403* (P). **COMOROS. Island of Grande Comore:** South Center, between Kourani and Dembeni, 450 m, 15 February 1975, *J. J. Floret 965* (L); Hahaia Seaside, 21 October 1975, *P. Coulon 177* (L). **MAYOTTE. Bandraboua Commune:** Handrema, Handrema Point, 22 April 1999, *C. Mas 35* (L). **Chiconi Commune:** Sohoa, Zone Dégradée, 19 April 1999, *M. Pignal 1224* (L). **Bandrélé Commune:** Sommet, Chissoua Bambo, 22 April 1999, *M. Pignal 1264* (L). **Dzaoudzi Commune:** Petite Terre, Dziani Dzaha Lake, 20-60 m, 27 April 1999, *M. Pignal 1302* (L). **SEYCHELLES. Multiple:** Mahé, Police Point, 07 December 1961, *Jeffrey & Zelia 690* (K, L); Mahé, Grand Anse, 50 ft, July 1977, *Mrs. S. A. Robertson 2439* (L, P). **Mont Fleuri:** Long Island, 0-300 ft, June 1936, *F. L. Squibbs G21* (K). **MAURITIUS. Rivière Noire District:** Corps de Garde, below north-facing cliffs, 300 m, 24 April 1976, *I. B. K. Richardson 4023* (K); Trois Mamelles, April 1974, *J. Bosser 21878* (P). **Port Louis District:** Petite Riviére, *s.d.*, *R. E. Vaughan A7* (K). **Rodrigues:** Pointe Mangues, July 1970, *T. Cadet 2660* (K, P). **Grand Port District:** La Saline, June 1957, *J. Bosser 11810* (P). **RÉUNION. Saint-Paul:** Cap La Houssaye, 20 December 1971, *J. Bohez 20905* (K, P). **Saint-Joseph:** Commerson Crater, *s.d.*, *anonymous* (P). **NAMIBIA. Kavango East:** Caprivi Strip, 45 miles from Katima, on road to Singalamwe, 3000 ft, 30 December 1958, *Killich and Leistner 3196* (K). **Erongo:** Karibib, 1150 m, 01 April 1957, *Dr. R. Seydel 1081* (K); Karibib, Otjosondu, 1300 m, 28 February 1963, *Dr. R. Seydel 3415* (L). **Hardap:** Bullspoort, base of Naukloof Mountains, 4000 ft, 16 December 1947, *R. J. Rodin 2794* (K); Kyfferhäuser, north northwest of Maltahöhe, on road D850 to Bü llspoort, 12 March 1995, *L. Smook 9371* (L). **Otjozondjupa:** Grootfontein, Lughawe, 1300 m, 02 March 1970, *P. J. Le Roux 1132* (K); Okahandja, Farm Omupanda, 8 km east of Hochfeld, 07 March 1983, *G. Russell and Smook, 5373* (K); Nama Pan, 14 August 1955, *R. Story 5201* (K). **ǁKaras:** Groot Karasberge

Mountains, 128 km south of Keetmanshoop, 32 km north of Grünau, 945 m, 27 February 1996, *N. Snow & P. Burgoyne 7174* (K). **Oshikoto:** Tsumeb, southern boundary of Etosha Game Park, near Farm Renex, 19 February 1966, *K. L. Tinley 1303* (K); Namaqualand, Groot Karasberge Mountains, Kreikloof, 31 June 1924, *I Örtendahl 486* (K, L). **Khomas:** Windhoek Bergland, Bodenhausen, 1600 m, 07 May 1960, *Dr. R. Seydel 2403* (L). **SOUTH AFRICA. Bantustan:** Bophuthatswana, Pilanesberg National Reserve, 17 January 1984, *Sydney and James 8* (K); Kwandebele, Diana Ranch, Farm Goederede, 16 March 1981, *L. Smook 3055* (K); KaNgwane, Songimvelo Gane Reserve, Farm Dunbar, Mtsoli River, 08 December 1992, *L. Smook 8108* (L). **Limpopo:** Saselandonga, Kruger National Park, 460 m, 23 January 1974, *G. Davidse 5878* (K); Nylsvley Nature Reserve, T. P. A. Camp, 3500 ft, 02 March 1975, *P. C. V. de Toit 634* (K, L, P); Vhembe, Makhado, Louis Trichardt, Mutali area, near Masisi, 25 January 1961, *H. P. v. d. Skijff 5247* (K); Ellisras, Darby Grootgelukmyn, read adjacent to mine property, 22 December 1982, *L. Smook 4303* (K); Vygeboomspruit, near Shokolles Kraal, June 1917, *Dr. H. S. Breyer s.n.* (K); Messina, Government Rauching Station, 15 March 1933, *J. A. du Plessis s.n.* (K); Kruger National Park, 9.5 miles southeast of Punda Maria, 1400 ft, 14 March 1949, *L. E. Codd 5297* (K); Capricorn, Lepelle-Nkumpi, Zebediela, Percy Fufe Nature Reserve, 04 February 1967, *B. J. Huntley 965* (K); Mopani, Greater Letaba, Duivelskloof, 22 May 1980, *H. C. D. de Wit 1093* (L); Nylstroom, Vaalwater, Farm Commando Nek, 1390 m, 27 February 1986, *R. Westfall 2128* (P); Zoutpansberg, February 1935, *A. P. de Klerk s.n.* (L); Experimental Farm Ermelo, November 1905, *J. B. Davy 3915* (L). **Mpumalanga:** Nelpruit, Kruger National Park, Shabeni Mount, 03 February, *L. E. Codd 457* (K); Lydenburg, top of Long Tom Pass, 2150 m, 13 December 1975, *P. C. V. du Toit 1015* (K); Ehlanzeni, Mbombela, Barberton Game Reserve, on the farm hillside 459 JT, 760 m, 11 October 1997, *K. Balkwill, S. Williamson & S. Smith 10007* (K). **Northwest Province:** Lichtenburg, White's Quarry, 04 February 1970, *Moris and Engelbrecht 1044* (K); Pilanesberg, Saulspoort, 27 November 1977, *L. Smook 916* (K); Pilanesberg, Buffelskloof Farm, 29 November 1977, *L. Smook 966* (K); Southern District, JB Marks, Potchefstroom, October 1903, *J. B. Davy 2173* (L); Thoming, 45 miles north of Kimberly, west of Harz River near Taungs, 13 February 1948, *R. J. Rodin 3652* (K, P). **Gauteng:** Roodeplaat Dam, section of Roodeplaat Research Station, near entrance to Transvaal, 02 December 1973, *B. Clarke 580* (K); Pretoria, Eloffsdal, Property 51-53, 14 December 1971, *W. J. Hanekom 1683* (K, L); Pretoria, Onderstepoort, Pyramid Koppies, 30 November 1908, *R. Leendertz 1673* (K); Pretoria, Garsfontein, February 1977, *L. C. C. Liebenberg 8772* (K); Pretoria, Wonderboompoort, 26 January 1929, *J. Hutchinson 2888* (K); Farm Gladysvale, about 9 miles west of Krugersdrop, 22 February 1948, *R. J. Rodin 3815* (K, P)); Johannesburg, Frankenwald Station, 5000 ft, March 1939, *H. C. D. de Wit 669* (L). **Free State:** Xhariep, Mohokare, Zastron, Aasvoëlberg, behind Caravan Park, 27 March 1980, *Smook and G. Russell 2286* (K); Xhariep, Kopanong, Fauresmith, about 3 miles west northwest of G Farmhouse, 4650 ft, May 1927, *C. A. Smith 4015* (K). Hoopstad, Bultfontein, Oppermansdrifdam, 1220 m, 15 December 1974, *T. G. O'Connor 113* (K, P); Mangaung, Bloemfontein, 25 January 1971, *J. A. V. D. Berg 3687* (K); Bethlehem, Golden Gate Hoogland Park, Glen Reenen Camp, 16 January 1966, *L. C. C. Liebenberg 7463* (K); Windburg, Willem Pretorius Game Reserve, 4500 ft, 23 February 1963, *Van Zinderen Bakker 1152* (K); Senekal, Ferrara, 17 December 1931, *A. P. Goosseus 959* (K); 12 km east of Verwoerd Dam Wall on road to Bethulie, Falls Upper Karroo roadside, March 1981, *L. Smook 2914* (L); Luckoff, Farm Bleskop, 29 km south of Luckoff on road to Heuningkop, February 1981, *L. Smook 2825* (L). **KwaZulu-Natal:** Harry Gwala, Dr Nkosazana Dlamini-Zuma, Underberg District, Garden Castle Forest Reserve, 6000-6200 ft, 05 December 1980, *O. M. Hillard & B. L. Burtt 13831* (K); Harry Gwala, Dr Nkosazana Dlamini-Zuma, Underberg District, vicinity of Tarn Cave, Bushman's Nek, 8000 ft, 20 January 1984, *O. M. Hillard & B. L. Burtt 17411* (K); Ndumu Game Reserve, Ndumu Hill, 19 February 1971, E. S. Pooley 1278 (K). **Western Cape:** Cape Winelands, Witzenberg, Bella Vista, Nkonjane/Abekorn Drift, 1000 ft, 31 October 1969, *E. J. Moll & E. S. Pooley 4170* (K); Zululand, Abaqulusi, Ngotshe, Pongola Bridge, on Coudouer-Gollet Road, 500 ft, 09 March 1964, *D. Edwards 3265* (K, L); Uthukela, Inkosi Langalibalele, Estcourt Research Station, 17 March 1938, *O. West 719* (K); Langeberg Range, 22 March 1920, *I. B. Pole-Evans 79* (K); City of Cape Town, Durbanville, Peaslake, on the property of Mr. Colin Taylor, 3 miles from Durbanville on the Langeberg road to Kraaifontein, 400 ft, 21 October 1963, *H. C. Taylor 5451* (K); Shaapenberg, Somerset West, Stellenbosch, 08 December 1951, *R. N. Garken 4697* (K); Swellenodam, Bontebok National Park, near Old Garden (Ou Tuin), 100 m, December 1962, *L. C. C. Liebenberg 6712* (K); City of Cape Town, Gordon's Bay, January 1927, *A. O. D. Mogg s.n.* (L). **Eastern Cape:** Uitenhage, on the fields near the Zwartkop River, *s.d., anonymous 185* (K); Amathole, Mnquma, Kentani, 10 October 1914, *A. Pegler 2088* (K); Sarah Baartman, Kouga, Humausdorp, Company's Drill, 1200 ft, November 1923, *H. G. Fourcade 2871* (K); Sarah Baartman, Makana, Grahamstown, 24 May 1901, *Miss D. Daly 73* (K); Faraway, portion 3 of Coldsprings, Witteberg quartzite ridge, 700 m, 22 November 1981, *A. J. Guillarmod 8935* (K); Nelson Mandela Bay, Port Elizabeth, Koega, 09 December 1976, *M. C. Olivier 1721* (K); **Northern Cape:** Pixley ka Seme, Siyathemba, Prieska, April 1931, *E. G. Buyant 622* (K); Frances Baard, Dikgatlong, Barkley West, Boetsap, 19 February 1945, *A. Brueckner 141* (K); Frances Baard, Dikgatlong, Barkley West, Koopmansfontein Agricultural Research Station, 4500 ft, 14 January 1963, *P. D. Hattingh H22* (K); Pixley ka Seme, Emthanjeni, Britstown, Donkiekampkop, 14 km north of Britstown, just on turn off to Farm Waterval, 10 March 1988, *L. Smook 6821* (K, L, P); Pixley ka Seme, Emthanjeni, De Aar Farm, 25 km from De Aar on road to Phillipstown, April 1981, *L. Smook 3405* (L); Marydale area, Neeldale farm, Low mountain range, 1067 m, January 1996, *L. Smook 9592* (L). **ESTIWANI. Hhohho:** Lobambo, Tshaneni, 900 ft, January 1974, *S. Townsend s.n.* (K); Mbabane, 4500, ft, 03 November 1961, *R. H. Compton 30971* (K). **Mansini district:** 1500 ft, 07 February 1964, *R. H. Compton 31933* (K). **LESOTHO.** Maluti mountains, 6500 ft, s.d., *R. R. Staples 130* (K); Leribe district, LHDA Phase 1A, 2170 m, 11 January 1996, *P. B. Phillipson 4483* (K, P); Leribe district, Teyateyaneng, 5500 ft, December 1964, *A. J. Guillarmod 4826* (K); Rietfontein, Bloemhofdam Nature Reserve, 4000 ft, 25 January 1978, *J. I. de Wit 15* (K); Seaka Bridge, 10 km from Quthing on road to Mohale's Hoek, 10 December 1977, *P. C. V. du Toit 2689* (K). **USA. Arizona:** Pima County, Gila River Basin, 26 August 1940, *R. T. Clausen & H. Trapido 5185* (K); Pima County, Sabino Canyon, 26 October 1957, *P.O. Schallert 7584* (L); Chiracachua Mountains, Paradise Road, 1558 m, 29 October 1991, *M. Newman 334* (K); Chiracachua Mountains, Maxon's Peak, 5500 ft, 02 October 1907, *J. C. Blumer 1753* (K, L); Coshise County, east end of the Dos Cabezas Mountains, near entrance to Fort Bowie Area, Apache Pass, 1460 m, 09 August 1990, *J. R. Reeder & C. G. Reeder 8536* (K); St. Catalina Mountains, Giant Cachen Camp, 21 September 1913, *T. J. Stomps s.n.* (L); Yuma County, about 35 miles south of Mohawk, Tule Mountains, 14 July 1955, *H. E. Ahles 9080* (K). **Texas:** Brooks County, King Ranch, Santa Fe, Julian Pasture, 03 November 1949, *J. R. Swallen 10598* (K); El Paso County, 30 August 1915, A. S. Hitchcock 552 (K, L); Uvalde County, 05 August 1949, *Geo. L. Fisher 49200* (L); Starr County, 9.7 miles north of Junction FM2294, 21 October 1996, *W. E. Fox III 571* (L). **New Mexico:** Dona Ana County, Organ Mountains, 6000 ft, 04 September 1897, *E. O. Wootan 448* (K, P). **Florida:** Monroe County, Middle of Cape Sable, 03 November 1963, *F. C. Craighead s.n.* (L). **MEXICO. Baja California:** 24 June 1921, *I. M. Johnson 4199* (K); Isla Espiritu Santo, Bahia de Candelero, 01 November 1959, *I. L. Wiggins 15257* (K); 6.4 miles south of Todos Santos, 25 December 1958, *I. L. Wiggins 14526* (K); Arroyo de Tabor, Sierra de la Giganta, west of Puerto Escondido, 125 m, 03 December 1950, *A. Carter & L. Kellogg 2863* (K, US); Dritroto del Sur Llano de Magdalena, 11.5 km south of San Domingo, 06 December 1947, *A. Carter, A. M. Alexander & L. Kellogg 2140* (K). **Colima:** Revillagigedo Islands, Binner's Cove, 07 May 1925, *H. L. Mason 1647* (K); Revillagigedo Islands, Clarion Island, Sulphur Bay, 23 March 1932, *J. T. Howell 8362* (K); Revillagigedo Islands, Socorro

Island, Braithwaite Bay, Mesa, west side of landing cove, 28 March 1932, *J. T. Howell 8425* (K); Cerralvo Island, west side of island, about 1/3 way down from the north end, 15 April 1962, *I. L. Wiggins 17710* (US). **Chihuahua:** 16.1 km west of Balleza, 1990 m, 18 September 1991, *P. Peterson & al. 10743* (K); Meoqui, 08 August 1936, *H. Lesueur 141* (K); Sierra Madre Occidental, west of Munérachi, 1200-1600 m, 07 September 1903, *P. M. Peterson 17716* (K); Guasaremos, Rio Mayo, 3500-4000 ft, 28 September 1936, *H. S. Gentry 2890* (K). **Coahuila:** La Rosita, 85.4 km northwest northwest of Muzquiz, on highway 53 towards Boquilla del Carmen, 810 m, 12 September 1991, *P. Peterson & al. 10575* (K). **San Luis Potosí:** Sierra de Alvarez, between Santa Maria del Rio and Tierra Nueva, 1700-1800 m, 07 September 1954, *E. R. Sohns 1121* (K, P); Morales, August 1876, *Dr. J. G. Schaffer 7057* (K). **Jalisco:** between Acatlán and the basin of Laguna de Atotonilco, about 25 miles southwest of Guadalajara, near El Molino, 1650 m, 02 October 1952, *R. McVaugh 13323* (K); Bolaños, 10-19 September 1897 (K); Tecalitlán, Barranco de San Juan de Dios, near Los Corales, Sierra de los Corales, 1300 m, 23 October 1963, *J. Rzedowski 17361* (US). **Nayarit:** 10 miles southeast of Tepic, 1650 m, 06 October 1952, *R. McVaugh 13383* (K); Punta Mita: 23 July 1932, *J. T. Howell 10385* (K, US). **Guanajuato:** about 8 km west of San Felipe, 27 October 1952, *E. R. Sohns 464* (K); about 2 km northeast of San Miguel, on top of Cerro de la Presa, 01 November 1952, *E. R. Sohns 513* (K, US). **Tamaulipas:** Mpio, Matamoros, Isla Mula, east of Santa Teresa, 5 m, 27 September 1981, *P. A. Fryxell 3734* (K). **Morelos:** Xochitepec, Mor, 24 September 1938, *E. Lyonnet 2637* (K, US); between La Concepcion and Aldama, on the Aldama-Soto la Marina road, 50-150 m, 27 September 1956, *F. M. Martinez & G. B. Luyando F-2191* (K); Yautepec, Canyon del Lobo, 6 miles west of Yautepec, 1372 m, 12 August 1970, *P. J. Lyons 97* (US); Sierra de San Carlos, El Rosario, vicinity of Marmolejo, 701 m, 10 August 1930, *H. H. Bartlett 10870* (US). **Zapotitlan:** 2.2 km from Colonia San Martin towards Caltepec, 1700 m, 15 September 1902, *J. I. Calzada 23244* (K). **Sonora:** El Rancho de la Nacha, 25 miles west of La Angostura, 4300 ft, 14-20 August 1941, *J. V. Santos 1809* (K, US); Bavi Cora, in canyon west of Rio de Sonora, 17 November 1939, *F. E. Drouet, D. Richards & W. A. Lockhart 3630* (US); region of the Rio de Bavispe, El Rancho del Cumarito, Sierra de la Cabellera, 1189 m, 05 October 1941, *J. V. Santos 2073* (US). **Oaxaca:** 42 km from Oaxaca, on road to Mexico City, 1820 m, 11 December 1963, *H. S. McKee 11025* (K, P). **Tabasco:** Tenosique, Estapilla, 27 June 1939, *E. Matuda 3509* (K). **State of Mexico:** Temascaltepec, Luvianos, 1100 m, 05 December 1933, *Geo. B. Hinton 5306* (K); Temascaltepec, Chorrera, 1080 m, 24 September 1932, *Geo. B. Hinton 1821* (K). **Guerrero:** Pungarabato, Coyuca, 02 October 1934, *Geo. B. Hinton 6700* (K). **Puabla:** Manzanilla, 14 August 1909, *Nicolas s.n.* (P). **Michoacán:** Cerro Potrerillos, about 5 miles north of Cotija, 1829-1890 m, 05-06 October 1961, *R. M. King & T. R. Soderstrom 4666* (US). Hidalgo: Metepec, from Tenango de Doria, 10 km east of Metepec, 2240 m, 07 August 1980, *R. Hernández-Magaña & J. V. Hernandez 4713* (US). **HONDURAS. Yoro:** Morazán, 10 km south of La Venta, 870 m, 20 June 1970, *R. W. Pohl & G. Davidse 12015* (K). **GUATEMALA. Huehuetenango:** Huehuetenango, 1350 m, 17 August 1942, *J. A. Steyermark 50762* (K). **NICARAGUA. Léon:** Santa Clara Volcano, near Highway 26, 600 m, 19 July 1970, *R. W. Pohl & G. Davidse 12376* (K). **Rivas:** Omotepe Island, 500 m, October 1869, *P. Levy 1148* (P). **HONDURAS. Madriz:** 12 km south of Ocotal, 680 m, 06 July 1970, *R. W. Pohl & G. Davidse 12193* (K). **BELIZE. Cayo:** Millionario-Augustine Road, north bank of Macal River, near Guacamallo bridge, 1400 ft, 21 November 1968, *R. R. Innes RRI24* (K). **PUERTO RICA. Cabo Rojo:** Boqueron, slopes just west of Punta Melones, 50 m, 05 February 1995, *F. Axelrod & A. Axelrod 8741* (K, US). **ANTIGUA AND BARBUDA. Saint Paul:** Sugar Loaf Mountain, 13 September 1931, *H. E. Box 71* (K, L) **SAINT KITTS AND NEVIS. Saint John Capisterre:** Morne Hills, near Frigate Bay, 250 feet, 26 January 1932, *H. E. Box 154* (K). **ANTILLES. Lesser Antilles:** Martinique. Commune de Bellefontaine, towards Vétiver, 175 m, 15 November 1916, *C. Delnatte, G. Viscardi & C. Potiron 3664* (P); Curaçao, s.d., *I. Boldingh 4784* (L). **GUADELOUPE. Saint-**

Barthélemy Island: Charwelle, 08 January 1952, *C. Le Gallo 208* (L); St. Jean, 12 February 1952, *C. Le Gallo 480* (L); Pointe de Chauvette, 50 m, 30 September 1952, *C. Le Gallo 1023* (L). **Basse-Terre:** Baillif, Vieux-Habitants, 25 m, 11 September 1934, *H. & M. S. 713* (P). **BRAZIL. Northeast:** Maranhão, Loreto, region between the Balsas and Parnariba Rivers, 35 km south of Loreto, west of main house of Fazzanda Morros along trail to Gigante, 300-350 m, 25 February 1970, *G. Eiten & L. Eiten 10790* (K). **Center-West:** Goiás, Luziâna, 08 April 1898, *A. Glaziou s.n.* (P). **GUYANA. Upper Takutu-Upper Essequibo:** Rupununi District, foot of Mount Shiriri, 140 m, 16 June 1995, *M. J. Jansen-Jacobs & al. 4116* (K, L, P); basin of Rupunubni River, near mouth of Chairwair Creek, 1-4 November 1937, *A. C. Smith 2363* (K, L, P); Rupununi Savanna, Febuary-March 1952, *Ir J. G. P. Driven LP174* (L). **CUBA. Santiago de Cuba:** on the top of the hill La Pedreda, 28 September 1916, *E. L. Ekman 7754* (K). **Sancti Spíritus:** Sancti Spíritus, 27 August 1909, *F. Léon s.n.* (P). **JAMAICA. Manchester:** May Hill, Lititz, 300-900 m, 07 July 1914, *W. M. Harris 11738* (K). **St. Andrew:** Hope Botanical Gardens, 600 ft, 10 July 1958, *A. D. Skelding 4816* (K); Surrey, Gordon Town, 30 September, *A. S. Hitchcock 9374* (L); Hall's Delight, 750 ft, 10 October, *W. M. Harris 11259* (P). **St. Catherine:** the Portland Bight Protected Area, Hellshire Hills, 31 October, *W. M. Harris 11351* (K, L). **HAITI. West Region:** Prince-au-Prince, 03 July 1941, *H. H. Barlette 17487* (K). **ECUADOR. Loja:** Catamayo, 1300 m, 17 February 1987, *I. Grignon 84251* (K); close to bridge across Río Limones, Cariamanga-Amalusa Road, 20 March 1998, S. Laegaard & al. 18571 (K, L); 8 km west of Malacatus, on road to Purinuma and Gonzanama, 1600 m, 01 June 1990, *P. M. Peterson & E. J. Judziewicz 9449* (K, US); San Pedro de la Bendita, Catcocha KM 6, 2000 m, 29 April 1992, *S. Laegaard 102515* (K). **Azuay:** at bridge of Panamerica across Río Leon, 1800 m, 27 March 1999, *S. Laegaard 19713* (K); 10.2 km north of Ona, on the Panamerica Highway, at the bridge crossing Río Leon, 1880 m, 24 April 1990, *P. M. Peterson, C. R. Annabel & M. E. Poston 8916* (K). **EI Oro:** below Piñas, 750 m, 20 March 1955, *E. Asplund 15846* (K). **Chimborazo:** Cañon of the Río Chanchan, near Huigra, 4000-4500 ft, 7-14 May 1945, *W. H. Camp E3207* (K, P). **Imbabura:** Near Lake Cuicocha, 3000-3100 m, 14 March 1988, *S. Laegaard & S. Renvoize 70883* (L). **VENEZUELA. Sucre:** Peninsular de Araya, 6 km west of corner where road from Cariaco to Chacopata meets ocean, 100 m, 18 May 1981, *R. Liesner & A. González 11984* (K). **COLOMBIA. Andean Region:** Huila, 3 km southeast of Neiva, 1700 ft, 23 February 1945, *E. L. Little, Jr. & al. 9481* (K); Huila, upper basin of Río Magdalena, 6 km north of Villavieja, near camp Cerbatana, 400 m, 20 July 1983, *S. G. Smith, 1224* (K); Boyacá, Sachica, Parque de Los Olivares, 2400 m, 23 July 1983, *J. R. I. Wood 3893* (K). **Caribbean Region:** Magdalena, Santa Marta, July 1903, *H. H. Smith 191* (K). **PERU. Cajamarca:** Jaen, 1 km north of Chamayo on Highway 5N towards Jaen, 500 m, 23 March 2000, *P. M. Peterson & N. Refulio Rodriguez 15049* (K); 30 km from Celendin towards Río Marañon, 2300 m, 23 March 1988, *S. A. Renvoize & S. Laegaard 4890* (K). **La Libertad:** Santiago de Chuco, 22 km east of Huamachuco on road towards Sarin above Río Chusgon, 2500 m, 29 March 1997, *P. M. Peterson & N. Refulio Rodriguez 13983* (K). **Ancash:** Sihuas, just west of junction of Río Sihuas and Río Chinchobamba, 7 km south of Sihuas on road towards Pomabamba, 2520 m, 24 March 1997, *P. M. Peterson & N. Refulio Rodriguez 13910* (K). **Huánuco:** Huánuco, 7000 ft, 05-08 April 1923, *J. F. Macbride 3239* (K). **Cusco:** Cusco, Anta, Limatambo, Mollepata, 963 m, January 1904, *W. Galiano 5504* (L). **BOLIVIA. La Paz:** Sud Yungas, Chicaloma, 1700 m, 06 February 1996, *St. G. Beck 22566* (K); Larecaja, Sorata, between Poquerani and San Pedrol, 2700 m, March 1861, *G. Mandon 1387* (L, P). **Tarija:** Avilez, Ventolera, 26 km of Tarija to Padcaya, Zona El Angosto, 1692 m, 14 February 1908, *M. Mendoza & al. 2846* (K); Cercado, near Tolomosa Chico, Paz Property, 1900 m, 02 January 1986, *E. Bastian 385* (K); Cercado, Camino Junacas, 3 km after St. Ana, 1980 m, 14 May 1986, *E. Bastian 1280* (K). **Cochabamba:** Narciso Campero Leyes, Soto Loma community, 2200 m, 17 February 1990, *R. C. Pardo 63* (K). **Chuquisaca:** Camataqui, 2500 m, 10 February 1904, *M. Fiebrig s.n.* (L, P). **ABC ISLANDS. Sint Eustatius:** near

Boven, 200 m, 30 June 1906, *I. Boldingh 1238* (L). **ARGENTINA. Córdoba:** Sierra de Pocho, Route 20, 05 December 1958, *Rosengurtt 7618* (K) San Roque Lake, 28 January 1876, *G. Hieronymus 374* (P). **San Luis:** La Capital, Cerro "El Linco" exposicion NO, 30 October 1968, *D. L. Anderson & E. B. Pontis 1364* (K). Corrientes: Empedrado, Estancia Las Tres Marias, 03 August 1956, *T. M. Pederson 3782* (K, L, P). **La Rioja:** General Ocampo, Dique de Anzulón, surrounding of the wall, 25 March 1977, *F. Biurrun, R. Montes de Oca & R. Corzo 741* (P). **PARAGUAY. Presidente Hayes:** Menno, Nueva Vida Mission, 02 February 1976, *P. Arenas 1517* (K). **Concepción**: Villa Concepción, 23 March 1876, *B. Balansa 220* (L). **Chaco:** Zalazar, 10 January 1952, *Rosengurtt 6067* (P).

B. ***Heteropogon triticeus***

INDIA. Central Province: Khanduma District, September 1888, A. R. Lowrie 8514 (K); **Maharashtra State:** Mumbai, Khandala, Monkey Hill, October 1945, *H. Santapau s.n.* (K); Mumbai, Khondala, St. Xavier Villa, October 1908, *E. Blatter 9390* (K); Mumbai, Satara, November 1908, *W. A. Talbot s.n.* (K); Puna, 13 December 1953, *H. S. Gentry 13245* (K). **MYANMAR. Magway:** near Obauk, November 19xx, *U Thein Lwin 2921* (K); **Central Northwestern:** Sagaing, 1200 ft, October 1928, *Sulwr 7876* (K). **SRI LANKA. Central Province:** Kandy District, near Madugoda, about 18 miles east of Kandy on Mahiyangana road, 800 m, April 1970, *F. W. Gould 13382* (K); Kandy District, about 8 miles northeast of Hunasgiriya, near mile post 29/10 along the Kandy-Mahiyangana Road, 810 m, November 1974, *G. Davidse & A. H. M. Jayasuriya 8407* (K). **THAILAND. Chiang Mai:** Chiang Dao, 27 September 1957, *K. Bunchuai 695* (K); Doi Suthep, 550 m, 16 October 1958, *T. Sørensen, K. Larsen & B. Hansen 5722* (K). **Sakaeo:** Watana, 15 October 1928, *Put 1959* (K). **Petchaburi:** Tung Luang, 1100 m, 05 November 1931, *A. F. G. Kerr 20602* (K). **Chaiyapum:** between Tung Kramang and Nam Pherm, 700 m, 16°20' N 101°45' E, 18 December 1971, *C. F. van Beusekom, C. Phengkhlai, R. Geesink & B. Wongwan 4411* (K). **Kanchanaburi:** Khao Salop National Park, 18 November 1970, *M. Lazarides 7425* (K). **INDONESIA. Maluku:** Aru Islands, Pulau Trangan, Meroor, sea level, 6°50' S 134°20' E, 14 April 1993, *M. van Balgooy & J. Mamesah 6261* (K); Maluku Barat Daya, Wetar, 650 m, 06 April 1939, *S. Bloembergen 3609* (K). **East Java:** Situbondo, Besuki, 19 April 1920, 200-300 m, *C. A. Backer 30763* (K). **East Nusa Tenggara:** Sumba, Lewa, 400 m, 27 May 1950, *Monod de Froideville 1797* (K). **PAPUA NEW GUINEA. Western Province:** Fly River, April 1936, *L. J. Brass 6538* (K). **AUSTRALIA. Queensland:** Mackay Region, Sarina, 50 ft, 14 January 1931, *C. E. Hubbard & C. W. Winders 6504* (K); between Ingham and Toobanna, 35 ft, 26 January 1931, *C. E. Hubbard & C. W. Winders 6926* (K); Palm Island, 01 April 1931, *T. L. Bancroft s.n.* (K); Shire of Flinders, Torrens Creek, 19 March 1933, *C. T. White 8728* (K); Cook District, Crest of Newcastle Range, West of Einasleigh, 660 m, 14 July 1954, *S. T. Blake 19527* (K); Lockerbie, 10 miles West Southwest of Somerset, 30 m, 23 April 1948, *L. J. Brass 18371* (K); Portland Roads, 20 m, 31 May 1948, *L. J. Brass 18947* (K); Cook District, Springmount Station, about 13 km from the Mareeba-Dimbulah Road, On the road to Collins Weir, 580 m, 17°13' S 145°17' E, 19 April 1983, *J. R. Clarkson 4606* (K); Burke District, near source of Poison, creek about 90 miles north of Hughenden, 12 April 1935, *S. T. Blake 8610* (K); Cook District, Cairns, 15 June 1935, *S. T. Blake 9419* (K); Port Curtis District, near Rockhampton, 300-700 ft, 04 March 1935, *S. T. Blake 7892* (K); Cook District, Cairns, Yorkey's Knob Beach, 13 April 1962, *H. S. McKee 9023* (K).

C. ***Themeda anathera***

PAKISTAN. Khyber-Pakhtunkhwa Province: Lower Dir District, Chakdara, 10 July 1995, *S. Harris 16770* (K); Kurram District, Kurram Valley, 1894, *Harsukh 15511* (K); Manshera, About 34 miles from Balakot to Kaghan Road, October 1970, *S. A. Farooqi & M. Qaiser*

3355 (K); Hazara, Khanpur, 14 September 1959, *R. R. Stewart 28905* (E); Hazara, Nilishang, 4000 ft, 23 September 1958, *L. B. Burtt B1400* (E); Mansehra, Kaghan Valley, 15 August 1996, *Zuayat 20362* (IBSC) **Punjab Province:** Faisalabad District, March 1960, *A. Jalis 1300* (E); Rawalpindi District, Bhurban, 11 September 1959, *R. R. Stewart 5317* (E); Kulu, Banjar, 5000 ft, 06 November 1931, *W. Koelz 3127* (E); Jhelam District, Chakwal Subdistrict, Choya Ganjali Shah, 14 October 1902, *J. R. Drummond 14754* (K); Faisalabad, 05 March 1960, *A. Jalis s.n.* (E). **Islamabad Capitol Territory:** Margalla Hills National Park, Margalla Hills, North of Rawalpindi, March 1928, *R. R. Stewart 9556* (K). **INDIA. Arunachal Pradesh State:** Lohit District, Di Chu, Lohit Valley, 4500 ft, 14 July 1950, *F. Kingdon-Ward 20081* (K). **Uttarakand State:** Dehradun District, Mussoorie, September 1999, *J. F. Duthie 3043* (K); below Mussoorie, Alglar River Valley, 4000 ft, 01 August 1931, *R. R. Stewart 12333* (K); Valley of Flowers, Bhyundar Valley, 20-2600 m, 19 October 1962, *U. C. Bhattacharyya 24548* (K); Kumaon, Almora District, 5300 ft, *s.d.*, *R. Strachey & J. E. Winterbottom 932* (K); Kumaon, Nainital, 1650 m, July 1970, *M. L. Sharma 234* (K); Tehri, 4000 ft, 14 September 1948, *Thakur Rup Chand 1099* (K); Dehradun District, Mussoorie, Gracemount, July 1915, *A. Audesu 113* (E); Juansar, Mundali to Kathian road, 8000 ft, 24 September 1936, *M. B. Raizada 7335* (E); **Jammu and Kashmir:** Baramulla District, Tangmarg, 6000 ft, 17 August 1956, *O. Polunin 56/410* (E); Anantnag District, Upper Bringhi Valley, 7000 ft, 01 September 1940, *F. Ludlow & G. Sherriff 8040* (E); **Himachal Pradesh State:** Karsog, October 1987, R. McBeath 01933 (E); Chamba, Dalhousie, 6000 ft, 19 September 1874, *C. B. Clarke 22723* (E). **NEPAL. Dolpa District:** Karnali Zone, 2200 m, 83° 50’ E 28° 50’ N, 11 October 1991, *M. Minaki & al. 9109313* (E); Karnali Zone, Thuli Bheri River, 2310 m, 28° 53’ 58’’ N 82° 58’ 42’’ E, 02 September 2014, *C. A. Pendry& al. BRD B120* (E). **Karnali Province:** Mugu District, Mugu Karnali Valley, between Lumsa and Mangri, 7000 ft, 15 August 1952, *O. Polunin, W. R. Sykes & L. H. J. Williams 5235* (E). **Mustang District:** between Ghasa and Kaiku, about 2050 m, 14 September 1981, *M. A. Farille 81-295* (E); **Myagadi District:** Tatopani, about 1190 m, 12 September 1981, *M. A. Farille 81-276* (E, K); Dhaulagiri Zone, 1400 m, 83° 35’ E 29° 30’ N to 83° 40’ E 29° 30’ N, 04 September 1988, *M. Suzuki & al. 8881740* (E); Dhaulagiri Zone, 1265 m, 28° 29’57’’ to 36° 00’ 05’ N to 83° 38’ 16’’ to 39° 00’ 30’ E, 18 September 1995, *M. Mikage & al. 9552244* (E); Dhaulagiri Zone, 1390 m, 83° 42’ E 28° 24’ N to 83° 39’ E 28 30’ N, 27 July 1996, *T. Hoshino & al. 9670024* (E); Dhaulagiri Zone, Beni, Kali Gandaki River, 2500 ft, 04 September 1954, *J. D. A. Stainton, W. Sykes & J. Williams 7031* (E); near Lumsum, 6000 ft, 26 August 1954, *J. D. A. Stainton, W. Sykes & J. Williams 4025* (E); near Mayangdi Khola, 4000 ft, 28 October 1954, *J. D. A. Stainton, W. Sykes & J. Williams 9175* (E); Ghasa (South of Tukucha), Kali Gandaki, 7500 ft, 05 July 1954, *J. D. A. Stainton, W. Sykes & J. Williams 1571* (E).

D. *Themeda arguens*

INDIA. Andaman and Nicobar Islands: South Andaman District, Ferrargunj Tehsil, Aniket, December 1893, *King’s Collector s.n.* (K); South Andaman, Port Blair, Dhanikhari Dam, about 25 m, 13 November 1977, *N. P. Balakrishnan & al. 6290* (IBSC). **SRI LANKA. Central Province:** Kandy, Peradeniya Botanic Garden, 500 m, 05 January 1970, *D. Clayton 5035* (US). **North Central Province:** Polonnaruwa, Alut Oya, 91 m, 29 November 1969, *T. R. Soderstrom & S. Kulatunge 1757* (US). **Uva:** Monaragala, 4 miles north of Wellawaya, 100-200 m, 19 April 1970, *F. W. Gould 13489* (US). **THAILAND. Chumphon Province:** Pathiu, Bang Son, January 1927, *A. F. G. Kerr 11322* (K). **Kanchanaburi Province:** Mueang, Ban Kao, November 1961, *K. Larsen 8146* (K); Huay Bankau, November 1971, *C. F. van Beusekom & al. 3603* (K). **Amnat Charoen Province:** 6 km south of Khammarat, October 2001, *S. Laegaard & al. 21855* (K). **Petchaburi Province:** December 1926, *A. F. G. Kerr 11090* (K). **Saraburi Province:** Kaeng Khoi, December 1923, *A. F. G. Kerr 7956* (K).

Prachuap Khiri Khan Province: Hua Hin, December 1927, *A. F. G. Kerr 13520* (K). **Chiang Mai Province:** at pass about 25 km along road Mae Rim to Samoeng, October 2001; **Chonburi Province:** Siracha District, Mount Khao Kheow, 13°16' N 101°05' E, 100 m, 23 October 1976, *J. F. Maxwell 76-690* (L). **Trang Province:** Palien, Lipang, Ban Tahkao, 25 m, 21 November 1986, *J. F. Maxwell 86-960* (L); Udon Thani: Ban Phue, Ban Klang Yai Village, along route 2348, between km 9 and 10, 177 m, 17°43'49"N 102°23'45"E, 29 November 2013, *P. Traiperm & al. 595* (BKF, MO). **LAOS. Champasak Province:** Pakse District, route from Pakse to Paksong, 23 November 1938, *E. Poilane 28514* (K, L)**. CAMBODIA**. **Kratié Province:** Sambour District, Mekong River, Rohng Ngiew Island, east side at Wae Wah, 30 m, 15 November 2006, *J. F. Maxwell 06-852* (L). **VIETNAM. Southeast Region:** Saigon, Cholon (Chợ Lớn), 02 November 1886, *B. Balansa s.n.* (L); Saigon, June 1909, *A. C. d' Alleizette s.n.* (L). **Dong Nam Bo Region:** Bà Rịa-Vũng Tàu Province, Vũng Tàu (Cap Saint-Jacques), 02 January 1971, *Nguyen van Khiêm s.n.* (L). **South Central Coast Region:** Bình Thuận Province, Phan Thiết, 27 October 1924, *F. Evrard 1607* (L). **MALAYSIA. Selongor State:** University of Malaya, Kuala Lumpur campus, March 1979, *Benjamin C. Stone 14058* (L). **Johor State:** Segamat District, 26 October 1965, *John Carrick 1412* (K, L). **Negeri Sembilan State:** Tampin, Tebong, 25 April 1939, *Forest Research Institute KEP FRI 19836* (L); **Penang State:** George Town, George Town Botanical Garden, 17 January 1950, *S. J. van Ooststroom 12509* (L). **Sabah State:** Elopura Forest District, Lubang Batu, Sandakan, January 1950, *Kadir A2690* (L). **SINGAPORE**. **Bukit Timah District:** Bukit Timah Forest Reserve, at railway bridge, January 1950, *J. Sinclair s.n.* (L). **INDONESIA.** Sumatra, November 1876, *E. de la Savinierre s.n.* (K)**; East Java Province:** Lumbang, August 1922, *J. Jeswiet 188* (WAG); Sumenep Regency, Kangean Islands, 1920, *C. A. Backer 28018* (L); Sampang Regency, Madura (Madoera) Island, Karang Pinang, 1910, *C. A. Backer 20088* (L); Pasuruan (Pasoeroean), Loembang, 12 April 1925, *J. Jeswiet 704* (WAG). **West Java Province:** Cianjur Regency, Cipanas, LPH Research Garden, 7 April 1972, *A. P. Everaarts 43* (WAG); Bogor, 06°35'22" S 106°47'28" E, 01 September 1899, *H. Dihm s.n.* (L); Sumedang Regency, West Preanger, Cikeruh (Tjikeroeh), 10-235 m, 14 April 1938, *P. F. Franck 88*; **West Sumatra Province:** Padang, Faculty of Medicine (Komplex Facultas Kedokteran), 00°57'00" S 100°20'59" E, 4 October 1998, *H. Siwon 1032* (L); Padang, near campus of Andalas University, about 13 km east from Padang city, Limau Manih, 04 September 2010, *Nurainas & J. F. Veldkamp 2360* (L). **East Nusa Tenggara Province:** Sumba, Waikabubak, 31 May 1950, *C. Monod de Froideville 1916* (L); Sumba, between Waingapu and Melolo, June 1950, *C. Monod de Froideville 1994* (L); Timor, South Central Timor Regency, between Soe and Kapan, May 1950, *C. Monod de Froideville 1495* (L). **Papua Province:** Jayapura Regency, Sentani, Cyclops Mountains, August 1957, *D. Veemantri 18* (L). **West Papua Province:** Manokwari Regency, Bukit Bamsam, between Sungai Apni and Kampong Anjai II, 00°48'00'' S 133°04'0'' E, 620 m, 15 May 1994, *M. J. S. Sands 6650* (K, L); Manokwari Regency, Kebar Valley, Andjai village, 550 m, 12 September 1954, *C. B. W. Versteegh 715* (L). **Jakarta Province:** North Jakarta, Port of Tanjung Priok, 23 June 1946, *A. G. de Wilde 2947* (L). **South Sulawesi Province:** Lombasang, 05°15'43" S 119°51'07" E, 23 May 1921, H. A. *B. Bünnenmeijer 11688* (L). **Central Sulawesi Province:** between Palu and Parigi, 30-40 km from Palu, 00°52'59" S 120°00'00" E, 16 April 1975, *W. Meuer 9262* (L). **Bangka-Belitung Province:** West Bangka Regency, Muntok (Mentok), 10 October 1917, H. A. B. *Bünnenmeijer* 1397 (L); Bangka Island, Muntok, 10 m, 10 October 1917, *H. A. B. Bünnemeijer 1397* (L). **Maluku Province:** Aru Islands Regency, Palau Trangan, between Kerei and Beltubun, 5-10 m, 06° 45' 00'' S 134° 19' 59'' E, 18 April 1993, *M. M. J. van Balgooy & J. A. B. Mamesah 6369* (L). **North Maluku Province:** Ternate, Lagoena, 300 m, 00°45'56" N 127°20'33" E, 05 May 1920, *V. M. A. Béguin 642* (L). **North Sumatra Province:** Medan, 15-20 m, 18 January 1928, *J. A. Lörzing 12895* (L); Atjeh, Gunung Leuser Nature Reserve, Vicinity of Penosan, about 25 km southwest of Blang Kedjeren, 1000 m, 15 April 1975, *W. J. J. O. de Wilde & B. E. E. de*

Wilde-Duyfjes 16442 (L); Karo Regency, Brastagi, along Alasweg river to Kota Tjane, January 1923, *T. J. Stomps s.n.* (L). **THE PHILIPPINES. Central Luzon Region:** Zambales Province, Iba, Bucao, 40 m, 02 December 1988, *N. O. Aguilar 974* (L)**. Cordillera Administrative Region:** Mountain Province, Bontoc, 24 February 1914, *M. F. J. P. M. Vanoverbergh 301* (L). **Northern Mindanao Region:** Misamis Oreintal, Cagayan de Oro, Barrio Lumbia, 27-28 December 1975, *J. V. Santos 7806* (L). **TIMOR LESTE** Manatuto: Laclo, between Metinaro to Manatuto, Beheda, 08°29'48" S 125°57'02" E, 26 February 2005, *J. A. R. Paiva, P. Silveira & J. Pratas T706* (L)**. AUSTRALIA. Northern Territory:** South Bay, Bickerton Island, in the Gulf of Carpentaria, 13°45'00" S 136°05'59" E, 17 June 1948, *R. L. Specht 585* (L); Glen Luckie Creek, South of Darwin, on Stuart Highway, 24 April 1956, *N. T. Burbidge 5297* (L); Elcho Island, Warangaiyu Lagoon, 11°56’04’’ S 135°41’59’’ E, 02 July 1975, *P. K. Latz 6057* (L); East Arnhem Region, Yirrkala, 12°11’59’’ S 136°46’59’’ E, 13 August 1948, *R. L. Specht 878* (L). **Queensland:** South Kennedy, along the Mount Coolon-Suttor Development Road, 400 m south of its junction with Gunn Ck, 235 m, 21°30'00" S 147°30'00" E, 20 January 1996, *A. B. Pollock & I. G. Champion 314* (L); Cook District, Ingram Island, Sand Cay, 14°25'00" S 145°52'59" E, 2 m, 27 July 1973, *D. R. Stoddart 4078* (L); Cook District, 4.8 km north of Little Laura River, on Peninsula Development Road, 120 m, 15° 30’ 00’’ S 144° 17’ 00’’ E, 24 April 1983, *J. R. Clarkson 4785* (K, MO, IBSC)**. PAPUA NEW GUINEA. Central Province:** 10 miles north-northwest of Port Moresby, near Waigani village, Tovobada Hills area, 300 ft, 10 May 1967, *R. Pullen 6949* (K, L). **Western Province:** Mabaduan, April 1936, *L. J. Brass 6474* (L); along Arufi Road, about 2 miles east of Morehead Patrol Post, 80 ft, 02 September 1967, *R. Pullen 7237A* (L). **Madang Province:** Madang District, near Bili Bili village, on the coast south of Madang, 10 m, 03 June 1955, *R. D. Hoogland 4855* (L); Josephstaal FMA area, Josephstaal Road, near the village of Wadaginum, 04°43'59" S 145°00'00" E, 13 September 1998, *W. N. Takeuchi & E. Saxon & al. 13075* (L); Madang, Schering Peninsula, 5° 13’ 00’’ S 145° 48’ 00’’ E, 13 April 1987, *J. Lambinon 87/373* (L). **New Britain Island:** Rabual District, Keravat Plantation, 02 December 1954, *H. S. McKee 1557* (L). **NEW CALEDONIA. South Province:** Nouméa, Toutazimut, Mount Koghi, 500 m, *s.d.*, *I. Franc 348* (US). **JAMAICA.** Saint Andrew: Hope Grounds, 700 ft, 05 December 1916, *W. M. Harris 12461* (L); Prospect, near Morant Bay, 25 ft, 02 January 1913, *W. M. Harris 11538* (L, MO); Saint Thomas, southeast of Seaforth along road to Morant Bay, 20 m, 25 November 1971, *G. Davidse 3267* (MO); Saint Thomas, near White Horses, 0-10 ft, 02 January 1958, *G. Y. Truman 17872* (MO); Saint Thomas, about 2 miles east of Arcadia Junction, 100-250 ft, 18 March 1958, *G. Y. Truman 18438* (MO); Hanover, Dias, 600 ft, 19 December 1960, *C. D. Adams 8528* (MO); Clarendon, Trout Hall to Crooked River, 800 ft, 26 June 1960, *C. D. Adams 7333* (MO).

E. *Themeda arundinacea*

CHINA. Guangxi Zhuang Autonomous Province: Baise, Leye County, Tonglezhen, 750 m, 24°45'53.4" N 106°37'13.28" E, 21 January 2015, *H. Xueyan, P. Yude & W. Rongchang 451028150121002JY* (GXMG)**;** Guilin, Guangxi, Lipu, 637 m, 24°43'20" N 110°17'36" E, 08 November 2018, *Lipu County Census Team 450331181108022LY* (KUN). **Yunnan Province:** Pu’Er, 1446 m, 22°35'45" N 101°03'03.7" E, 11 June 2012, *Simao District Census Team 5308020625* (IMDY); Pu’Er, Jingdong Yi Autonomous County, Taizhongxiang, 1568 m, 24°28'01" N 100°54'33" E, 09 December 2009, *L. Zhonghua & al. JDNR09095* (KUN); Linshan, Yongde County, Dedangzhen, 1385 m, 24°01'22.8" N 99°16'52" E, 23 November 2010, *Li Yongliang & al. YDDXS0667* (KUN); Baoshan,Tengchong, Daju Town, 1747 m, 25°06'36" N 98°33'00" E, 22 November 2008, *Zhou Yingzi Zhyz-365* (KUN); near Manxicun, 1250 m, 21°43'37.89" N 100°02'21.86" E, 07 September 2012, *Menghi Census Team 5328220945* (IMDY). **INDIA. Assam State:** Palasbari, 04 November 1949, *W. N. Koelz 24173* (US). **West Bengal/Assam State:** Dooars, January 1898, *Dr. D. Prain s.n.* (L)**.**

Jharkhand State: Singhbhum District, Saranda, Karampada Plateau, 2800 ft, 3 February 1935, *H. F. Mooney 20* (K). **Meghalaya State:** Mawphlang Khasi Hills, 1829 m, 16 August 1954, *T. R. Chand 8025* (US); below Mawphlang, Khasi Hills, 1219 m, 15 September 1949, *W. N. Koelz 23971* (US). **Tripura:** Barjalai Hills, Tipperah, 396 m, 23 June 1912, *anonymous 269* (US). **Uttarakhand:** Dehradun and vicinity, Mittribbers Tea Estate, 10 October 1928, *U. Singh 484* (US). **West Bengal:** Darjeeling, Sukna, 14 December 1876, *C. B. Clarke 31741* (E). **NEPAL. Bagmati Province:** Chitwan District, Sauraha, 400 m, 5 November 1975, *A. Laurie 48* (L); Chitwan District, Chitwan National Park, Lake Lamital, 27°32'02" N 84°21'03" E, 19 November 2004, *Second Darwin Nepal Fieldwork Training Expedition A12* (E). **Sudurpashchim Province:** Suklaphanta Wildlife Reserve, Kanchanpur area of terai in far west, in mud on border of Ranital, 28°45'00"N 80°15'00"E, 30 October 1975, *C. Rice 8* (US). **Madhesh Province:** Chitwan National Park, Bhawanipur, 230 m, 27°33'00" N 84°29'00" E, 11 November 1974, *T. R. Soderstrom 2091* (US). **MYANMAR. Bago Province:** Pegu District, Pegu Township, Wungabaw, 22 January 1948, *U. Thein Lwin 433* (L). **Shan State:** Saga, *s.d.*, *A. Khalil s.n.* (US). **Sagaing Region:** Mawlaik (Upper Chindwin) District, from Chamg to Khoung Kyew and Kyokta, southeast of Mawliak, Khoduang stream near Khaung Kyew, 16-27 January 1921, *J. F. Rock 825* (US). **THAILAND. Chanthaburi:** Mueng District, Plabpla Subdistrict, 12°35'59"N, 102°9'0"E, 25 November 1970, *M. Lazarides 7488* (K, L); **Prachinburi:** Krabin Buri District, Ban Keng, 25 m, 10 November 1930, *A. Marcan 2586* (K). **Loei:** Phu Kradueng, near Rest House, 1300 m, 15 November 1954, *T. Smitinand 2106* (K); Phu Kradueng, 1200 m, 11 February 1931, *A. F. G. Kerr 20070* (K); Phu Kradueng, Wang Kuang Waterfall, 1240 m, 16°49'59" N 101°43'00" E, 31 August 1988, *H. Koyama T61464* (L) Phu Kradueng, on the plain at its summit, 1200 m, 16°52'16"N, 101°43'07"E, 04 September 1967, *T. Shimizu, M. Hutoh & D. Chaiglom T8882* (L). **Chumphon:** Ban Pak Khlong, 20 m, 12 January 1927, *A. F. G. Kerr 11387* (K). **Chiang Mai:** Mae Rim, Above Training Center of Queen Sirikit Botanical Garden, 700-1000 m, 18°54'00"N 98°52'00"E, 05 October 2001, *S. Laegaard 21675* (K, L); Doi Suthep, 900 m, 04 March 1966, *B. Sukkri 80* (K); Mae Rim, east of nursery of Queen Sirikit Botanical Garden, 900 m, 18°53'00"N 98°52'00"E, 24 September 2001, *S. Laegaard & M. Norsangsri 21615* (K, L, US); Doi Suthep, September 1958, *Th. Sørensen, K. Larsen & B. Hansen 4731* (K); Km 24-28 along road Mae Rim-Samoeng, 1000-1100 m, 18°52'00"N 98°47'00"E, 21 October 2001, *S. Laegaard 21762* (K, L, US); Mae Tang, 47 km north of Chiang Mai, 420 m 19 October 1958, *Th. Sørensen, K. Larsen & B. Hansen 5767* (K); Mae Rim District, Doi Suthep-Pui National Park, Doi Mon Luang, above Nong Hoi Village, 1375 m, 24 December 1996, *J. F. Maxwell 96-1680* (L); Doi Inthanon, along Mae Klang Phat river, 940-1010 m, 5 August 1988, *H. Koyama T61097* (L); Doi Suthep, near Maeo village, 1300-1500 m, 19 September 1967, *M. Tagawa & al. T10518* (L); Muang, Doi Suthep-Pui National Park, east side of Palaht Temple Area, 670 m, 24 October 1993, *A. Phuakam 60* (L); Mae Tang District, Doi Chang, 1550-1600 m, 22 October 1979, *T. Shimizu & al. T20202* (L); Doi Suthep, summit of Doi Chom Cheng, 1500-1650 m, November 1920, *J. F. Rock 208* (US); Doi Suthep, Hoi Chan Kiang Camp, 600 m, 25 October – 1 November 1920, *J. F. Rock 109* (US). **Nakhon Ratchasima:** Pak Thong Chai, 200 m, 26 December 1923, *A. F. G. Kerr 8121* (K); **Chaiyapum:** Chatturat, 26 January 1931, *A. F. G. Kerr 19944* (K). **Songkla:** Tepa, 22 March 1928, *A. F. G. Kerr 14688* (K). **Lampang Province:** Wahng Nua District, Doi Luang National Park, just below the summit of Doi Luang, 1650 m, 02 July 1998, *J. F. Maxwell 98-715* (K); Muang Bahn (Pan) District, Chae Son National Park, Mae Jam Yao Village, 1225 m, 18°19'59" N 99°52'00" E, 14 December 1996, *J. F. Maxwell 96-1616* (L). **Saraburi Province:** Muang District, Sahm Lahn Forest, 75 m, 7 December 1974, J. F. Maxwell 74-1018 (L); **Lamphun Province:** Doi Khun Tan National Park, 1200-1374 m, 18°19'59" N 99°13'00" E, 05 September 1967, *M. Tagawa & al. T9268* (L). **VIETNAM. Lâm Đong Province:** Da Lat, 27 November 1924, *F. Evrard 1915* (L); 2 km south of Da Lat, 1200 m, 11°54.9’00’’N 108°26.7’00’’E, 14 November 1998, *J. B. Hacker 1610* (L). **Đắk Lắk**

Province: 15 km east of M’Drak, road to Nha Trang, 500 m, 12°41.9’00’’ N 108°47.0’00’’ E, 06 November 1998, *J. B. Hacker 1558* (L); **Southeast Region:** Ho Chi Minh City (Saigon), 01 November 1886, *B. Balansa 4* (L); Sài Gòn, 01 November 1886, *B. Balansa 70* (L). **CAMBODIA. Kampong Chhnang Province:** Hô-hhil, 04 October 1938, *Müller 415* (L); **Siem Reap Province:** Chikreng District, Chikreng Grassland, 26 April 2003, *Anonymous s.n.* (L). **MALAYSIA. Sabah State:** West Coast Division, Ranau District, about 8 miles from Kampung Merungin, 25 November 1975, *L. Madani & L. Saikeh SAN82695* (K, L); West Coast Division, Ranau District, Kampung Nabutan, 19 July 1979, *A. Gibot SAN91005* (L); Telupid District, Berkat Setia Estate, 44 m, 18 May 2012, *J. F. Veldkamp & J. B. Sugau SAN153306* (L); Kalabakan District, Hap Seng logged area, 18 November 1983, *S. Jimpin 101404* (L); Ranau District, Mamut, 15 July 1987, *Amin & Jarius SAN118218* (L). **THE PHILIPPINES. Nueva Écija Province:** Caranglan, Barrio Maringalo, 23 October 1958, *J. V. Santos 6772* (L). **Calabarzon Region:** Rizal Province, Novaliches, Hacarin Llairy Farm, 18 November 1951, *J. V. Santos 5134* (L). **Llocos Region:** Pangasinan, Rosales, 23 May 1902, *E. D. Merrill 262* (US); La Union Province, Pugo, October 1925, *A. Balbin 30205* (US). **INDONESIA. West Nusa Tenggara Province:** Sumbawa, November 1879, *P. F. A. Colfs 308* (L). **South Kilimantan Province:** Martapoera, Riam Kiwa District, Pengaron, 40 m, February 1938, *F. C. van Loenen 16* (L).

F. *Themeda avenacea*

AUSTRALIA. Western Australia: Gill Pinnacle, Rawilson Range, 24°53'32.5" S 128°46'7.3" E, 23 June 2007, *L. S. J. Sweedman 7112* (K); Bowes State Farm, 01 November 1903, *A. Morrison K252* (K).**Northern Territory:** 4 miles south of Yambah Station, near Burt Creek, 10 March 1953, *R. A. Perry 3370* (K); Ayers Rock, 19 June 1926, *H. Basedow 84* (K); Uluru National Park, Kata Tjuta, on the Docker River Road, 45 km Western Northwest of the Ranger Station, 25°18' S 130°41' E, 14 May 1988, *M. Lazarides & J. Palmer 077* (K); 29 miles southwest of Lucy Creek Station, 08 May 1955, *M. Lazarides 5226* (K); Mount Chappel Bore to Limestone Bore, near Redbank Hill, 26 September 1955, *Burbridge & Gray 4343* (K); Alice Springs, Peterman Ranges, 27 km southeast Docker Range, 25°04' S 129°11' E, 07 November 1979, *T. S. Henshall 2802* (K); Kakadu National Park, about 37 km south southeast of Jabiru, 12°58'59" S 132°55'05" E, 30 March 1981, *L. A. Craven 6636* (L). **Queensland:** Torrens Creek, 19 March 1933, *C. T. White 8736* (K); Mitchell District, Tambo-Augathella Road, 13 km from Tambo, 24°55' S 146°22' E, 18 May 1975, *B. K. Simon & J. R. Clarkson 2809* (K); Leichhardt District, Area surrounding State Wheat Board, installations Moura, 26 February 1967, *R. Henderson 206* (K); Mitchell District, Jericho and vicinity, 06 March 1946, *M. S. Clemens s.n.* (K); near Gurulmundi, *s.d.*, *E. Belson s.n.* (K); near Mundubbera, *s.d.*, *E. Belson* s.n. (K); North Kennedy District, Alpha, 1144 ft, 23 February 1931, *C. E. Hubbard 7869* (K); Leichhardt District, Dingo, by railway enclosure, 372 ft, 26 February 1931, *C. E. Hubbard 8018* (K); Maranoa District, Mungallala, 1390 ft, 31 December 1930, *C. E. Hubbard & C. W. Winders 6069* (K); Darling Downs District, between Tooburra and Rose Hill, north of Warwick, 10 March 1931, *C. E. Hubbard 5647* (K, L); Cook District, Chillagoe, 1154 ft, 22 January 1931, *C. E. Hubbard & C. W. Winders 6814* (K, L); Mitchell District, Jericho, 1200 ft, 27 November 1935, *S. T. Blake 10261* (K); Burke District, Hughenden, 1100 ft, 07 April 1935, *S. T. Blake 8456A* (K); Maranoa District, Noondoo, near Dirranbandi, 29 February 1936, *S. T. Blake 10620* (K); Darling Downs District, between Inglewood and Milmerran, 20 January 1934, *C. T. White 6753* (K); Clemont, 02 March 1927, *C. T. White 3428* (K); Mitchell District, Prairie, 1450 ft, 22 May 1936, *S. T. Blake 11596* (K); Clermont, Peak Downs, *s.d.*, *W. C. Goose 88* (K); Burke District, Fairlight Station, 34 miles north of Hughenden, 12 February 1931, *C. E. Hubbard & C. W. Winders 7480* (L); North Kennedy District, Alpaa, 23 February 1931, *C. E. Hubbard 7869* (L); Rockhampton, 23°22'49"S 150°30'21"E, *s.d.*, *R. Simmons s.n.* (L); Leichhardt

District, near Wandoan, 15 November 1930, *C. E. Hubbard 4961* (L); Mitchell District, Prairie, 01 February 1931, *C. E. Hubbard & C. W. Winders 7022* (K, L); Darling Downs District, Wyreema, 1750 ft, 17 March 1931, *C. E. Hubbard 5884* (L); South Kennedy District, Causeway-Collinsville, 20°45'00"S 147°49'59"E, 14 September 1950, *L. S. Smith 4568* (L). **New South Wales:** New England, January 1890, *F. T. McFarland s.n.* (L); Warrego District, Morven, April 1936, *S. T. Blake 11004* (K); Warrego District, Chesterton, April 1936, *S. T. Blake 11083* (K); North Kennedy District, Pentland, April 1935, *S. T. Blake 8389* (K); Maranoa District, Boatman Station, March 1947, *S. L. Everist 2929* (K).

G. *Themeda caudata*

INDIA. Meghalaya State: Shillong, Laithyngkot, 5 December 1943, *N. L. Bor* 18082; Eastern West Khasi Hills District, Mairang, 22 August 1885, *C. B. Clarke 40002A*. **Uttarakand State:** Dehradun District, Lachhiwala Range, October 1891, *J. S. Gamble 23135*; Kumaon, Valley of Sarja, 1067 m, *s.d.*, *R. Strachey & J. E. Winterbottom s.n.*; Tehri District, Senwali, 25 September 1948, *Thakur Rup Chand 1202*; Tehri District, Madhes, 2286 m, 15 October 1948, *W. N. Koelz 22198* (US).**Karnataka State:** Belgaum District, Kapoli, 1821, *anonymous s.n.* **West Bengal State:** Howrah District, Khalia, 17 October 1930, *Joseph D. Hooker s.n.* **Odisha (Orissa) State:** Kalahandi District, Upar Ampodar Valley, 23 December 1948, *H. F. Mooney 3210*. **Himachal State:** Bailadilla, 25 April 1937, *H. F. Mooney 379*. **NEPAL. Bagmati Province:** Ramechhap District, Bhuji Khola, 7000 ft, 15 October 1954, *A. Stainton, J. D. Adam, W. Sykes & J. Williams 9055* (E). **Lumbini Province:** Parasi District, Kusma, 05 September 1954, *W. L. Chew, E. J. H. Corner & A. Stainton 7048* (E, K). **BHUTAN. Tongsa District:** between Bubja and Kinga Rapden, 1950 m, 27°25’00’’ N 90°30’00’’ E, 19 September 1998, *Noltie & al. 271* (E); between Shingkhar and Thrisa, 1750 m, 07 September 2002, *K. Wangdi 2002.G37* (US). **Punakha District:** above Awakha Bridge, east of Wangdi Phodrang, 1650 m, 20 September 1998, *Noltie & al. 288* (E). **CHINA. Fujian Province:** near Fuzhou, Kuliang Hills, 305-914 m, July-August 1919, *J. B. Norton 1152* (US). **Guangdong (Kwangtung) Province:** Dinghushan (Tinghushan) Biosphere Reserve, 1978, *K. S. Chow & al. 78059* (K); Hwei-Yang District, Lin Fa Shan, Sam Hang Shek T’au Village, October 1935, *W. T. Tsang 26006* (L); 60 miles west from the Port of Shantou, 2000 ft, July 1900, *J. M. Dalziel s.n.* (L); Qingyuan, 31 October 1929, *Y. K. Wang 30249* (US).**Guangxi Province**: Baise, Tianyang District, Leixu Town, 722 m, 23°28'47.43"N 106°48'19.21"E, 14 November 2016, *Debao County Census Team 451024161114036LY* (IBK). **Guizhou Province:** Qianxinan Buyei and Miao Autonomous, Xingyi, Jushan Residential District, 1180 m, 25°05'26.76"N 104°55'20.64"E, 16 October 2011, *L. Yanchun 782* (KUN). **Hong Kong:** New Territories, Lead Mine Pass, 02 November 1971, *P. But 274* (K). **Hunan Province:** Huaihua, Hongjiang, Yuanjiang Road Residential District, 360 m, 27°07'45"N 109°59'24"E, 09 November 2008, *L. Shenghua, W. Xianjin & al. WuXJ1085* (KUN). **Jiangxi Province:** Lu Shan, Kuan Yin Ch’iao, 18 October 1932, *H. C. Cheo 478* (L); Jiujiang, Lianxi District, 94 m, 29°30'24.17"N 116°00'41.23"E, 16 November 2012, *D. Anmiao & W. Congmei TanCM1403* (KUN). **Sichuan Province:** Xichang, Nyingchi, Mêdog County, Damuluobazuxiang, 1248 m, 29°29'3.9"N 95°26'47.22"E, 15 November 2016, *G. Yongjie & al. 16CS14445* (KUN).**Yunnan Province:** Tengchong, Goaliang Shan State Nature Reserve, Taipingpu area, west side of Goaligong Shan, on the road from Baoshan to Tengchong via Dahaoping, 2260 m, 24°57’27’’ N 98°44’22’’ E, 04 September 2003, *Gaoligong Shan Biotic Survey Expedition 18720* (E); Honghe Hani and Yi Autonomous Prefecture, Mengzi, 0-1866 m, 23°27'23"N 103°38'51"E, 31 August 2011, *L. Qing & al. 213* (IBSC); Wenshan Zhuang and Miao Autonomous, Xichou County, 1120 m, 23°15'58.68"N 104°33'8.28"E, 28 October 2011, *L. Yanchun 826* (KUN). **Zhejiang Province:** Zhoushan, Dinghai District, 57.98 m, 30°04'34"N 121°51'20"E, 21 March 2013, *B. Yuke & al. BYK3803* (CSH). **SINGAPORE. Central Region:** Novena, Balestier Plain, 21

January 1994, *R. J. Hullett s.n.* **MYANMAR. Mandalay Region:** Pyin Oo Lwin District, Maymyo Plateau, 10 October 1908, *J. H. Lace 4293*; **Tenasserim Division:** Dawei (Tavoy) District, Hills west of Paungdaw Power Station, 12 miles from Paungdaw, October 1961, *J. Keenan, U. Tun Aung & R. H. Rule 1708* (E). **THAILAND. Chiang Mai Province:** Chiang Dao District, Doi Chiang Dao Hills, along road below park wardens house, 1400-1500 m, 19°22’00’’N 98°50’00’’E, 28 September 2001, *S. Laegaard & M. Norsangsri 21630* (L). **Loei Province:** Phu Kradueng, 27 November 1965, *M. Tagawa, K. Iwatsuki & N. Fukuoka T370* (K). **Kanchanaburi Province**: Thong Pha Phum, Huai Khayeng, road to Phatsadu Klang (Central Post), 24 October 2004, *S. Sirimongkol 169* (L). **Khonkaen Province:** Phu Khieo Game Reserve, about 80 km east of Petchabun, 101°58’00’’E 16°50’00’’N, 850 m, 07 November 1984, *G. Murata & al. T41624* (L). **VIETNAM. Lâm Đồng Province:** Da Lat, April 1969, *Vu-Van-Cuong s.n.* (K); Bảo Lộc, Đại Lào, Haut Donai, 900 m, 20 December 1966, *Pételot 8829* (US). **MALAYSIA. Pahang State:** Temerloh District, 21 April 1931, *R. E. Holttum 24655* (L); Pekan District, Kuala Pahang, 24 August 1935, *E. J. H. Corner 29902* (K). **Kelantan State:** Gua Musang District, Sungai Ketil, 12 August 1929, *M. R. Handerson 22675* (L); Bukit Batu Papan, Sungai Lebir, 07 July 1935, *M. R. Henderson 29594* (K). **Selangor State:** Gombak District, Ulu Klang, 03°01’59’’N 101°27’00’’E, 20 August 1953, *R. Melville 4717* (L). **Sabah State:** Tenom Forest District, Tenom Pangie, 06 June 1951, *A. Cuadra A3276* (US). **INDONESIA. West Java Province:** Tjikampek, December 1920, *Beumie 1594* (L). **North Sumatra Province:** between Porsea and Siruangkuk, 13 November 1975, *S. Soenarko 401* (L); Central Habinsaran, southeast Lake Toba, Batuhoda, 29 March 1929, *J. A. Lörzing 15442* (L); Habinsaran, Parsoburan, 13 November 1920, *J. A. Lärzinger 7771* (L). **South Sulawesi:** Masamba, northeast of Singkalong, 1100 m, 01 August 1937, *Eyma 1468* (US). **Bangka Belitung Islands:** Petaling, Pangkal Pinang, 12 November 1917, *H. A. B. Bünnemeijer 1985* (L). **NEW CALEDONIA. South Province:** Nouméa, September 1870, *B. Balansa 3074* (L).

H. *Themeda cymbaria*

INDIA. Andhra Pradesh: 6 miles east of Trivandrum, Tirumala Hill, 6 January 1934, *E. W. Erlanson 5166* (L). **Karnataka State:** Dupabarry, East slope, September 1939, *E. Barnes 823* (L); Uttara Kannada, Bailur, 24 August 1905, *C. E. C. Fischer* 333 (K). **Kerala State:** Idukki District, Munnar, 2 December 1959, *J. Christopher A401* (K). **Tamil Nadu State:** Salem District, Sanyasimalai RF, 17 September 1965, *K. N. Subramanian 1983* (L); Nilgiris District, Ooty (Ootacamund), May 1940, *E. Barnes s.n.* (K); Tirunelveli District, Sengalteri to Kalkad, 16 February 1913, *D. Hooper & M. S. Ramaswami 39277* (K); Nilgiris District, Gudalur, September 1899, *anonymous 84* (K); Gudalar, on the Nilgiris, 10 April 1900, *C. A. Barber 2644* (US); Nilgiris District, Periyashola, 18 June 1898, *anonymous s.n.* (K); Erode District, Sathyamangalam, March 1902, *B. Oollu 6404* (K); Erode District, Thalavadi Taluk, Hassanur, 914 m, 09 March 1931, *K. C. Jacob 153* (US); Coimbatore District, Bahvani Range, Burgur Hills, March 1902, *A. G. Bourne 6428* (K); Dindigul District, Kodaikanal, Palamai-Machur slopes, 12 August 1987, *K. M. Matthew & K. T. Mathew 50105* (K); Nilgiris District, Nilgiri Hills, Kunjapani Village, 19 February 1937, *W. Koelz 11074* (K). **SRI LANKA. Central Province:** Matale District, Erawalagala Mountain, just east of the Kandalama Tank, about 6 miles directly east of Dambulla, 29 October 1974, *G. Davidse & D. B. Sumithraarachchi 8096* (K, MO, US); Nuwara Eliya District, Hakgala, 17 February 1970, *D. Clayton 5789* (K, US); Kandy District, Hairpin bends west of Mahiyangana, 19 February 1970, *D. Clayton 5856* (K, US). **North Central Province:** Anuradhapura District, Mihintale, top of hill, 16 January 1970, *D. Clayton 5318* (K, US); Anuradhapura District, Ritigala Strict Natural Reserve, 198 m, 09 August 1973, *A. H. Jayasuriya 1288* (US). **Uva Province:** Moneragala District, about 11 miles west of Tanamalwila, 24 November 1974, *G. Davidse & D. Bhithiya Sumithraarachchi 8808* (K, L, MO, US); 4 miles north of Wellawaya (about 56 miles north of

Hambantota), trunk road A4 marker 135/3, 19 April 1970, *Frank W. Gould 13491* (K, US); Monaragala District, Nilgala, Galoya National Park, 1 May 1975, *A. H. M. Jayasuriya 1965* (K, US); about 15 miles southwest of Badulla, about ½ mile below Ella Rest House, 8 April 1970, *F. W. Gould 13328* (K, US); Monaragala District, near Badalkumbura 17 February 1970, *D. Clayton* 5798 (K); **Southern Province:** Sinharaja Forest, near Weddagalle, November 1978, *A. J. G. H. Kostermans 27160* (L).

I. *Themeda gigantea* var. *gigantea*

THE PHILIPPINES. Central Visayas Region: Negros Oriental Province, Siaton, Barrios Bundo, 06 August 1980, *Jose Vera Santos 8262* (L); Negros Oriental Province, Mount Katugasan, March 1954, *G. E. Edaño 21790* (L); **Eastern Visayas Region:** Eastern Samar Province, Suluan Island, 20 March 1996, *Franz Seidenschwarz 06-01* (L). **Western Visayas Region:** Panay Island, southwestern range of Mount Baloy, Anunang, 5.5. km south of Lublub, 04 August 1987, *G. S. Varadarajan & al. 1509* (L). **Bicol Region:** Sorsogon Province, Irosin, Mount Bulusan, July 1916, *A. D. E. Elmer 16764* (L); Albay Province, Taqui River, San Bernardo, Tiwi Side, 27 October 1995, *Reynoso, Sagcal & Fernando 21295* (L). **National Capital Region:** Quezon City, Mesa Heights Station, *Jose Vera Santos 4009* (L). **Mimaropa Region:** Oriental Mindoro Province, 2 km west of Puerto Galera and vicinity, 03 May 1952, *Jose Vera Santos 5303* (L); Oriental Mondoro Province, Mount Badyang, 30 April 1958, *H. C. Conklin 37923* (L); Palawan Province, Aborlan, Malasgao River, March-April 1951, *G. E. Edaño 14090* (L). **Cordillera Administrative Region:** Mountain Province, Bontoc Subprovince, 13 May 1953, *Jose Vera Santos 5743* (L); Mountain Province, Bontoc Subprovince, 07 May 1914, *Father Morice Vanoverbergh 410* (L); Ifugao Province, Banaue, Batad, 14 January 1963, *H. C. Conklin & Buwaya 78734* (L); Ifugao Province, Lloge Banaue, 31 July 1961, *H. C. Conklin & Del Rosrio 72644* (L). **Calabarzon Region:** Batangas Province, August 1914, *M. Ramos 1864* (L); Laguna Province, Santa Cruz, Acoje Mine Concession Area, 25 May 1986, *C. E. Ridsdale 1512* (L); Rizal Province, Antipolo, November 1909, *M. Ramos 127* (L). **Cagayan Valley Region:** Cagayan Province, San Juan, Santa Praxedes, 11 August 1995, *Garcia, Fuentes & Romero 18444* (L); Santa Ana, Palaui Island, San Vicente, 14 December 1995, Barbon, *Garcia & Romero 18885* (L). **Northern Mindanao Region:** Bukidnon Province, Impasugong, along Atugan Kanyon, 13 May 1960, *J. V. Santos 6926* (L). **INDONESIA. West Java Province:** way up to Tjibodas (Cibodas), 03 July 1923, *T. W. A. Stomp s.n.* (L); Bogor (Buitenzorg) City, on the river Tjilivong, 14 December 1893, *V. Schiffner 1586* (L). **North Sumatra Province:** Medan, 20 March 1928, xxxx s.n. (L); Medan, 20 March 1928, *J. A. Lörzing 13010* (L). **PAPUA NEW GUINEA. Morobe Province:** Morobe, January 1948, 07°45’00’’S 147°35’00’’E, *J. Womersley NGF2949* (LAE).

J. *Themeda gigantea* var. *intermedia*

CHINA. Guangdong Province: Tingwushan, March 1978, K. *C. Ting & K. L. Shih 1076* (L)**. INDIA. Assam State:** Umran, Mount Khasia, *s.d.*, *J. D. Hooker s.n.* (L). **Meghalaya State:** Khasia Hills, Pomrang, September 1852, *J. D. Hooker s.n.* (E). **BANGLADESH. Chittagong:** Hathazari, Baluchara**,** 22°30'18" N 91°48'48" E, 17 March 1999, *M. A. Rahman 4707* (E); Jaldi, 22°20'18" N 91°49'54" E, 24 October 1920, *J. M. Cowan 1780* (E). **BHUTAN. Punakha District:** between Punakha and Lobesa, 1300 m, 03 October 1987, *J. R. I. Wood 5929* (E). **MYANMAR. Sagiang Region**: Katha District, Bilumyo Nature Reserve, 10 November 1911, *J. H. Lace 5536* (E). **VIETNAM. Ninh Binh Province:** Cuc Phuong National Park, 20°14.82'00" E 105°42.57'00" N, 08 October 1999, *N. M. Cuong, D. T. Kien & M. V. Sinh 601* (L). **MALAYSIA. Sabah State:** Kinabatangan District, along road about 5 km east of Sukau, 10 m, 13 March 2001, *S. Laegaard & al. 151185* (L); Tenom District, Agricultural Research Station, 200 m, 116°00'00" E 05°10'00" N, 28 March 2011, *S. Laegaard & al. 151327* (L). **INDONESIA. Central Kalimantan Province:** Sinting, HPH km 87, south along Sungai Posang, 100 m, 112°03'38.8" E 00°49'25.8" N, 25 April 1994, *A. C. Church & al. 1118* (L). **East Kalimantan Province:** Berau, 01 November 1963, *A. J. G. H. Kostermans 21730* (L). **East Nusa Tenggara Province:** Alor Island, Pirigomo to Lantoka, 650 m, 12 May 1938, *O. Jaag 998* (L); West Timor, between Kefamenanu and Sekon, 600 m, 20 May 1950, *C. Monod de Froideville 1690* (L); Manggarai, 750 m, 10 May 1983, *E. Schmutz 5837* (L); Flores Island, Mok, 750 m, 10 May 1983, *E. Schmutz 5837* (P). **Maluku Province:** West Serum, Seram Barat, Kaibobu, 0-100 m, 19 September 1910, *L. M. R. Rutten 1683* (L). **North Sumatra Province:** Dairi, Tanah Pinem, Pasir Tengah, 5 m, 20 May 1919, *H. A. B. Bünnemeijer 5881* (L). **Papua Province:** Balim River, 1600 m, 01 December 1938, *L. J. Brass 11678* (L); Jayawijaya, Wamena, 06 April 1973, *J. Raynal 16969* (L). **South Sulawesi Province:** Tanah Toraja, Rantepao-Palopo divide, 02 February 2004, *J. J. Vermeulen 2397* (L). **West Kalimantan Province:** Pontianak, 5 m, 28 September 1948, *M. Enoh 386* (L). **THE PHILIPPINES. Cagayan Valley Region:** Cagayan Province, Gattaran, April 1927, *J. Clemens s.n.* (L). **Davao Province:** Mount Apo, 01 June 1909, *A. D. E. Elmer 11000* (L). **Mimaropa Region:** Romblon Province, Lone District, above Magdiwang, on ridge leading to Mayos Peak, 28 August 1989, *G. Argent & E. J. Reynoso 89150* (K, L). **North Mindanao Region:** Bukidnon Province, Malaybalay, Barrio Valencia, 24 October 1957, *J. V. Santos 6583* (L); Bukidnon Province, Maramag, Farm Project of the Rice and Corn Production Administration, 31 May 1958, *J. V. Santos 4967* (L). **Palawan Province:** Palawan, lower slopes of Mount Matalingahan, Macagua River, 13 October 1994, *N. Snow & E. Sagcal 16309* (L). **PAPUA NEW GUINEA. Central Province:** Kairuku, about 5 miles north-west of Kanosia Plantation, 15 ft, 24 July 1962, *P. J. Darbyshire 723* (L). **Eastern Highlands Province:** Goroka, 5600 ft, 19 November 1954, *H. S. McKee 1302* (L). **Morobe Province:** Aseki Patrol Area, near Kwaimengu, 3800 ft, 23 April 1966, *L. A. Craven & R. Sehodda 1393* (L); Morobe, vicinity of Kajabit Mission, 07°43'39" N 147°35'53" E, 14 September 1939, *M. S. Clemens 40756* (E). **Northern Province:** about 1 km west of Devatutu Village, 10 m, 21 July 1953, *R. D. Hoogland 3400* (L). **TIMOR-LESTE. Atauro Island:** Dili, southeast side of mount Manucoco ridge, 500 m, 125°34'56" E 08°16'22" S, 13 May 2015, *I. D. Cowie & F. Santana 13824* (L). **Lautém:** Lospalos, Port Timor, Plateau of Fuiloro, site of Mehara, 400 m, 18 December 1953, *C. G. G. J. van Steenis 18089* (L). **VANUATU. New Hebrides:** Santo, Nokowoula, 1100 m, 03 September 1971, *J. Raynal 16364* (P).

K. *Themeda hookeri*

CHINA. Sichuan Province: Confluence of Wengshi river & Yangtze, 28°09’48’’N 99°24’00’’E, 15 September 1995, *Forestry Commission, Royal Botanic Garden Edinburgh to Dêqên Prefecture 245* (E); Garzê Tibetan Autonomous Prefecture, Dêrong Xian, Downstream from city of Derong towards Jinsha Jiang, along Ding Qu in deep gorge, 2315 m, 28°37'52"N, 99°17'9"E, 21 July 2004, *D. E. Boufford & al. 31057* (MO). **Tibet (Xizang) Autonomous Region:** Markam County, Ningjing Shan, Markham Range, between Mekong and Yangtze river drainages, 2880 m, 29°43’12’’N 98°52’12’’E, 14 October 1997, *R. J. Soreng, P. M. Peterson & S. Hang 5672* (K, US); Diqing Prefecture, Deqin County, on the way from Benzilan to the pass of Baima snow Mountain, at the east entrance of Baima National Park, near the Yueliang Wan, 25 July 2007, *J. Wen & al. 1272* (US). **Yunnan Province:** Tungshan, Yangtze Drainage Basin, east of Likiang, *s.d.*, *J. F. Rock* 10462 (E, K, US); North of Mosoyu (Lan Kong), 15 September 1885, *P. J. M. Delavay 1784* (P, US); Luchun, Mount Huanglianshan, Ma-yu, 840-1300 m, 29 October 1995, *S. K. Wu & al. 354* (PE); Kunming, Heilongtan, grounds the Kunming Institute of Botany, 2000 m, 20 August 1984, *B. M. Bartholomew & D. E. Boufford 1979* (E). **INDIA. Meghalaya State:** Khasi Hills, *J. D.*

Hooker & T. Thomson s.n. (L). **Sikkim State:** North Sikkim District, Lachung, 2591 m, 30 August 1892, *G. A. Gammie 1061* (K, US); Choontang, 16 September 1892, *G. A. Gammie 1243* (K, L); Gangtok District, Domang, 10 August 1943, *J. Pradhan s.n.* (K). **NEPAL. Gandaki Province:** Gorkha District, Gup, 03 August 1994, 1920 m, 28°26’00’’N 84°52’00’’E, *M. Suzuki & al. 9485256* (E); Baglung District, Plain of Dhorpatan, 2800 m, 19 August 1981, *M. A. Farille 81-208* (P). **Province No. 1:** Sankhuwasabha District, south slopes of Pawa Khola Valley, on west side of Panch Pokhari Khola, 1540 m, 27°35’00’’N 87°24’00’’E, 17 October 1991, *D. G. Long & al.* 845 (E); north of Taplejung, Thapabu Khola, Tamur Valley, 02 August 1954, *J. D. A. Stainton* 1207 (K). **THAILAND**. **Chiang Mai Province:** Chom Thong District, Mae Soi Subdistrict, Mae Soi Ridge, west of Ban Bah Gluay, 1350 m, 27 September 1992, *J. F. Maxwell 92-568* (L, P); Chiang Dao, Chinag Dao Hills, along trail above park wardens house, 28 September 2011, *S. Lægaard & M. Norsaengsri 21645B* (K). **Lampoon Province:** Doi Khun Dahn National Park, ridge above Daht Muey Falls, 825 m, 27 August 1993, *J. F. Maxwell 93-967* (K). **VIETNAM. Central Highlands Region:** Lam Dong Province, Da Lat, creek ravine of Preul, 07 December 1924, *F. Evrard 2087* (L); Lam Dong Province, 5 km South of Da Lat, 11°52’59’’N 108°27’00’’E, 14 November 1998, *J. B. Hacker 1615* (L).

L. *Themeda huttonensis*

INDIA. Assam State: banks of the Nanteilek River, near Laruri, *s.d.*, *N. L. Bor s.n.* (K). **Nagaland State:** Naga Hills, *s.d.*, *N. L. Bor 6717* (K); Akhegwo, *s.d.*, *N. L. Bor 6704* (K). **Odisha (Orissa) State:** Koraput District, near Pottangi, 10 October 1950, *H. F. Mooney 4064* (K).

M. *Themeda idjenensis*

INDONESIA. East Java Province: Semonkrong, *s.d.*, *J. Jeswiet 1940* (L, WAG); Ijen (Idjen), Gending Waloch, August 1923, *J. Jeswiet 359* (WAG); Situbondo Regency, Ijen (Idjen), on the way to the crater, 1464 m, 25 May 1931, *C. Laarman E49* (L); Idjen plateau, Mount Tenger, 11 July 1916, *S. H. Koorders & A. Koorders 42922* (L); Situbundo Regency, Besuki, Idjen Plateau, 1200-1400 m, 20 June 1918, *C. A. Backer 25150* (L); east of Pasuruan, Semongkrong, on the south slope, 25 m, 24 May 1927, *C. A. Backer 36946* (L); Situbundo Regency, Baluran National Park, at the crater of Mount Baluran, 1120 m, 23 May 1949, *F. W. Rappard s.n.* (L).

N. *Themeda melanocarpus*

INDIA. Odisha: Sambalpur, Taprang Forest, 20 December 1939, *H. F. Mooney 1183* (K). **Uttarakand:** Tehri-Garhwal, September 1898, *J. S. Gamble 27252* (K). **Uttra Pradesh:** Saharanpur, November 1892, *J. S. Gamble 23985* (K). **BOTSWANA. Central District:** 95 miles north of Nata, on the road to Duru, 25 February 1966, *A. Blair Rains 27* (K); 43 km north of Nata, on the road to Kazangula via Pandamatenga, 23 March 1976, *R. P. Ellis 2755* (K). **Ngamiland:** Chobe Nature Park, Mababe Depressions, 2 km north of Tsotsoroga Pan, 18 May 1977, *R. P. Ellis 3007* (K); Chobe Nature Park, central hill of the Goha Hills, 19 May 1977, *R. P. Ellis 3033* (K). Aha Hills, 19°46.4' S, 21°2.35' E, 24 April 1980, *P. A. Smith 3420* (K); Tsodilo, 18°45' S, 21°45' E, 02 May 1975, *P. A. Smith 1371* (K). **Okavango Delta:** Gcwihaba, on the floor of fossil river valley, 20°00.8' S, 21°21.50' E, 21 April 1980, *P. A. Smith 3369* (K); Okavango Native Territory, Shamvura Camp, 11 February 1956, *B. de Winter & W. Marais 4601* (K). **CAMEROON. North Province:** Mayo-Louti, Guider, Bossoum, 19 October 1974, *G. Fotius s.n.* (K); Laéndé, 08 November 1984, *A. P. M. van der*

Zon 2495 (WAG); Tsancho, Mayo Oulo, 90 km north of Garoua, 9°38' N 13°53' E, 29 October 1987, *A. P. M. van der Zon 3709* (WAG). **DEMOCRATIC REPUBLIC OF THE CONGO. Kinshsa:** Kisanto, southwest of Kinshasa, 05 May 1926, *Vanderyst 17623* (K); Masina, Mapela, 23 November 1980, *Nkunga 6348* (WAG). **ETHIOPIA. Oromia:** Genale Gorge, Bale side, 10 May 1982, *I. Friis, M. Tadesse & K. Vollesen 2713* (K); Bale, Sof Omar Gorge, 2 km from crossing of Web River towards Ghinir, 19 June 1986, *M. G. Gilbert, D. Sebsebe & K. Vollesen 8309* (K); Sidamo, 54 km from Negele Borena, along road to Melca Guba and Moyale, 41 km from Dawa River and Melca Guba, 05 June 1988, *M. G. Gilbert & D. Sebsebe 8677* (K). **GHANA. Ashanti:** Ejura, Ejura Nkoranza, 2 km east of Ahiaem, 276 m, 7°28.2' N 1°31.2' W, 20 October 1912, *A. P. M. van der Zon 7132* (WAG). **Bauchi:** Darazo Forest Reserve, 27 October 1967, *P. N. de Leeuw & S. O. Magaji 1994* (K). **Brong-Ahafo:** Nkoranza, 16 km west of Ahiaem, 4 km west of Kyikaman, 195 m, 7°29.7' N 1°39.6' W, 27 October 1912, *A. P. M. van der Zon 7403* (WAG); Nkoranza, 2 km east of Ahiaem, 176 m, 7°31.0' N 1°34.7' W, 27 October 1912, *A. P. M. van der Zon 7422* (WAG). **KENYA. Kwale:** Buda Mafisini Forest, 8 miles west southwest of Gazi, 21 August 1953, *R. B. Drummond & J. H. Hemsley 3949* (K). **Kilifi:** Malindi, 18 August 1949, *A. Bogdan AB2614* (K). **SUDAN. Blue Nile:** Roseires, 28 October 1952, *S. A. G. Jarr 1814* (K). **West Darfur:** Jebel Marra, Kibi, Sketuga, 09 September 1963, *I. J. Blair 153* (K). **Central Darfur:** Jebel Marra, Zalinge, 11 September 1964, *G. E. Wicken 2495* (K); Jebel Marra, Golo, 04 May 1964, *G. E. Wickens 1566* (K). **MALAWI. Northern Region:** Nkhata Bay, Bandawe Point, 1550 ft, 08 June 1974, *J. Pawek 8700* (K, WAG); Myimba, Kasitu Valley, 3400 ft, 26 Janaury 1938, *J. E. L. Fenner 214* (K). **Southern Region:** Blantyre, Shiri Valley, Matope Road, 08 February 1951, *G. Jackson 412* (K); neighbourhood of Zomba, 3000 ft, *s.d., A. B. Cormack 44* (K); Mangochi, Monkey Bay Road, 1600 ft, 18 April 1949, *P. O. Wieke 67* (K); Nsanje, 500 ft, 25 March 1960, *J. B. Phipps 2734* (K). **MOZAMBIQUE. Cabo Delgado:** Montepuez, Matuta, about 5 km south of M'salo River, near Nantulo, 400 m, 09 April 1964, *A. R. Torre & J. Paiva 11802* (K). **Inhambane:** Inhampossa, 10 km south of Inhambe town, 01 March 1938, *A. de Figueiredo, Gomes & Sousa 2112* (K); Govuro, about 3 km between Mabote to Mapinhane, 30 March 1974, *F. Correia & A. Marques 4294* (WAG). **Sofala:** Beira, near Camara, 04 June 1956, *M. Myre & A. Balsinhas 2354* (K), Beira, Gorongosa National Park, 120 m, 19°00' S, 34°11' E, 08 July 1972, *C. J. Ward 7789* (K). **Tete:** between Inhacapirire and Chicoam 15.1 km of Inhacapirire, 19 February 1972, *J. M. de Aguiar Macedo 4864* (K); Cabora Bassa, Mueengádzi River, 330 m, 17 May 1972, *A. Pereira & M. F. Correia 2639* (WAG); Cabora Bassa, a part of Barragem and the mountain, north of Zambezi River, 330-365 m, 14 April 1972, *A. Pereira & M. F. Correia 2052* (WAG); Angónia, around Ulongwe, *E. Stefanesco & H. Nyongani 1242* (WAG).**Zambezia:** Mocuba, Namagoa, 200-400 ft, 01 May 1945, *H. G. Faulkner 15* (K). **NAMIBIA. Oshikoto:** Etosha Pan, 39 km southeast of Okakuejo, near Olifantsbad, 17 March 1984, *L. Smook 5121* (K); Etosha National Park, border to Rietfontein, 21 April 1971, *Le Roux 363* (K). **Otjozondjupa:** towards Kombat, 9 km south on D2863 from junction on D3022, 1680 m, 19°32'37.28" S 17°44'15.68" E, 31 May 1914, *H. Kolberg HK3659* (K). **TANZANIA. Dodoma:** Mpwapwa, Kikambo Valley, 4000 ft, 22 April 1932, *B. D. Burtt 3948* (K); Kondoa, Sambala, Sambala Hill, 5000 ft, 19 May 1929, *B. D. Burtt 2608* (K); Dodoma Urban, Matumbulu Reservoir, 1200 m, 6°17' S, 35°44' E, 27 May 1975, *I. Backeus 1254* (K). **Iringa:** Iringa, Ruaha National Park, 1000 m, 7°40' S, 34°57' E, 19 May 1971, *B. Mhoro 1309* (K). **Mbeya:** Mbarali, Chimala, 1240 m, 12 May 1963, *S. B. Boaler 928* (K). **Morogoro:** Ulanga, Luhombero Junction, 1500 ft, 09 June 1967, *A. F. Rees 98* (K). **Rukwa:** Milepa, 3200 ft, 27 May 1951, *A. A. Bullock 3912* (K); Lake Rukwa, Kalumbalesa, 15 April 1934, *A. P. G. Michelmore 1025* (K). **Ruvuma:** Songea, near Mshangano fishponds, Waterfall on Luhira River, 1030 m, 25 April 1956, *E. Milne-Redhead & P. Taylor 9812* (K); Tunduru Road, 8 miles of Masasi, 390 m, 05 May 1962, *S. B. Boaler 566* (K). **Songwe:** Kamsamba Game Camp, just southwest of Lake Rukwa, 850 m, 24 May 1971, *B. N. N. Mbano & M. A. Ndolanga 104* (L). **Ufipa:**

Kasanga, 30 March 1959, *M. M. Webster T231* (K). **ZAMBIA. Central Province:** Kafue National Park, Ngoma, 11 June 1960, *A. Angus 2403* (K). **Muchinga:** Mpika, Luangwa Game Reserve, upstream of Mfuwe, 28 April 1965, *B. L. Mitchell 2728* (K). **Eastern Province:** Luangwa Valley Game Reserve Station, south of Lubi River, 2000 ft, 10 April 1967, *S. B. Prince 455* (K); Luangwa Valley, Chilongozi, 14 April 1963, *W. C. Verboom 951* (K). **Luapala:** Kalasa Mukosa Flats, Masenga Causeway, south of Katumba, 1200 m, 22 February 1996, *S. A. Renvoize 5668* (K, WAG). **Southern Province:** Siavonga, Zambesi Escarpment, 3000 ft, 13 March 1962, *W. L. Astle* 1536 (K); Namwala, Shawba, 3800 ft, 22 February 1964, *W. L. Astle 2953* (K); Sinazongwe, 1850 ft, 18 April 1965, *W. L. Astle 3092* (K). **Western Province:** Kalabo, in the Lukona local forest, 3.3 km west from Lukona Basic School, 1140 m, 15°24'7.3" S 22°49'31.4" E, 20 March 1996, *B. Luwiika, D. K. Harder, M. G. Bingham & N. B. Zimba 356* (WAG). **ZIMBABWE. Masvingo:** Ndanga, western end of Chionja Hills, 1200 ft, 28 March 1961, *J. B. Phipps 2891* (K); Gronatudzaywa National Park, Nuanetsi, 04 April 1961, R. Goodier 1055 (K). **Mashonaland Central:** Sipolilo, Nyamunyeche, 24 April 1979, *P. Nyariri 805* (K). **Mashonaland West:** Kariba, Charare Fish Camp, 10 April 1966, *P. J. Jarman B14* (K); Lomagundi, 10 km east of Banket, on road to Whindale Farm, Mangula, 24 March 1969, *H. M. Biegel 2891* (K). **Matabeleland North:** Nyamayendlovu, 13 April 1953, *D. C. H. Plowes 1599* (K); Hwange, Kazuma Range, 1000 m, 09 May 1972, *B. K. Simon 2163* (K); Hwange, Matetsi Safari Area, 3200 ft, 14 March 1978, *P. Gonde 136* (K); Hwange, Victoria Falls, 12 March 1932, *C. K. Brain 5589* (K). **Matabeleland South:** Matobo, Matopos Research Station, 4500 ft, 24 February 1954, *J. M. Rattray 1646* (K). **MADAGASCAR. Vakinankaratra:** Betafo, 1600 m, 01 May 1912, *P. de la Bathie 10714* (P). **SOUTH AFRICA. Transvaal:** Punda Maria, 18 February 1954, *H. P. van der Schyft 2363* (K); Kruger National Park, Dzundwini Hills, 20 km north of Babalala picnic area, along the road to Punda Milia, 420 m, 23 January 1974, *G. Davidse & R. Ellis 5853* (K). **Western Cape:** Grootfontein, Vogelsang Farm, 12 April 1950, *H. G. Schweickerdt 2147* (K). **USA. Arizona:** Santa Cruz, Patagonia Mountains, Sycamore Canyon, 7.5 km east of National Forest, 1300 m, 13 September 1990, *J. R. Reeder & C. G. Reeder 8595* (K).**Florida:** near Jacksonville, Old Fields, 01 October 1978, *A. H. Curtis 3641* (K); Lake County, vicinity of Eustis, 1-15 August 1894, *Geo. V. Nash 1563* (K); Manatee, Terra Ceia Island, 13 November 1891, *J. H. Simpson 413* (K); Lake City, north of Alligator Lake, 04 October 1907, *A. Chase 281* (K). **MEXICO. Chihuahua:** Canyons, Mapula Mountains, October 1886, *C. G. Pringles 820* (K). **Guerrero:** Balsas, 09 September 1910, *A. S. Hitchcock 282* (K). **Jalisco:** Rio Blanco, *Dr. E. Palmer 589* (K). **Michoacán:** north of Jungapeo, 3000-5000 ft, 01 October 1953, *E. R. Sohns 716* (K); on steep slopes of Barrancas, on road from Uruapan to Nueva Italia, 05 October 1953, *E. R. Sohns 840* (K). Morelos: near Yantepec, 4500 ft, 22 October 1902, *C. G. Pringle 8678* (K). **Nayarit:** 10 miles southeast of Tepic, 2 miles southeast of El Refugio, 1000 m, 06 October 1952, *R. McVaugh 13380* (K). **Querétaro:** about 2.5 km west of Pueblito, 02 November 1952, *E. R. Sohns 516* (K). **Sonorra:** Leo, 500 m, *s.d.*, *A. Coulier 373* (K); Fronteras, 4550 ft, 25 September 1890, *C. V. Hartman 55* (K). **HAITI. Ouest Department:** Port-au-Prince, Furcy, Massif de la Felle, 1200 m, 16 September 1924, *F. Chase H1909* (K). **BRAZIL. North Region:** Acre, Rio Branco, Surumu, 01 July 1909, *anonymous 8012* (K).

O. ***Themeda mooneyi***

INDIA. Odisha State: Koraput District, near Pottangi, above Nelpadu Village, 1067-1219 m, 08 October 1950, *H. F. Mooney 4034* (K, US); Koraput District, near Pottangi, from Deo Mali to Turia Konda, 1219 m, 10 October 1950, *H. F. Mooney 4064* (K). **NEPAL**. **Province No. 1:** North of Taplejung District, Thapabu Khola, Tamur Valley, 7000 ft, 02 August 1956, *J. D. A. Stainton 1207* (K).

P. *Themeda novoguineensis*

INDONESIA. Maluku Province: Maluku Barat Daya Regency, Wetar Island, Kali Kuning River, 13 May 1993, *G. J. Leach & C. R. Dunlop 3773* (L). **PAPUA NEW GUINEA. Central Province:** Nunumai, about 12 km north of Amazon Bay, 15 m, 19°11'00" S, 149°23'00" E, 15 June 1969, *R. Pullen 7606* (K, L, PE); Rubulogo Creek, about 18 miles north of Port Moresby, 12 April 1967, *R. Pullen 6711* (K, L); Nakeo District, Baroka, 50 m, April 1933, *L. J. Brass 3710* (K, US); Motupore Island, 09°31'59" S, 147°16'59" E, 15 March 1987, *J. E. J. Lambinon 87/126* (L); Eastern footslopes of Tovobada Hills, 12 miles north of Port Moresby, June 1965, *P. C. Heyligers 1277* (K, L); Rigo Subdistrict, about 3 miles southeast of Tave, 50 ft, 15 August 1962, *R. Schodde 2789* (L); Port Moresby, January 1936, *L. J. Brass 8782* (L). **Eastern Highlands Province:** Goroka, 31 May 1972, *J. F. Veldkamp & P. F. Stevens 5506-a* (US). **Milne Bay Province:** Normanby Island, Sewa Bay, February 2008, *J. M. Simaga with R. Johns, T. Kuria & J. Gagul 09715* (K, L). **Port Moresby District (National Capitol District):** Kanosia, 10 February 1935, *C. E. Carr 11235* (K).

Q. *Themeda ritchiei*

INDIA. Karnataka State: Belgaum District, the Deccan, south of Ghat Hills, *s.d.*, *D. Ritchie 884* (K). **Maharashtra State:** Pune District, Hill near Pune, 23 September 1996, *G. M. Woodrow s.n.* (E). **MYANMAR. Mandalay Region:** Kyaukpadaung Township, Mount Popa Park, in the vicinity of the Environment Education Center, 600-800 m, 20°55'37.9" N 95°13'00.8" E, 12 November 1997, *W. J. Kress & al. 97-6021* (US).

R. *Themeda tremula*

INDIA. Karnataka State: Bisle (Bisale) Ghat, December 1927, Unknown (K); Mangalore, Jan 1902, *anonymous 4837* (K); Hassan District, Shiradi Ghats, peak above Panorama Point, 28 October 1969, *C. J. Saldanha 15394* (K); Hassan District, Genikalbetta, 04 December 1970, *C. J. Saldanha & T. P. Ramamoorthy HFP1172* (E, K); Hassan District, Genikalbetta, 19 December 1969, *C. J. Saldanha 15927* (E, K); South Canara, Mercara-Sampagi Ghat, 13 November 1900, *C. A. Backer 2335* (US). **Maharashtra State:** Mumbai (Bombay), Girgaon (Ghirgaum), 13 October 1893, V. Schiffner 1556 (K); Kattekan Forest, 27 July 1958, J. Fernandez s.n. (K); Mumbai (Bombay), Dudh Sagur Falls (Portuguese side), 23 November 1949, *J. Fernandez* 506 (K); **Tamil Nadu State:** Dindigul District, Kodaikanal, Berijam to Vembadi Peak, 19 November 1985, K. M. Matthew et al. 42717 (K); Dindigul, Kodaikanal, Pulney Hills, 17 May 1898, *A. G. Bourne 3132* (US); Tamil Nadu State: The Nilgiris District, near Naduvattam town, September 1934, *S. Bauer* 878 (K); Tamil Nadu State: Anaimalais, on the way to Konalaar, from Akkamalai Estate, 27 October 1982, *J. Klackenberg & R. Lundin* 486 (K); Dindigul, Kodaikanal, Pulney Hills, Pillar Rocks, 19 July 1898, *A. G. Bourne 1951* (US). **Kerala State:** Idukki District, Sabarimalaya (Sabarimalai), 24 December 1980, *P. V. Sreekumar* 69457 (K); Kerala State: Eravikulam National Park, Turner’s Valley, 25 November 1979, *C. G. Rice* 54 (K); Kerala State: Kochi (Cochin), Vittelapara Forest, December 1952, *J. Fernandez* JF17 (K); Kerala State: Idukki District, Madupatti, 1964, *ƒ* 3 (K); Malabar, in first clearings in deciduous forest, Mattanur to North Malabar, 28 November 1931, *E. K. Janaki 464* (US); Kanara District, Pilicode, 05 December 1919, *anonymous 16279* (US). **SRI LANKA. Central Province:** Kandy District, Kotmale, 12 September 1992, *Clayton & Weerasooriya 6046* (K); Nuwara Eliya District, Ramboda Pass, 17 December 1950, *F. Ballard 1159* (K); 23 miles east of Kandy on road to Mahiyangana, near Urugala, 700 m, 12 April 1970, *F. W. Gould 13379* (US); about 28 miles south of Kandy on Gampola-Nuwara Eliya road A-5, marker 28, 800 m, 05 April 1970, *F. W. Gould 13268* (K); Kandy District, Peradeniya, University of Ceylon campus, 500 m, 27 March 1970, *F. W. Gould*

13182 (K); Kandy District, Peradeniya, Royal Botanic Garden, 500 m, 07 March 1970, *F. W. Gould 13026* (K); Kandy District, at Highway A5 between Pusselawa and Ramboda, at road marker 32/8, 1000 m, 13 September 1967, *D. Mueller-Dombois 67091306* (US); Nuwara Eliya District, between Ramboda and Pussellawa, 07 November 1969, *T. R. Soderstrom and S. Kulatunge 1651* (K); between Pusselawa and Ramboda, along Nuwara Eliya Road, near the Milestone 32/8, 15 May 1968, *Tetsuo Koyama 13615* (K); Kandy District, Peradeniya, Royal Botanic Garden, 5 January 1970, *D. Clayton 5034* (K); Nuwara Eliya District, at road to Ambawela from Hakgala, road marker 5/3, 1640 m, 14 September 1967, *D. Mueller-Dombois 67091410* (US); Nuwara Eliya District, near Ramboda, Weddemulle, 1300 m, 28 January 1970, *D. Clayton 5542* (K); Khandwa District, side of stream near Hewra, 20 December 1888, *J. F. Duthie 8478* (US); Kandy District, Upper Hantane, 1000 m, 20 January 1970, *D. Clayton 5360* (K); Kandy District, Upper Hantane, 1200 m, 20 January 1970, *D. Clayton 5349* (K); Nuwara Eliya District, about 15 miles northwest of Nuwara-Eliya at mile post 32/8, on the Gampola-Nuwara-Eliya road, 1036 m, 24 October 1974, *G. Davidse & D. B. Sumithraarachchi 7933* (US). **Southern Province:** Galle District, ascend to Haycock Mountain, just west of Hiniduma, 305 m, 21 October 1974, *G. Davidse 7858* (K, US); near Haycock Mountain, 22 January 1951, *F. Ballard 1557* (K); Galle District, 2 miles north of Hiniduma, 150-300 m, *M. Lazarides 7345* (US); Galle District, Kanneliya Forest, 2-3 miles into forest from forestry bungalows, 90 m, 06°15'00" N 80°22'12" E, 19 February 1977, *B. Bremer & K. Bremer 839* (US). **Uva Province:** Badulla District, Mounstainside above mile post 10/3 along the road between Ohiya and Boralanda, 18 October 1974, *Gerrit Davidse 7702* (K); Rendapola, Badulla Road, below Hakgala, 25 December 1950, *F. Ballard 1227* (K); Badulla District, Haputale, Thotulagalla tea estate, 4 January 1970, *D. Clayton 5018* (K); Badulla District, Eastern slopes of Hakgala, 06°55'14" N 80°49'48" E, 09 March 1969, *R. D. Hoogland 11523* (E, L). **Sabaragamuwa Province:** Belihul Oya, near Rest House, 2 January 1951, *F. Ballard 1362* (K); Ratnapura District, Kalawana, 8 February 1970, *D. Clayton 5713* (K, L); Kegalle District, Kegalle, 07 February 1970, *D. Clayton 5686* (K); along eastern trail to Adam's Peak, 1900 m, 25 April 1970, *F. W. Gould 13599* (US).

S. *Themeda triandra* var. *triandra*

ALGERIA. Anaba: Anaba, Edough Massif, June 1890, *J. A. Battandier 581* (L); near Bone, at the base of Mount Edough, 36°53'00" N 07°37'00" E, 27 June 1861, *R. Le Tourneux & H. de la Perraudière 153* (E). **YEMEN. Al Bayda:** Radda, 2050 m, November/December 1979, *E. Westinga s.n.* (AMD); **Sanaa:** 2 km south of al Hayfah, 15°43'00" N 44°15'00" E, 24 February 1979, *D. Wood Y1079* (E); north of Sanaa, south side of mouth of Wadi Dhahr, 15°26'24" N 44°07'15" E, 02 April 1974, *J. J. Lavranos 11368* (E). Taiz: near Turbah, Gaheli, 13°12'00" N 44°10'00" E, 10 November 1995, *M. Thulin, M. Ghebrehiwet & A. N. Gifri 9273* (E). **SAUDI ARABIA. Al Bahah:** Wadi Habaquah, 04 April 1982, *J. Grainger 482* (E). **'Asir:** 22 km southwest of Abha, 8 km northeast of Al-Qara'a National Park, 23 May 1980, *L. Boulos & A. S. Ads 14198* (E). **LEBANON. Mount Lebanon:** Ein Anub-Choneifat, 33°47'30" N 35°31'30" E, 412 m, 06 February 1943, *P. H. Davis 5221* (E); near Beirut, on the mountain slopes of Mukallis, 33°51'52" N 35°33'02" E, 16 June 1901, *E. Hartman 183* (E); Lower Brummana, 33°53'00" N 35°37'50" E**,** June 1897, *J. Bornmüller 1590* (E); Matn District, Brummana, June 1897, *J. Bornmüller 1590* (US). **TURKEY. Mediterranean:** Adana, Seyhan, about 100 km east northeast of Adana, 300 m, 24 May 1959, *E. Hannipman & al. 1360* (WAG); Adana, Seyhan, about 15 km south of Haruniye, about 100 km east northeast of Adana, 300 m, 24 May 1959, *E. Hennipman & al. 1360* (L); Hatay, Antakya, southwest of Antakya, on Karacay-Tekmepinari road, 36° 5' 26" N 36° 2' 3" E, 13 July 1973, *F. Holtz, P. Hänel & T. Kesercioglu 654* (E); Hatay, Castle of Payas, near Dörtyol, 36°45'44" N 36°13'35" E, 03 May 1965, *M. J. E. Coode & B. M. G. Jones 391* (E); Hatay, Mount Amanus, Hasan Veyli Region, 36°45'00" N 36°20'00" E**,** June 1908, *M. Haradjian 2206* (E);

Hatay, coastal plain on western Amaros, 5-6 miles north of Iskenderun, 36°35'13" N 36°10'24" E, 29 July 1971, *Aberdeen University Amanus Expedition LI773* (E); Hatay, Amanus Mountains, Nurdaglari, 1 mile north of Kaypak, 36°45'00" N 36°20'00" E, 24 July 1971, *Aberdeen University Amanus Expedition J2 658* (E). **Düzce:** Gölyaka, border of Güzeldere, near village in Kechlik, about 5 miles from Mersina, 29 May 1855, *B. Balansa 740* (E, K, L). **CHINA. Guizhou:** near Liping, Marneo, 500 m, *s.d.*, *Dr. H. F. van Handel-Mazzatti 1731* (L). **Hebei:** Tientsin, Leichwang, 23 August 1912, *M. S. Clemens 1572* (E). **Hong Kong:** Lantau Island, Lin Fa Shan, 01 October 1935, *W. T. Ts'ang 25980* (E). **Jiangkou Xiang:** Shaoxiding, immediately west of Jiangkou, *Sino-American Guizhou Botanical Expedition 728* (L). **Jiangxi:** Lu Shan, Huang Yen Sau, 05 September 1932, *H. C. Cheo 272* (E). **Kwangtung:** Tinghushan, s.d., *K. S. Chow 78059* (E). **Shandong:** Tien Tai Shan, Kinoh Ching Sze, July 1927, *C. Y. Chiao 14590* (E); Laoshan, Tai Chin Kung, 17 August 1930, *C. Y. Chiao 2936* (E). **Yinjuang Xiang:** along trail between Zhangjaba and Huguoshi, on the west side of the Fanjing Shan Mountian Range, 850-1300 m, 25 September 1986, *Sino-American Guizhou Botanical Expedition 1672* (L). **Yunnan:** Barren Mountain, pastureland on the divide between Yun-Peng-Hsien, at the Mekong Valley, Talifu-Feng-Yueh Road, September 1903, *G. Forrest F889* (E). **TAIWAN. Tainan:** Tainan City, 09 October 1981, *C. S. Kuoh s.n.* (E). **JAPAN. Kantō:** Chiba, Kadzusa, Mobara, 07 September 1950, *J. Ohwi & T. Koyama 143* (E, L); Tokyo, Hachiōji, Mount Takao, 35°37'00" N 139°15'00" E, 29 September 1950, *M. Mizushima 496* (E); Gunma, Tatebayashi City, 1922, *T. Makino 93043 (*L); **Kyushu:** Fukuoka, Kasuya, Tachibama, 100 m, 30 October 1928, *K. Ichikawa 59* (L). **SOUTH KOREA. Jeju Island:** Hongno, 29 October 1908, *E. J. Taquet 1803* (E). **INDIA. Manipur:** Karong, 3500 ft, 17 October 1950, *W. N. Koelz 26632* (L). **Assam:** Mawryngkneng, Khasi Hills, 4000 ft, 21 November 1951, *W. N. Koelz 29096* (L); Longdong, November 1826, *N. Wallich 8764E* (E). **Himachal Pradesh:** Shimla Hills, 05 October 1849, *T. Thomson s.n.* (K). **Tamil Nadu:** Kongu Nadu, Coimbatore, 1 km west of Topslip, Mount Stuart, 750 m, 19 January 1979, *L. J. G. van der Maesen 3428* (WAG); Ootacamund, *s.d.*, *R. F. Hohenacker 1287* (K, L); Ootacamund, 29 February 1948, *W. N. Koelz 19744* (E). **Uttarakhand:** Chamoli, Badrinath, *s.d.*, *E. Madden 8* (E). **SRI LANKA. Monaragala:** Nilgala, Galoya National Park, sea level, 01 May 1975, *A. H. M. Jayasuriya 1966* (L). **NEPAL. Gandaki:** Baglung, 19 August 1981, *M. A. Farille 81-208* (E)**. Bagmati:** Dolkha, between Bigu and Khopa, 18 October 1981, *M. A. Farille 81-709* (E); Dolkha, between Syala and Gongar, 20 October 1981, *M. A. Farille 81-725* (E); Langtang Valley, 21 September 1972, *A. Maire 498* (E); Ganesh Himal, Dhading-Gorkha Border, 28°20'00" N 85°10'00" E, April 1974, April 1974, *Y. Bernard 229* (E). **Jumla:** Lumsa, 9500 ft, 10 August 1952, *O. Polunin, W. R. Sykes & L. H. J. Williams 5110* (E). **Sudurpashchim:** Bajhang, trail from Thalara to Budkhuri, 29°34'51" N 81°04'08" E, 11 July 2009, *Nepal Bajhang 2009 Expedition 20913096* (E). **BHUTAN. Chukka:** between Chulla and Chimakothi, 12 October 1988, *J. R. I. Wood 6813* (E). **Punakha:** Lobesa, Natural Resources Training Institute, 27°31'00" N 89°52'00" E, 04 September 1998, *Noltie, Pradhan, Sherub & Wangdi 58* (E); Wangdi Phodrang, 27°29'00" N 89°54'00" E, 18 September 1995, *R. Pradhan & T. Wangdi EG140* (E). **Mongar:** Kuri Chu, north of Lhuntse, 27°45'00" N 91°08'00" E, 20 August 1983, *C. Sargent 235* (E). **Thimphu:** road heading north from Thimphu, about 0.5 miles south of Tashichho Dzong, 27°30'00" N 89°38'00" E, 28 August 1998, *Noltie, Pradhan, Sherub & Wangdi 3* (E); Paro Chu, Drukgyel Dzong, 09 July 1983, *D. Keith 16* (E); Taba, 27°30'00" N 89°38'00" E, 17 July 1979, *J. C. A. Grierson & D. G. Long 2718* (E); Ramtokto, Namseling, 24 July 1991, *C. Parker 7059* (E). **MYANMAR. Mandalay:** Maymyo, 24 October 1908, *J. H. Lace 4364* (E). **THAILAND. Nakhan Ratchasima:** Pak Thong Chai, Sakaerat Forest Reserve, along Huai Krae Stream, 14°45' N 102°0' E, 400 m, 01 November 1969, *C. F. van Beusekom & C. Charoenpol 2012* (L); **Sa Kaeo:** Aran Prathet, 50 m, 09 August 1930, *A. F. G. Kerr 19581* (K). **Tak:** Raheng, near Tapotsah, Wang Chow Forest, 08 January 1904, *E. Lindhard s.n.* (K). **Chiang Mai:** Doi Suthep, 1120 m, 25 July 1958, *T. Sorensen, K. Larsen &*

B. Hansen 4394 (K); between Chiang Dao and Fang, 20 February 1958, *T. Sørensen, K. Larsen & B. Hansen 1369* (E). **Kanchanaburi:** Ta Salao, 100 m, 10 July 1930, *A. F. G. Kerr 19505* (K). **Nakohn Ratchasima:** Bua Yai, 01 November 1931, *Put 4249* (K); Pak Thong Chai, Sakaerat Forest Reserve, along Huai Krae Stream, 14°45'00" N 102°00'00" E, 01 November 1969, *C. F. van Beusekom & C. Charoenpol 2012* (E). **Loei:** Phu Kradueng, 1300 m, 16 October 1954, *T. Smitinand 2046* (K); Phu Kradueng, on the plain at its summit, 28 November 1965, *M. Tagawa, K. Iwatsuki & N. Fukuoka T557* (E). **LAOS. Salavan Province:** road to Ta Oy, 60 km from Salavan, 16°04' N 106°42' E, 14 November 1995, *J. B. Hacker JBH95.9D* (L). **INDONESIA. North Sumatra:** Padang Lawas, near Pertibi, s.d., *Horner 110* (L). **South Sumatra:** Palembang, Serilo, 400 m, 14 January 1933, *de Voogd 1516* (L). **THE PHILLIPPINES. Cordillera Administrative Region:** Benguet, Kabayan, Mount Pulag, 16°35'00" N 120°54'00" E, 24 February 1992, *G. Argent, J. A. S. Alvarez, E. M. Romera & L. Telino 9260* (E). **Zamboanga Peninsula:** Zamboanga, Santa Maria, 07°45'22" N 122°07'39" E, September 1912, *J. Reillo 16496* (E). **AUSTRALIA. Northern Territory:** Alice Springs, south side of Mount Gillen, 32°42'33" S 133°48'48" E, 24 March 1977, *R. Pullen 10467* (E). **Victoria:** Melbourne, Bayswater, 37°51'00" S 145°16'00" E, 03 December 1892, *Dr. A. Morrison s.n.* (E); Melbourne, Werribee, 37°54'00" S 144°40'00" E, 23 November 1889, *Dr. A. Morrison s.n.* (E); Melbourne, Frankston, 38°08'40" S 145°07'22" E, 24 December 1886, *Dr. A. Morrison s.n.* (E); Melbourne, Ringwood, 37°49'00" S 145°14'00" E, 30 November 1888, *Dr. A. Morrison s.n.* (E). **Western Australia:** Perth, Swan View, 31°52'16" S 116°02'45" E**,** 05 December 1903, *Dr. A. Morrison s.n.* (E). **PAPUA NEW GUINEA. Milne Bay:** Esa'ala, Fergusson Island, east of Lake Lavu, 09°33'00" S 150°37'00" E, 15 November 1976, *Lae Star Mountains Expedition 1975 68833* (E). **Central Province: Tapini Subdistrict, Tapini,** 08°18'00" S 146°58'00" E, 29 April 1971, *M. J. E. Coode 46167* (E). **CONGO. North Kivu:** Ishango, Virungu National Park, border of Lake Edward, deservoir of Semliki, 0°07' S 29°36' E, 930 m, 02 January 1978, *J. Lejoly 2617* (WAG); **Haut-Katanga:** Lubumbashi, Katanga, Katuba, January 1934, *P. Quarré 3775* (WAG). **BURUNDI. Muyinga:** Kigozi, 2°31' S 30°06' E, 1350 m, 31 May 1981, *M. Reekmans 10505* (WAG). **ETHIOPIA. Addis Ababa:** about 8 km north of Addis Ababa, along Blue Nile Road, Mount Entoto, 2800 m, 11 October 1965, *W. J. J. O. de Wilde & B. E. E. de Wilde-Duyfjes 8204* (WAG). **Amhara:** Begemder, along the road between Dirne and Dihurra, Semien Mountains National Park, 2850 m, 13 September 1974, *V. Magda 310* (WAG). **Harari:** Harar, about 9.5 km west of Jijga, along th**e** road to Harar, 9°21' N 42°45' E, 1875 m, 29 March 1970, *J. J. F. E. de Wilde 6445* (WAG). **Oromia:** Alemaya, Arboretum College of Agriculture, on the road to Kombolcha, 9°25' N 42°05' E, 02 July 1974, *J. J. Bos 8010* (WAG); West Arsi, 35 km east southeast of Shashemane, along the road to Dobollo, 7°03' N 38°49' E, 2600 m, 26 July 1970, *J. J. F. E. de Wilde 6848* (WAG); Ahmar Mountains, about 62 km east of Asbe Tafari, along thr road to Harar, 9°10' N 41°04' E, 2600 m, 18 April 1969, *J. J. F. E. de Wilde 4937* (WAG). **Shewa:** southern Addis Ababa, Mount Fure, 2500 m, 24 October 1974, *J. W. Ash 2653* (WAG). **Tigray:** 22 km on Axum-Chire Road, 14°10' N 38°30' E, 2130 m, 27 August 1973, *G. Aweke & M. G. Gilbert 833* (WAG). **KENYA. Rift Valley:** Masai Mara National Park, 1°31' S 35°08' E, 26 June 1994, *A. P. M. van der Zon 7661* (WAG). **Machakos:** Tsavo East National Park, Yatta Plain, 01°15'00" S 37°35'00" E, 02 July 1938, *I. B. Pole Evans & J. Erens 1070* (E). **Nyanza:** Londiani, Tinderet Forest Reserve, 0°5' S 35°27' E, 2260 m, 14 June 1949, *R. A. Mass Geesteranus 4929* (WAG); Kisii Central District, near Nyangasu, 0°50' S 34°48', 20 March 1978, 1835 m, 20 March 1978, A. C. Plazier 921 (WAG); **Nairobi:** Extra-provincial district, west end of Nairobi Dam Lake, 1°19' S 36°48' E, 5550 ft, 02 December 1966, *R. E. Perdue & S. P. Kibuwa 8171* (WAG); Jamhuri Park, beside access road from Kibera Station, 300 m south of main stand, 01°18'00" S 36°46'00" E, 16 July 1967, *D. Wood 843* (E). **Kajiado:** Oloolua Forest, 1°22' S 36°42' E, 1850 m, 15 June 1997, *B. Bytebier 894* (WAG, K). **UGANDA. Western Uganda:** Buhweju, Rugongo, 0°22' S 30°29' E, 1770 m, 31 March 1986, *P. K. Rwaburindore 2263* (WAG).

SOMALIA. Sanaag: Daalo Forest Reserve, 10°45' N 47°20' E, 24 June 1979, *O. J. Hansen & H. Heemstra 6246* (K, WAG); 11 miles west of Erivaro, Daloh Arap, 6800 ft, 27 October 1961, *C. F. Hemming 2319* (WAG). **Maroodi Jeex:** Gaanlibah, Forest Reserve, 09°53'00" N 44°47'00" E, 10 October 1978, *J. B. Allen & A. A. Elmi 468* (E). **MALAWI. Central Province:** Salima, north of Grand Beach Hotel, west shore of Lake Malawi, 13°46'49" S 34°27'31" E, 30 March 1985, *D. G. Long 12409* (E). **Northern Province:** Mzimba, 4 km southwest of Chikangawa, 5700 ft, 12 July 1978, *E. Phillips 3535* (WAG); Mzimba, Mzuzu, Marymount, 4500 ft, 11 March 1973, *J. Pawek 6493* (WAG); Mzimba Vipya Plateau, 37 miles southwest of Mzuzu, behind vernal pool dome, 5500 ft, 14 May 1973, *J. Pawek 6722* (WAG). **Southern Province:** Mount Mulanje, near Lychenya Hut, 2000 m, 07 November 1981, *L. van der Linden 46* (WAG); Phalombe, Mchese Forest Reserve, Mchese Mountain, 1140 m, 15°49'48" S 35°41'10" E, 02 June 2008, *J. Timberlake 5317* (K); Zambesia, Shiri Highlands, 15°30'00" S 35°15'00" E, July 1885, *J. C. M. G. Buchanan s.n.* (E). **MOZAMBIQUE. Cabo Delgado:** Pemba, about 15 km from Pemba, 27 January 1984, *E. M. C. Groenendijk, A. Maite & J. Dongo 836* (WAG). **Manica Province:** between Vocot river and Chireza, 950 m, 18 February 1966, *A. Pereira, A. Sarmento & A. Marques 1489* (WAG); Nova Sintra, Mount Macuina, 1020 m, 01 March 1966, *A. Pereira, A. Sarmento & A. Marques 1540* (WAG). **Nampula Province:** Malema, Nalume River Bank, 500 m, 28 May 1947, *L. G. Pedro s.n.*(WAG). **Niassa Province:** Bacino del Lugenda, Chiconono, 19 July 1979, *V. Leoncini & O. Matteucci s.n.* (WAG). **Tete Province:** Angónia, Dómué, Capsule circle, near Serra Dómué, 06 August 1979, *L. Macuácuá & E. Stefanesco 903* (WAG). **Zambezia Province:** Milange, Serra do Chiperone, below Marrega, 1100 m, 29 Jan 1972, *M. F. Correia & A. Marques 2394* (WAG). **RWANDA. Eastern Province:** Nyakayaga, Gabiro, Akagera National Park, 1500 m, June 1938, *Lebrun 9476* (L). **TANZANIA. Arusha:** Arumeru, southwest of Mount Meru, Kitaku, about 2 km north of Forestry Training Institute Olomotonyi, 3°16' S 36°40' E, 1785 m, 13 June 1912, *C. J. Kayombo 7545* (WAG); Monduli, Somali Maasai Centre of Endemism, Losimingori Village, about 1 km east of Tarmac Road to Babati, 3°25.0' S 36°13.0' E, 1398 m, 14 June 1912, *C. J. Kayombo & C. Makyao 7590* (WAG); Ngorongoro District, on top ridge of the Ngorongoro crater, 03°10'00" S 35°35'00" E, 24 June 1938, *I. B. Pole Evans & J. Erens 971* (E). **Iringa:** Kilolo, Mazombe, Image Ward, Image Mountains Forest Reserve, Iyai Village, Selebu Mountain Valley, Ihongole Area, 7°28.6' S 36°09.8' E, 1510 m, 02 September 1911, *C. L. Kayombo & E. Wimbe 6988* (WAG). **Kagera:** Ngara, Bugufi, Murgwanza, 5500 ft, 02 December 1960, *R. E. S. Tanner 5405* (WAG). **Kilimanjaro:** Marangu, 03°17'00" S 37°31'00" E, December 1893, *G. L. A. Volkens 1481* (E); Diehallasee, June 1893, *G. L. A. Volkens 303* (E). **Mara:** Musoma, Leonera Aerodrome, 5000 ft, 18 April 1958, *S. Paulo 293* (WAG). **Mbeya:** Makete, slopes of Matamba Mountains, 2800 m, 22 November 1986, *P. Goldblatt, R. K. Brummit & J. Lovett 8211* (WAG). Pwani: Kibaha, 49 km west of Dar Es Salaam, 6°46' S 38°55' E, 150 m, 30 May 1970, *T. M. T. Tadros DSM591* (WAG); Kikondo Camp, Poroto Mountains, 1950 m, 20 January 1961, *Mrs. H. M. Richards 13987* (WAG). **Morogoro:** Ulanga, Kisawasawa, 1964, *Haerdi 365/0* (WAG). **ZAMBIA. Luapula:** Kalasa Mukoso Flats, near the Luapula Bridge, 1200 m, 20 February 1996, *S. A. Renvoize 5633* (WAG). **Lusaka:** east southeast Lusaka, Kanyanja, about 5 km south of Kafue Powerline Road, near Game Ranch, 15°31'36" S 28°27'44" E, 1380 m, 25 February 1996, *D. K. Harder & M. Bingham 3502* (WAG). **ANGOLA. Cuanza Sul:** Antiga, between Munenga and Dondo, 300 m, 19 January 1971, *F. Raimundo, C. Matos & Figueira 598* (WAG). **ZIMBABWE. Manicaland:** Nyanga, Nyanga National Park, Mount Nyangani, 18°17' S 32°50' E, 2130 m, 20 December 1973, *P. Bamps, J. J. Symoens & C. Vanden Berghen 4* (WAG); Nyanga District, Nyanga, 18°12'57" S 32°44'28" E, 04 April 1944, *S. G. Corner s.n.* (E). **Masvingo:** Mushandike, Mushandike National Park, 28 January 1971, O. Chiparawasha 319 (WAG). **SOUTH AFRICA. Eastern Cape:** Uitenhage, Springs Nature Reserve, low lying area between Grootkop and Bayview, 07 September 1978, *M. C. Olivier 2288* (WAG); 22 km from Elliot, on road to Indwe, 31°22'09"

N 27°39'48" E, 1170 m, 11 January 1997, *A. M. Makwarela 75* (WAG); Chris Hani, 15 km from Dordrecht, on road to Queenstown, 31°29'88" S 26°59'316" E, 1554 m, 13 January 1997, *P. N. Sebothoma 48* (WAG). **Gauteng:** Pretoria, Waterkloof Ridge, 68 Eridanus Street, 1500 m, 19 December 1974, *A. O. Crook 2053* (WAG); Pretoria, Faerie Glen, near Bantu Village and Ruin, 25°47' S 28°18' E, 1350-1375 m, 27 November 1971, *anonymous s.n.* (WAG). **Gauteng:** Pretoria, top of Muclenuek Hill, 14 February 1938, *H. C. D. de Wit 2795* (WAG). **Limpopo:** Roedtan, southeast of Roedtan, Farm Delftzyl, 859 m, 09 February 1993, *G. L. Rossouw 18* (WAG). **Mpumalanga:** Songimvelo Game Reserve, Durrstede Farm, ridge below Lufafa Peak, 1410 m, 09 December 1992, *C. Reid 1881* (WAG). Cape Province: 25 km south southwest of Brodersput, 1250 m, 19 January 1987, *L. Smook 6178* (WAG); Ehlanzeni, Mbombela, Nelspruit Falls, 30 March 1938, *A. O. D. Mogg 1478a, 1478b* (WAG). **Northern Cape Province:** northwest of Campbell, in region of Downs and Broken Hill Farms, 25°42'638" S 23°36'200" E, 1341 m, 29 January 1996, *L. Smook 9690* (WAG); near Barkly West, 18 km on road to Potfontein, 28°26'44" S 24°03'45" E, 04 March 1998, *L. Smook 10193* (WAG); northwest of Kimberly, Koopmansfontein Agricultural Research Station, 28°12'22" S 24°04'45" E, 04 March 1998, *L. Smook 10133* (WAG). **Northwest Province:** Armoedsvlakte, north of Koppie Enkel, 01 May 1962, *A. O. D. Mogg G51* (WAG); Buffelpoort Dam, 1100 m, 06 October 1936, *L. en Meeuse 4852* (L). **Orange Free State:** 74 km east of Villiers on Vaal River, Farm Mandyville, Rolling Country, 29 January 1988, *L. Smook 6785* (WAG); 42 km southeast of Vrede, Farm Drie Kop, between Spitskop and Aasvoelkop, 2000 m, 05 February 1987, *L. Smook 6452* (WAG); Fickburg, area between Staffords Hill and Dam, 5300 ft, 15 January 1970, *N. Jarman 44* (AMD). **Transvaal:** Delareyville, at auction ground on south side of town, above salt pan, 1350 m, 22 January 1987, *L. Smook 6259* (WAG); Biesiesvlei, on southern side in area known as the Plots, 1400 m, 21 January 1987, *L. Smook 6235* (WAG); Benzuitenhoudskraal, 4500 ft, 25 Jan 1968, *J. W. Morrison 1102* (WAG); Barbeton, Kaapmuiden, 1340 ft, 21 May 1936, *A. O. D. Mogg 1447* (WAG); Babeton, Cythna Letty Nature Reserve, 1300 m, 03 January 1972, *P. J. Muller 2175* (WAG). **Western Cape:** Hermanus, Voëlklip, Klippies Baai, 3419 AD Caledon, 6 m, 06 October 1981, *S. L. Williams 738* (WAG); Cape Town, Kalk Bay Mountain, rocky east-facing slope above Boyes Drive, 15 September 1974, *P. Goldblatt 2666* (WAG); Central Karroo, Farm Daggafontein, main road to Victoria West, 46 km southwest of Britstown, 1346 m, 13 March 1988, *L. Smook 6919* (WAG). **NAMIBIA. Khomas:** Old Neudamn Experimental Farm, *s.d.*, *M. Müller 1688* (WAG); Windhoek, Bergland, Schoengelegen, 2000 m, 25 March 1959, *R. Seydel 1885* (WAG); Farm Regenstein, 2336 m, 06 May 1975, *W. Giess 13709* (WAG). **Zambezi:** Kongola, Caprivi Strip, Uramba, 11 April 1971, *E. Coppejans EC687* (WAG). **BOTSWANA. Ngamiland**: Vombara, Okavanga Delta, 18°56-57' N 22°40-41' E, 970 m, 10 May 1994, *P. A. Smith 5710* (WAG); **Gangi:** Okavango River, near the SWA border, 18°15.25' S 21°47.2' E, 14 February 1979, *P. A. Smith 2642* (AMD). **LESOTHO. Qacha's Nek:** Sehlabathebe National Park, Kubutseni, 2575 m, 15 February 1979, *F. K. Hoener 2173* (WAG).

T. ***Themeda triandra*** **var.** ***quadrivalvis***

OMAN. Dhofar Governorate: Zeisphoon, 20 September 1981, *M. G. Zaroug RMD27* (K); 30 km north of Salalah, on the Thumrait (Midway) road, near the Aqabat Hamir, 22 September 1977, 500 m, 17°13'00" N 54°06'00" E, *A. Radcliffe-Smith 5194* (K); south escarpment of Jebel Qara, 25 km north of Salalah, Wadi Nahiz, 500 m, 21 September 1979, *A. G. Miller & R. Whitecombe 2093* (K); Medina al Haq, 17°08' N 54°28' E, 27 October 1981, *J. R. Maconochie 2910* (K); about 5 km west of Hageif, 17°12'00" N 54°00'00" E, 24 November 1981, *J. R. Maconochie 2974* (K); Zeak, 17°15'00" N 54°09'00" E, 26 October 1981, *J. R. Maconochie 2919* (K); Medinat al Haq, Taqah, September 1981, *P. N. Allison 29* (K); Ashinhaib, 850 m, 17°15'01" N 54°16'43" E, 22 September 1993, *T. A. Cope 630* (K);

Jebel Al-Qamar, behind 2nd Military stop, 800 m, 16°43'00" N 53°13'00" E, 04 October 2001, *A. Patzelt & M. P. A. Al-Farsi MP123* (K); Tobruk, 27 September 1992, *I. McLeish77* (K); km 7 on the upper Sarfait to Dhalqut road, 02 October 1993, *I. McLeish 2807* (K); near Umberoff, 600 m, 16°44'00" N 53°20'00" E, 03 October 1991, *T. A. Cope 481* (K); Salalah to Thumrait road, near the Ayun turnoff, 900 m, 17°14'00" N 54°04'00" E, 06 October 1991, *T. A. Cope 519* (K); above Dhalqut, 800 m, 16°43'00" N 53°13'00" E, 04 October 1991, *T. A. Cope 513* (K). **YEMEN. Al Mahrah Governorate:** Hawf Mountains, Shah'rut, 03 October 2001, *N. Kilian, J. Meister & M. A. Hubaishan YP801* (WAG). **CHINA. Yunan Province:** Honghe Hani and Yi Autonomous Prefecture, Mengzi, 1450 m, 23°16'42" N 103°27'00" E, 31 August 2011, *L. Qing & al. 216* (IBSC). **NEPAL. Bagmati Province:** Dolakha District, between Gumbu Khola and Tenkhu, 1200 m, 28 October 1981, *M. A. Farille 81-803* (E). **Lumbini Province:** Dang District, Tulsipur, 2000 ft, 24 October 1952, *O. Polunin, W. R. Sykes & L. H. J. Williams 5871* (E, K). **Province No. 1:** Arun Valley, Tumlingtar, west of Chainpur, 1000 ft, 28 September 1956, *J. D. A. Stainton 1791* (E). **INDIA. Arunachal Pradesh State:** Changlang District, Namchik River Valley, mile 21 mark on Ledo Road, 27°20'12" N 96°2'55" E, 25 October 1945, *R. O. Belcher s.n.* (K). **Bihar State:** 14 km to Betla, 10 November 1983, *L. J. G. van der Maesen 5035* (K). **Chhattisgarh State:** Kanker District, 25 October 1938, *H. F. Mooney 823* (K); Rajnandgaon District, Khairagarh, near Bortalao, 09 November 1938, *H. F. Mooney 838* (K). **Gujarat State:** Sasan Gir, 05 October 1953, *H. Sautapau 16358* (K); Dang District, Waghai, 18 October 1954, *H. Santapau 19616* (K); Gir Forest, Hiran River, 06 October 1953, *M. B. Raizada 22779* (K, L). Haryana State: Jhajjar District, Beri, Majra, November 1912, *H. H. Haines 3627* (K). **Jharkhand State:** Sahibganj District, Rajmahal, October 1894, *S. Mokim 1499* (K, L); West Singhbhum District, Porahat Forest Division, January 1918, *anonymous s.n.* (K); Latehar District, Palamau Tiger Reserve, October 1915, *H. H. Haines 5332* (K). **Karnataka State:** Belgaum, *s.d.*, *D. Ritchie 886* (L). **Madhya Pradesh State:** Narmadapuram District, Pachmarhi, Satpura Range, between long Chakkar and short Chakkar, 26 October 1958, *R. C. Bharadwaja 24* (K); Narmadapuram District, Itarsi, 20 February 1947, *W. Koelz* 19736 (US); *Gwalior District*, s.d., *C. C. Wisner 102* (US). **Maharashtra State:** Mumbai (Bombay), Sanjay Gandhi National Park, Borivali, 30 September 1952, *R. R. Fernandez R677* (K); Jalgaon District, Jamanya, 29 September 1979, *P. Remanandan 4523* (K); Mumbai (Bombay), Girgaum, 5 m, 13 October 1893, *V. Schiffner 1554* (L). **Rajasthan State:** Sirohi District, Mount Abu, 27 April 1917, *Father E. Blatter 2682* (K). **Odisha State:** Kalahandi District, Gumer, Karlapat, *s.d.*, *anonymous 65* (K); West Sambalpur District, Khariar, 2150 ft, October 1949, *H. F. Mooney 3678* (K); Sambalpur, Redhakhol, Charmal, 15 October 1937, *H. F. Mooney 590* (K). **Punjab and Haryana State:** Chandigarh, Khandwa District, 26 January 1889, *J. F. Duthie 8479* (US). **Uttar Pradesh State:** Raebareli, 19 November 1978, *B. K. Misra 910* (K); Bundelkhand, near Jalaun, 01 December 1886, *J. F. Duthie 6571* (US). **BANGLADESH. Chittagong:** Bandarban, Alikadam, Thanei Road, 21°34'48" N 92°25'48" E, 13 October 1998, *M. A. Rahman & al. 3754* (E). **MYANMAR. Shan State:** Taunggyi, October 1939, *F. G. Dickson 9607* (L). **THAILAND. Chiang Mai:** Doi Suthep Mount, 600 m, 05 December 1957, *J. V. Santos 6706* (L). **Tak:** Raheng, Prachao Luang, 450 m, 18 November 1920, *A. F. G. Kerr 4589* (K). **VIETNAM. Hanoi Province:** Sơn Tây, Da Chong, October 1937, anonymous 2029 (US). **Thanh Hóa Province:** Thanh Hóa City, Đông Són, 1886, *Jansen & Wachter 27652* (L). **AUSTRALIA. Queensland:** Cook District, 2 miles west of Julatten, Mossman-Mareeba Road, 30 March 1962, *J. C. Tothill H178* (K); Cook District, 4.8 km north of Little Laura River, on Peninsula Development Road, 120 m, 15°30'00" N 144°17'00"E, 27 April 1983, *J. R. Clarkson 4776* (K); Cook District, 3 km south of Walkanin, on the Mareeba to Atherton road by the crossing of the main irrigation channel, 630 m, 17°10'00" S 144°26'00" E, 15 May 1987, *J. R. Clarkson & B. K. Simon 7227* (K); Cook District, Mareeba, 24 May 1938, *Stock Inspector Sibley 6* (K); Cook District, Lakefield National Park, 6 km north of Lakefield homestead, on the road to Bizant, 20 m, 14°53'00" S

144°10'00" E, 06 May 1987, *J. R. Clarkson & B. K. Simon 6950B* (K, L); Cook District, Mareeba, 1300 ft, 19 June 1935, *S. T. Blake 9519* (K); Habana, 14 miles northeast of Mackay, September 1935, *J. P. Kahler s.n.* (K); Cook District, Atherton, 14 April 1958, *Mrs. R. Weare s.n.* (K); Port Curtis District, Fitzroy Vale, 13 May 1956, *S. T. Blake 19948* (K); Port Curtis District, Cawarral, May 1932, *D. J. McDonald s.n.* (K); Port Curtis District, Farnborough School, 13 km northwest of Yeppoon, 23°04'00" S 150°44'00" E, 04 May 1975, *B. K. Simon & S. B. Andrews 2565* (K, L); Moreton District, 4 miles west of Kilcoy, 04 May 1967, *W. R. Gray s.n.* (K); Moreton District, Hendra, 17 May 1963, *G. Diataloff s.n.* (K); South Kennedy District, Keswick Island, north end of airstrip, 20°55'00" N 149°25'00" E, 18 September 1996, *G. N. Batianoff & I. G. Champion 960910* (K); South Kennedy District, Habana, near Mackay, May 1947, N. E. Goodchild s.n. (K); Burnett District, about 15 miles southwest of Mundubbera, April 1968, *A. D. Lindenmeyer s.n.* (K); Atherton District, near Talga, Northey Road, 600 m, 28 April 1962, *H. S. McKee 9395* (K); Leichhardt District, 10 miles from Clermont, on road to Emerald, 15 July 1963, *W. J. Bissett s.n.* (K, L); Leichhardt District, 9 miles south of Nedo Township, 18 June 1962, *Story & Yapp 8* (K, L); 28 miles (45 km) from Malborough, on inland highway to Sarina, 18 May 1970, *M. Fagg 657* (K). **Western Australia:** Fern Creek, 19 km east of Inglis Gap, King Leopold Ranges, 17°10'00" N 125°16'00" E, 09 April 1988, *B. K. Simon* 3853 (K). **SOLOMON ISLANDS. Guadalcanal Province:** Visale, on coast about 22 miles west of Honiara, 11 December 1954, *H. S. McKee 1630* (K). **NEW CALEDONIA. North Province:** near Canala, La Crouen, 100 m, 25 April 1964, *H. S. McKee 11453* (K, L). **South Province:** Thio, Dothio River Valley, 22 March 1983, *G. McPherson 5574* (K); about 5 am north of Bouloupari, along route 4, 07 March 1992, *H. Koyama & C. Tanaka 8252* (P). **FIJI. Ra Province:** Yaguara, Kings Road, 16 February 1951, *B. E. Parham 7154* (K). **MADAGASCAR. Boeny:** between Mahajanga and Marovoay, April 1967, *P. Morat 2712* (P). **Diana:** Ankarana Reserve, between Ambilobe and Anivorano, 200-350 m, 4-9 March 1951, *H. Humbert & R. Capuron 25576* (P). **Diego Suarez Province:** road along coast from Diego-Suarez to Ramenz, 23 May 1974, *A. Gentry 11931* (K). **MAURITIUS. Savanne District:** Souillac Village, park near Souillac, 17 February 1979, *R. E. Vaughau A112* (K). **Plaines Wilhems District:** Curepipe, 28 February 1888, *H. H. Johnston s.n.* (E). **Île Rodrigues:** route from Graviers, 08 April 1774, *J. Bosser 21944* (P); Plain Corail, July 1970, *T. Cadet 2617* (P). **MARTINIQUE. Schœlcher:** Madiane, 10 September 1943, *H. Stehlé 5453* (P). **USA. California:** Ontario, Plaza Serena, 24 November 1991, Timothy S. Ross 6026 (K). **Louisiana:** St. Landry, southeast of Opelousas, on Grant Road, 06 September 1984, *W. D. Reese, G. Landry & D. Waters 16889* (US); St. Landry, Bellview Grant, 7 miles southeast of Opelousas, 28 August 1943, *C. A. Brown 9780* (US). **CUBA.** Isla de la Juventud (Isla de Pinos), between Santa Ana and Rosalia, 19 November 1920, *E. L. Ekman 12261* (K). **HAITI. Artibonite Department:** Petite Rivière, Artibonite Plain, January 1925, *A. T. Sweet s.n.* (US); vicinity of Saint-Michel-de-l'Atalaye, 350 m, 15 November 1925, *E. C. Leonard 7000* (US). **Ouest Department:** Nouvelle-Touraine, Massif de la Pelle, Pétion-Ville, 1200 m, 31 August 1924, *E. L. Ekman H1728* (US). **BARBADOS.** Bridgetown: My Lords Hill, February 1939, *J. A. Allan 515* (K); Bridgetown: Garrison Savannah, 03 May 1927, *C. C. Skeete 156* (K); St. Michael, near Kingston, 02 October 1905, *anonymous 585* (K). **DOMINICAN. Monte Plata:** Sierra Prieta, 22 November 1966, *B. A. Lavastre 2343* (US). **San Juan:** Valle de San Juan, 22 August 1929, *E. L. Ekman H13400* (US). **Elías Piña:** Honde Valle, 3500 m, 02 September 1946, *R. A. Howard & E. S. Howard 8724* (US). **San Rafael:** road to Hondo Valle, near Cana River, 31 March 1969, *E. de J. Marcano Fondeur & J. J. Jiménez Almonte 5594* (US); **Peravia:** 2 km east of Baní, on the road to San Cristobal, 20-30 m, 18°16'00" N 70°16'59"W, 22 December 1984, *T. A. Zanoni & M. M. Mejía 33005* (L). **PUERTO RICO. Peñuelas:** Rucio, s.d., *L. M. Cruz-Pérez s.n.* (US); Tallaboa Alta, high point of development south of route 132, 150 m, 18°01'19.9" N 66°41'37" W, 22 November 2010, *F. S. Axelrod & Y. García 14444* (US). **Guayanilla:** Cedro, on north side of highway 2, 100 m, 18°01'4.1" N 66°44'28" W, 07 October 2006, *G. J. Breckon & I.*

Morales 8063 (US). **LESSER ANTILLES. Guadeloupe:** Basse-Terre, 24 August 1938, *A. Questel 2186* (K); Saint-François, Anse à la Barque, 20 m, 04 October 1936, *H. Stehlé 1089* (K). **ARGENTINA. Santa Fe Province:** General Obligado Department, El Rabon, 21 July 1975, *C. Quarín 3121* (K); General Obligado Department, Rutas Nacionales de Argentina No 11, 16 km north de Las Toscas, 04 May 1997, *M. Urbani 55* (US).

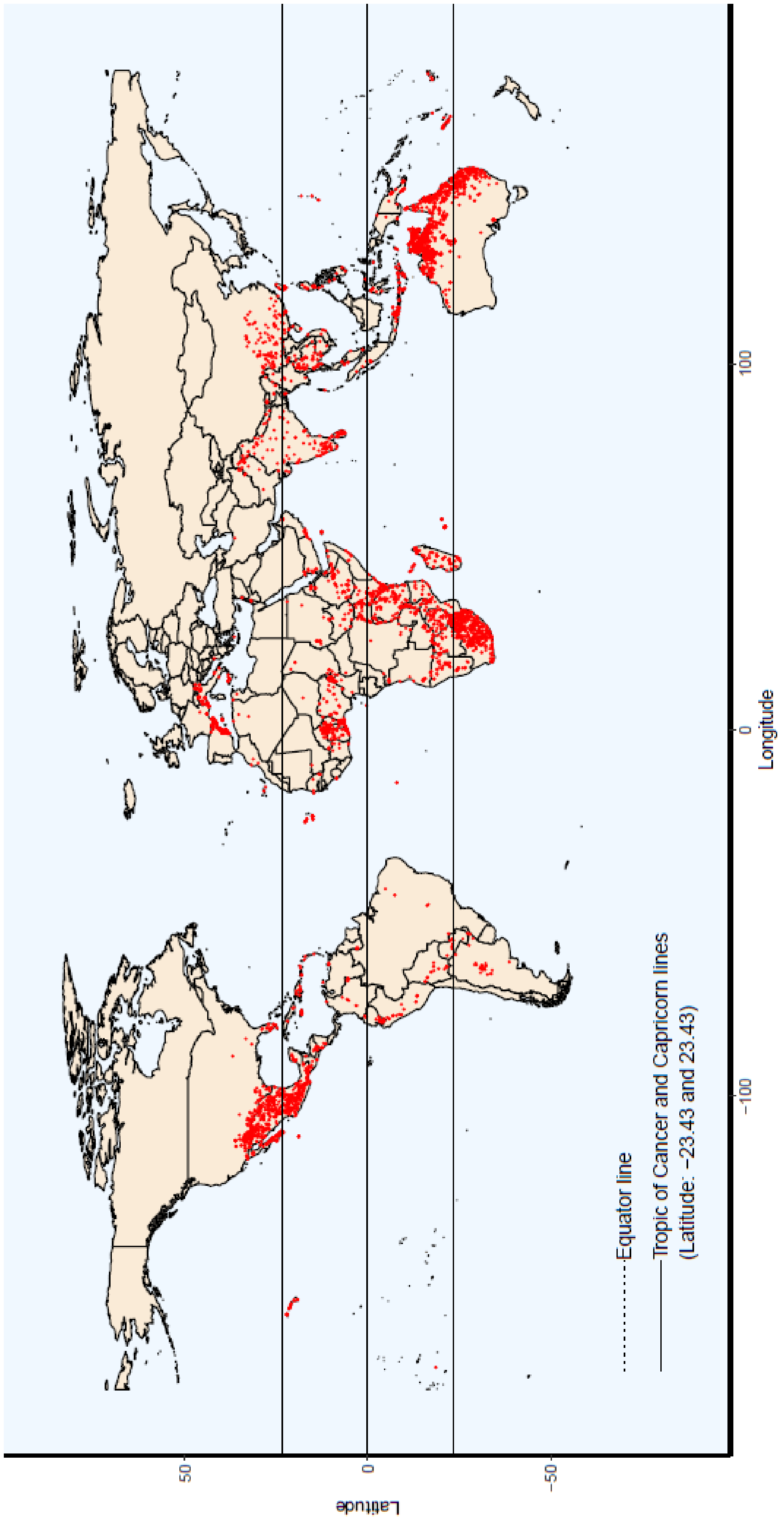
U. *Themeda villosa*

CHINA. Guangxi Zhuang Autonomous Region: Gaoloshan, Tian'e Xian, 15 November 1989, *Q. Hai-ning & al. 893234* (K, PE); Dar Shan Town, 24 li west of Hoo-Chih, 732 m, 21 July 1928, *R. C. Ching 6467* (US). **Guangdong (Kwangtung) Province:** Loh Ch'ang District, Chong Uen Shan, near Kau Fung, November 1932, *W. T. Tsang 20792* (K); Yung-Uen District, 1932, *S. K. Lau 620* (K). **Guizhou (Kweichow) Province:** Miao Wang, Kiangkou Hsien, 26 September 1931, *A. N. Steward, C. Y. Chiao & H. C. Cheo 534* (L); Nakan, Chengfeng, 18 October 1930, *Y. L. Keng 4729* (K). **Hainan Province:** Ling Shui District, Chim Shan, Fan Maan Ts'uen and vicinity, May 1932, *H. Fung 20120* (K); Ching Mai District, Pak Shik Ling and vicinity, Ku Tung Village, 25 October 1932, *C. I. Lei 176* (K); 25 miles above Kachek, edge of sand bank on Kachek River, 13 October 1921, *A. S. Hitchcock 19615* (US); Tsioh Biah, 14 October 1921, *F. A. McClure 10505* (US). **Hong Kong:** New Territories, Mount Golden Bell, 30 December 1970, *P. But 170* (K); New Territories, Taipo Forestry Station, 14 October 1968, *S. Y. Hu 5948* (K); Lim Tsuen, 16 April 1972, *S. Y. Hu 11880* (K). **Yunnan Province:** west of Talifu, Mekong watershed, en route to Youngchang to Tengyueh, September to October 1922, *J. F. Rock 6638* (US); Lunan Xian, Daduishui, 1650-1700 m, 24°45'00'' N 103°10'00'' E, 03 August 1984, *B. Bartholomew & al. 1643* (US). **INDIA. Sikkim State**: September 1882, *J. S. Gamble 10565* (K). **Orissa (Odisha) State:** Khordha District, Begunia Tehsil, Podadiha Village, 25 October 1949, *H. F. Mooney 3732* (K, L). **Jharkhand State:** West Singhbhum District, Saranda Forest, Karampada, 03 February 1935, *H. F. Mooney 16* (K). **Meghalaya State:** Garo Hills, Damalgiri, October 1929, *Mrs. N. E. Parry s.n.*(K); Nongpoh, Khasi Hills, 19 April 1949, *W. N. Koelz 22512* (K). **Nagaland State:** Kohima District, Naga Hills, August 1886, *D. Prain s.n.* (US). **ANDAMAN AND NICOBAR ISLANDS. Nicobar District:** Car Nicobar, Arong Village, 31 May 1975, *N. G. Nair 2641* (L)**. SRI LANKA. Central Province:** Kandy District, Peradeniya above University Campus, on hill across stream at lower Hantane, 29 December 1969, *R. G. Cooray 69122906R* (US). **Sabaragamuwa Province:** Ratnapura District, 11 miles east of Daniyaya, along Highway 17 to Ratnapura, near mile post 62, 750 m, 22 October 1974, *G. Davidse 7869* (L, US)**. NEPAL. Myagdi District:** near Lumsum, 27 October 1954, *Stainton, Sykes & Williams 9154* (K). **Chitawan District:** Royal Chitawan National Park, Dudhowra, 230 m, 27°33'00'' N 84°29'00'' E, 11 November 1974, *T. R. Soderstrom 2095* (K). **Taplejung District:** between Yamphudin and Mamamkhe, 29 September 1989, *S. Crawford & al. 1084* (E, K). **BHUTAN. Samtse (Samchi) Province:** Dhoan Khola, 18 December 1963, *K. Thothathri 10440* (K). **BANGLADESH. Chittagong:** Tintilla, Kassalong River, Chittagong Hill Tracks, 15 November 1934, *C. E. Parkinson 4270* (US). **MYANMAR. Kachin State:** Myitkyina, 25°23'17.2'' N 97°24'02.9'' E, 20 October 1945, *R. O. Belcher s.n.* (US). **MALAYSIA.** Selongor State: Hulu Selangor, Bukit Tunggal F.R., 26 m, 3°33.33' N 101°24.50' E, 27 April 2016, *M. Y. Chew & al. FRI73092* (L). **Selongor State:** Petaling District, Shah Alam, 03°05' N 101°30' E, 50 m, 06 February 1987, *R. D. Worthington 12386* (L); Kanching, Tin Mines, 03 November 1937, *M. R. Henderson 34413* (K). **Negeri Sembilan State:** Jelebu, Berembun F. R., Jeram Toi, Jeram Toi Recreational Forest, entrance, 250 m, 02°51'00'' N 102°00'00'' E, 250 m, 10 April 2008, *T. L. Yao & al. FRI65275* (L); Seremban, Port Dickson, 16 February 1946, *Monod de Froideville 748* (L). **Kelantan State:** Kuala Krai, Cobra Camp, Campsite, 5°20.16'00'' N 101°55.13'00'' E, 936 m, 08 February 2007, *T. L. Yao & al. FRI 55788* (L). **Johor State:**

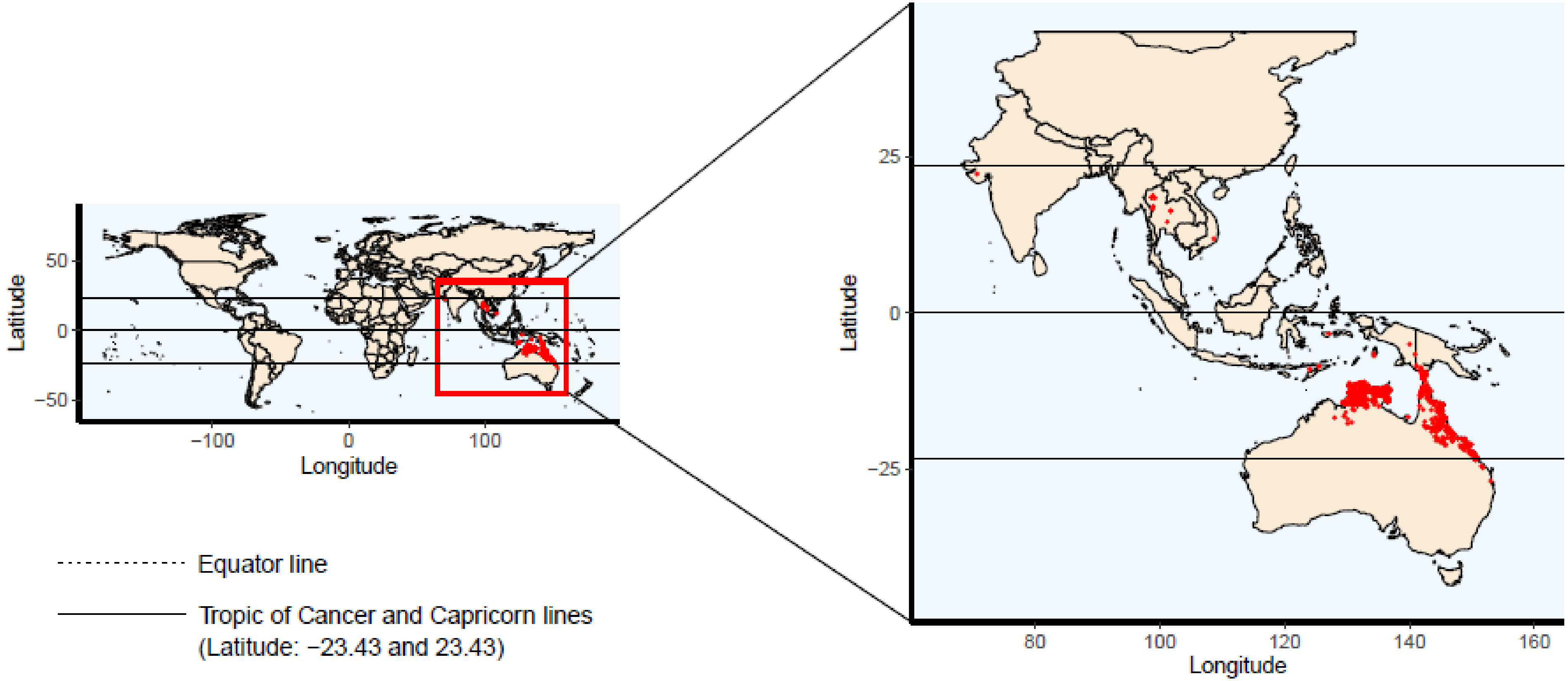
Segamat, 4 miles north of Labis, 17 November 1946, *M. R. Henderson 38214* (K); Labis District, Sungai Juasseh, 28 June 1970, *S. Ahmad S.267* (K, L). **Perak State:** Taiping, Tin Mines, 26 March 1924, I. H. xxx (K). **Kedah State:** Mount Jerai (Gunung Jerai), 3300 feet, 26 January 1964, *H. M. Burkill HMB.3289* (K, L). **Pahang State:** Cameron Highlands, 1500 m, February 1969, *A. O. s.n.* (L); Tasek Bera, Kampong Bapak, 28 October 1982, *R. Gainno A671* (L); near Temerloh, 21 April 1931, *R. E. Holttum 24655* (K); Lipis District, Kuala Lipis, May 1903, xxx 11523 (K). **SINGAPORE. Sungei Kadut area:** Mandai Quarry, off Woodland Road, 12 March 2022, *H. Duistermaat & K. Hillier S046* (L). **East Region:** Pasir Ris, 25 November 1980, *J. F. Maxwell 80-206* (L). **Central Region:** near 9th mile of Bukit Timah Road, 10 December 1949, *J. Sinclair s.n.* (L). **THAILAND. Narathiwat Province:** Sungai Kolok, Nikom Waeng, 03 March 1974, *K. Larsen & S. S. Larsen 32882* (K, L). **Satun Province:** Khuan Kalong District, Thung Nui, *A. F. G. Kerr 14643* (K). **Krabi Province:** Khao Panom District, Khao Panom, 23 March 1930, *A. F. G. Kerr 18648* (K). **Surat Thani Province:** 75 km north of Chumphon, July-August 1966, *K. Larsen, T. Smitinand & E. Warncke 1429* (K). **Chiang Mai Province:** Chiang Dao, Chiang Dao Hills, along road below park warden house, 28 September 2001, *S. Lægaard & M. Norsaengsri 21640* (K). **Trang Province:** Huai Yot District, Thale Song Hong, 09 April 2003, *D. J. Middleton & al. 2060* (K, L). **Mae Hong Son Province:** Mae Sariang District, 20 km west of Bo Luang, 04 July 1968, *K. Larsen, T. Santisuk & E. Warncke 2102* (K). **Nakhon Si Thammarat Province:** Lan Saka District, Kamlon, Khiriwong, 14 April 1952, *T. Smitinand 1288* (K, L). **Chumphon Province:** Pathio District, Ban Pak Khlong, 12 January 1927, *A. F. G. Kerr 11392* (K). **Songkhla Province:** Na Thawi District, 15 July 1928, *Rabil 78* (K). **Kanchanaburi Province:** Mueang Kanchanaburi District, Ban Kao Subdistrict, 09 November 1971, *C. F. van Beusekom & al. 3595* (K). **VIETNAM. Northeast Region:** Lang Son Province, mountain Cai Kinh, road from Than Moi to Tonkin, 04 December 1902, *D. Bois 145* (K). **Red River Delta Region:** Haiphong Province, 10 July 1885, *B. Balansa 486* (K, L); Nam Định Province, 22 November 1913, *Aug. Chevalier 29031* (K); Ninh Binh Province, Nho Quan District, Cuc Phuong National Park, 13 December 1998, *D. D. Soejarto & al. 11350* (L); Ninh Binh Province, Nho Quan District, CPNP, Sam Village, 17 November 2005, *M. V. Xinh MVX270* (L). **North Central Coast Region:** Thừa Thiên Huế Province, Huế, Jan-May 1927, *R. W. Squires 196* (K); Quảng Trị Province, 14 June 1924, *anonymous s.n.* (L); Mekong Delta Region: between An Giang and Hatien, 26 April 1939, *E. Poilane 27463* (K, L). **Northwest Region:** Lai Châu province, Pou Nhou, 1 June 1938, *M. Poilane 27002* (K, L). **South Central Coast Region:** 25 km from Da Nang (Tourane), Mount Bani, May-July 1927, *J. & M. S. Clemens 3732* (K, L). **INDONESIA. Jambi-Sumsel Province:** Hutan Harapan, Tanjakan kakak beradik, 04 April 2013, *Wardi, Ruhiyat & Jupri BOHK430* (K).**North Sumatra Province:** Tanah Karo Regency, Sipiso-piso and vicinity, 8 April 1929, J. A. Lörzing 15580 (K); Karo Regency, Berastagi, February 1920, *H. N. Ridley s.n.* (K); Karo Regency, Berastagi, 26 May 1923, *H. S. Yates 515* (US); vicinity of Rautau Parpat, Bila, 10 March to 28 May 1932, *R. S. Boeea 1843* (US); Asahan Regency, Serbangan (Si Horbangan), 12 October 1935, *R. S. Boeea 8395* (K); Asahan, vicinity of Loemban Ria, 05 February to 12 April 1934, *R. S. Boeea 7401* (US); Asahan, Aidang Rindang, vicinity of Hoeta Tomoen Dolok, 17 November to 10 December 1935, *R. S. Boeea 8553* (US). **West Sumatra Province:** 45 km from Padang, road to Batang Baras, 1000 m, 11 July 1999, *H. J. Siwon 1050* (L); road from Padang to Telasa Kembar, roadside near tea plantation, 1500 m, 11 July 1999, *H. J. Siwon 1055* (L); Gunung Talang, Laras Talang, 1300 m, 13 November 1918, *Bünnemeijer 5674* (L); West Sumatra Province: Solok Regency, Alahan Panjang, 04 October 1979, *J. C. Whitehead & J. R. Flenley JW187* (K). **Aceh Province:** Kampong Burni Bies, northwest of Takingeun, 1200 m, 03 September 1971, *K. Iwatsuki & al. S1572* (K, L). **West Java Province:** Parahyangan (Preanger), Tjidadap plantations, 1000 m, 29 April 1916, *R. C. B. van den Brink 3856* (L); Bogor, Baranangsiang, 250 m, 02 July 1982, *M. Rahayu 78* (L); Cianjur Regency, Ciwalen (Tjiwalen), Cibodas (Tjibodas), Mount Gedeh (Gunung Gede), 3 m, 25 March 1950, *S. J. van Ooststroom 13169* (L). **Central Java Province:** Cilacap Regency, Madjenang, Banyumas (Banjoemas), 30 m, 1915, *C. A. Backer 10515* (L). **Southeast Sulawesi Province:** Kolaka District, Uluiwoi Subdistrict, Pohanggu Village, Pohanggu Protected Forest, 500 m, 17 April 2011, *E. A. Widjaja & al. EAW9536* (L). **East Nusa Tenggara Province:** Manggarai, Ruteng, 1000-2000 m, *J. A. J. Verheyen 751* (L); Sumba, Waikabubak, 400 m, 28 May 1950, *C. Monod de Froideville 1838* (US). **East Kalimantan Province:** West Kutai Regency, Long Poehoes, 17 November 1925, *F. H. Endert 5031* (L); Western part of Samarinda, 0-50 m, 02 January 1979, *G. Murata & al. B-206* (L). **Central Sulawesi Province:** Poso Regency, Lore Timur Maholo Village, 01°28’54.7’’ N 102°23’04.9’’ E, 1130 m, 04 September 2013, *E. A. Widjaja & E. A. Hamzah EAW9971* (L). **Southern Sulawesi Province:** Maros, near Tompok Balang, 20 m, 27 September 1975, *S. Soenarko 324* (L). **Northern Sulawesi Province:** Menado, Paloe, east of Lindoe Lake, from kali Tokararoe to the lake, west slope of Gunung Ngilalaki, 1000 m, 11 July 1939, *P. J. Eyma 4049* (L). **BRUNEI.** Belait: Labi, Kampung Labi, 20 m, 10 March 1992, *S. Dransfield & al. 1272* (L). **TIMOR-LESTE. Kenutu:** about 1.5 km south of “Rock of Kapan”, 1000 m, 10 March 1939, *S. Bloembergen 3427* (US). **THE PHILIPPINES. Davao Region:** Lone District, Malita, Silangan Mountain, near Kabasalan, 26 December 1940, *L. E. Ebalo 854* (US). **NIGERIA. Taraba State:** Mambilla Plateau, 09 October 1971, *J. D. Chapman 2571* (L). **USA. Hawaii:** Oahu, Honolulu, Waipio Valley, 244 m, 20 January 1963, *O. Degener & I. Degener 29849* (US); Oahu, Honolulu, Mokuleia, southwest of Dillinghan Ranch, 12 March 1937, *O. Degener & al. 11058* (US); Hilo, Hilo Reserve Forest, 16-mile marker on Saddle Road, 200 m, 19°41’11’’ N 155°17’38.4’’ W, 07 July 1997, *C. R. Annable & al. 3604* (US).

Appendix XV. Distribution maps of *Heteropogon* and *Themeda*

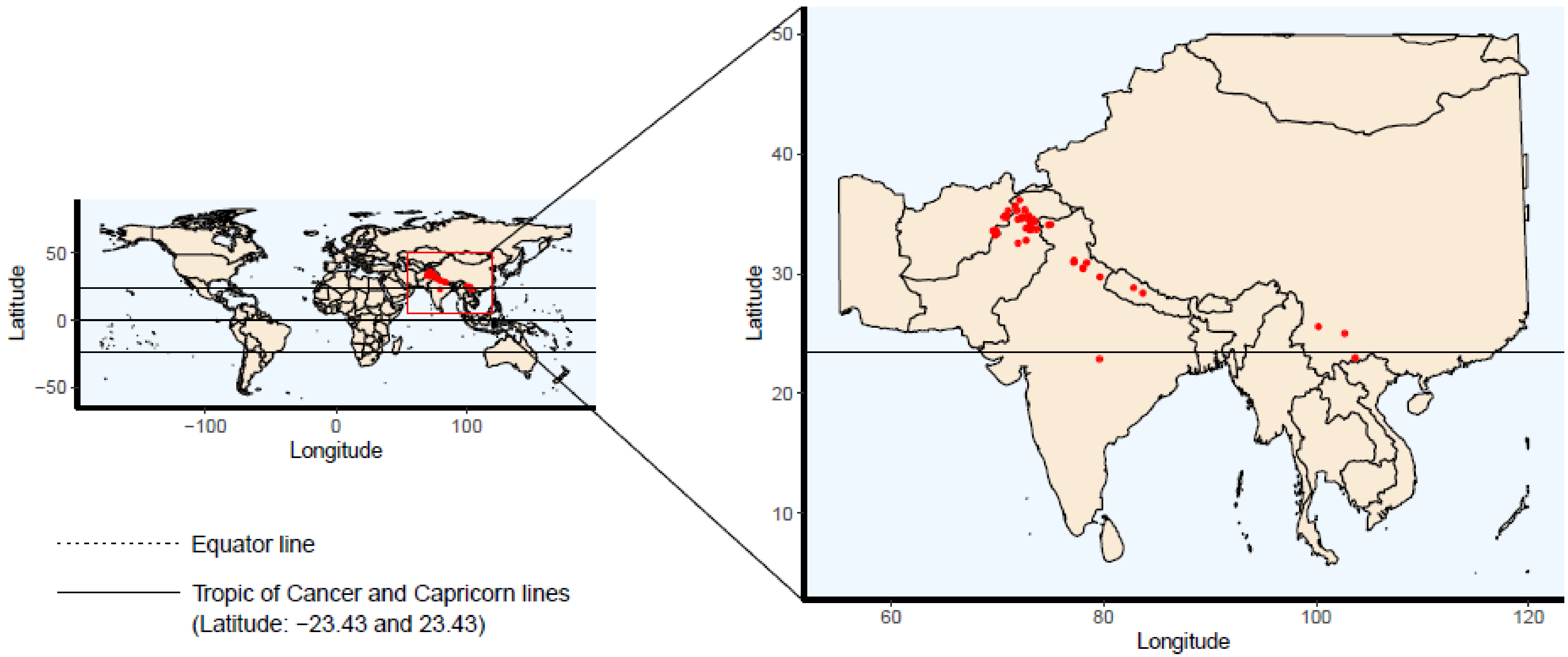
Distribution map of *Heteropogon contortus*



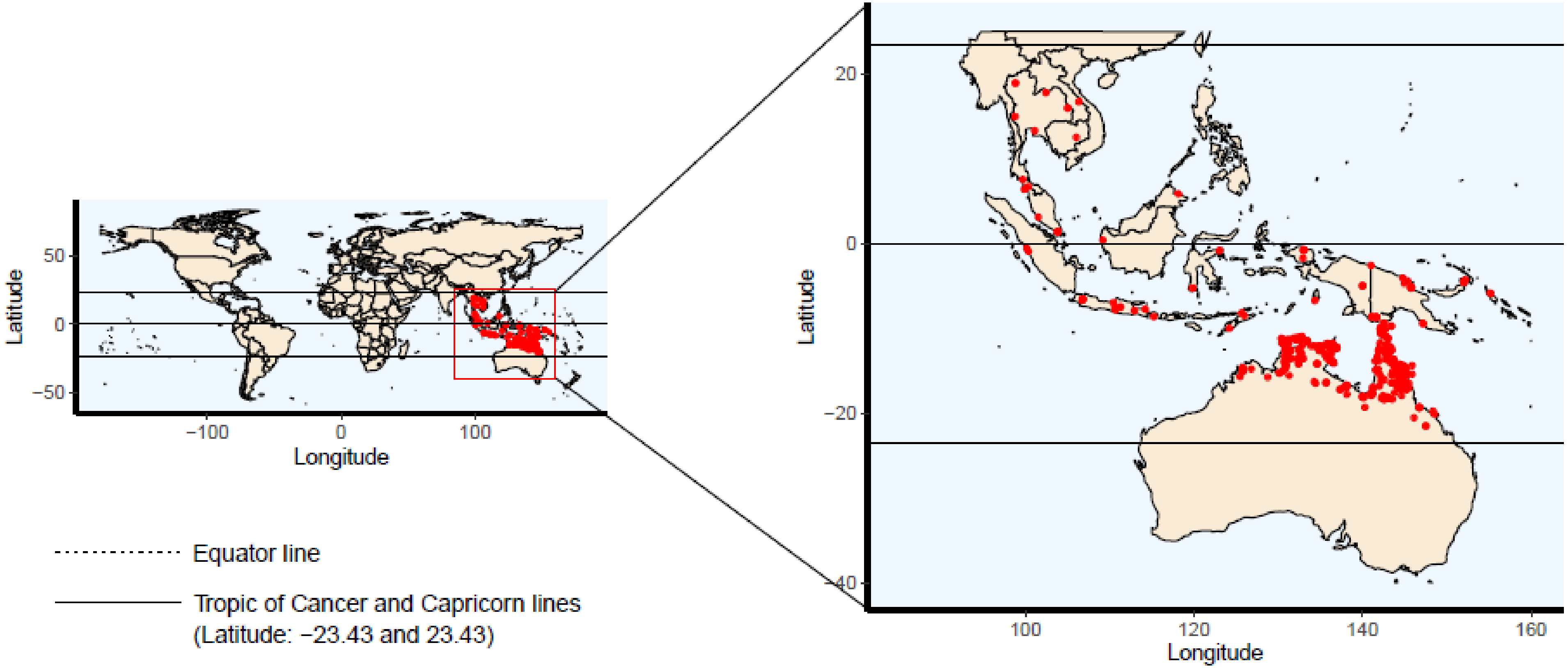
Distribution map of *Heteropogon triticeus*



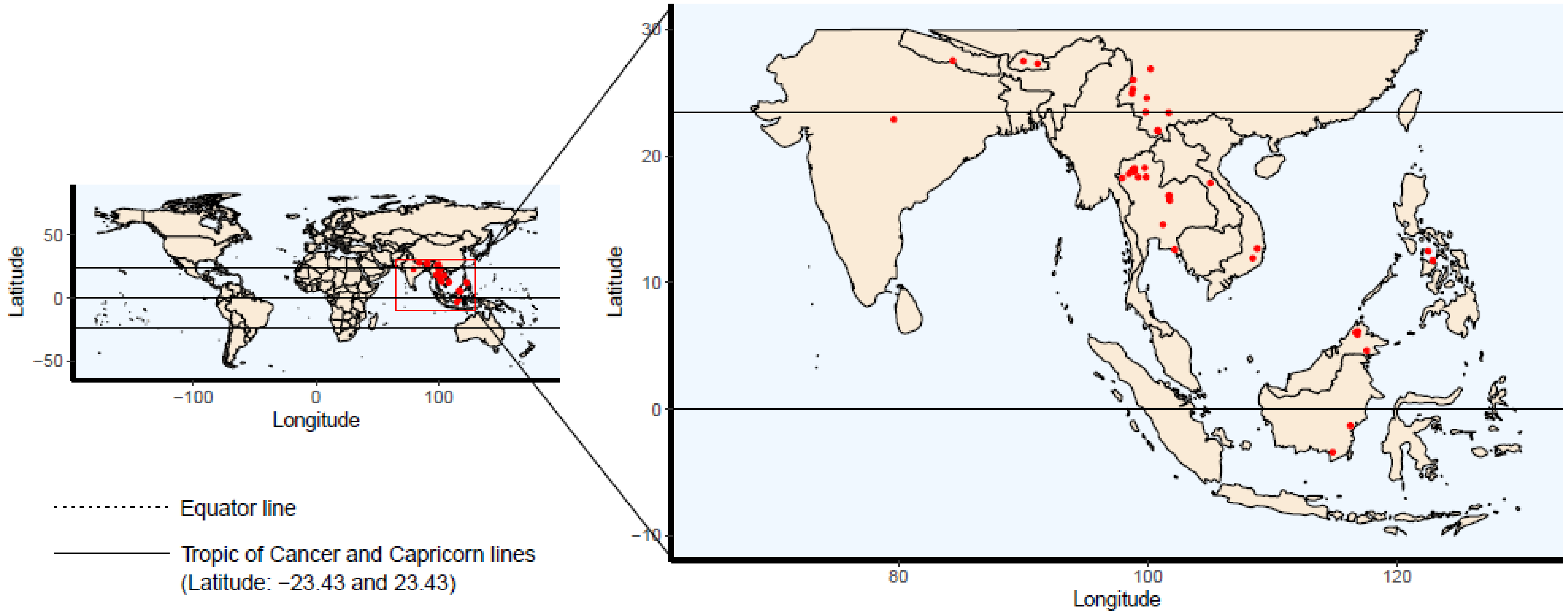
Distribution map of *Themeda anathera*



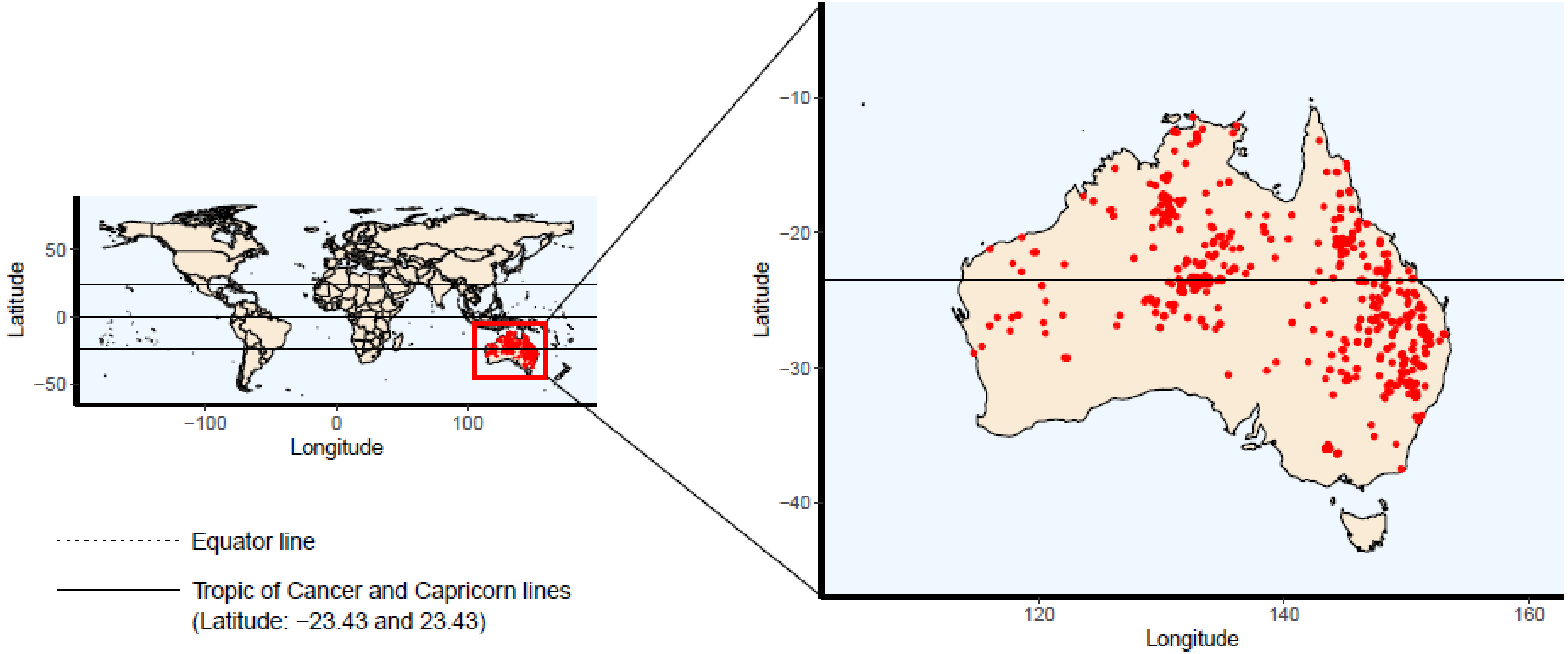
Distribution map of *Themeda arguens*



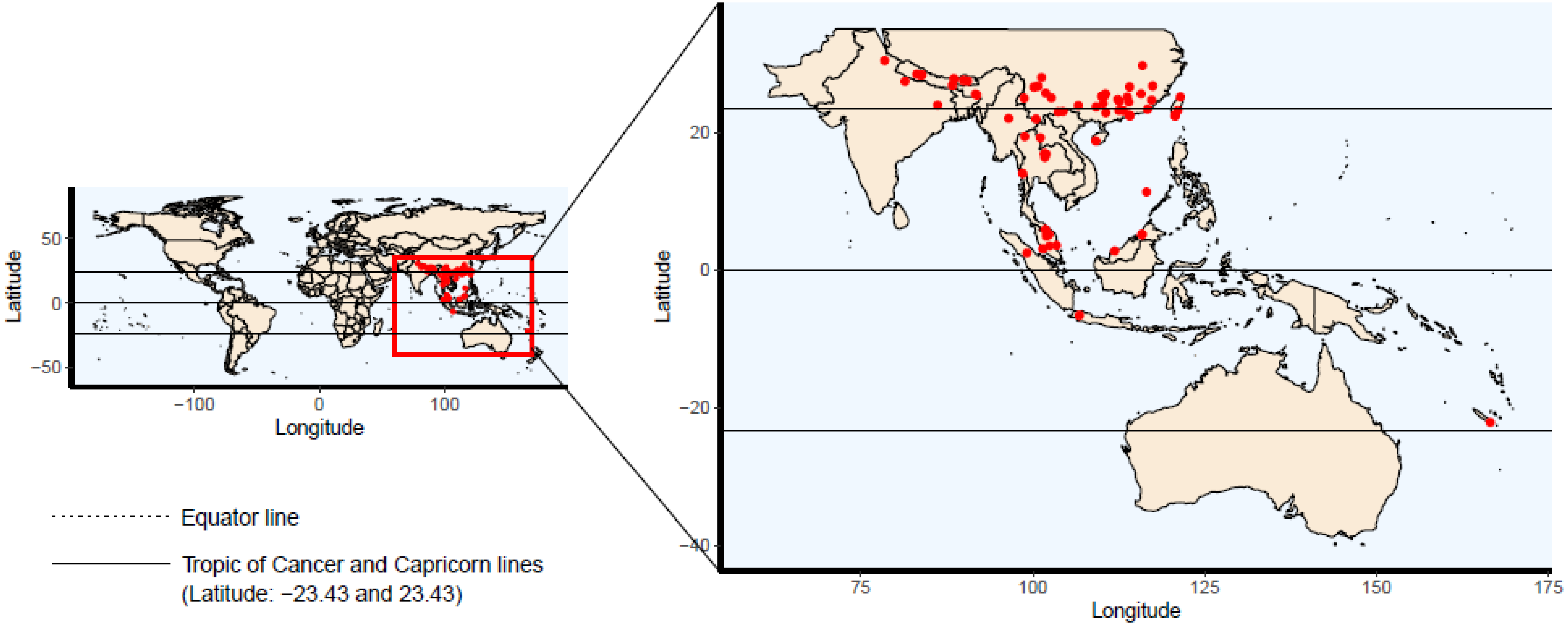
Distribution map of *Themeda arundinacea*



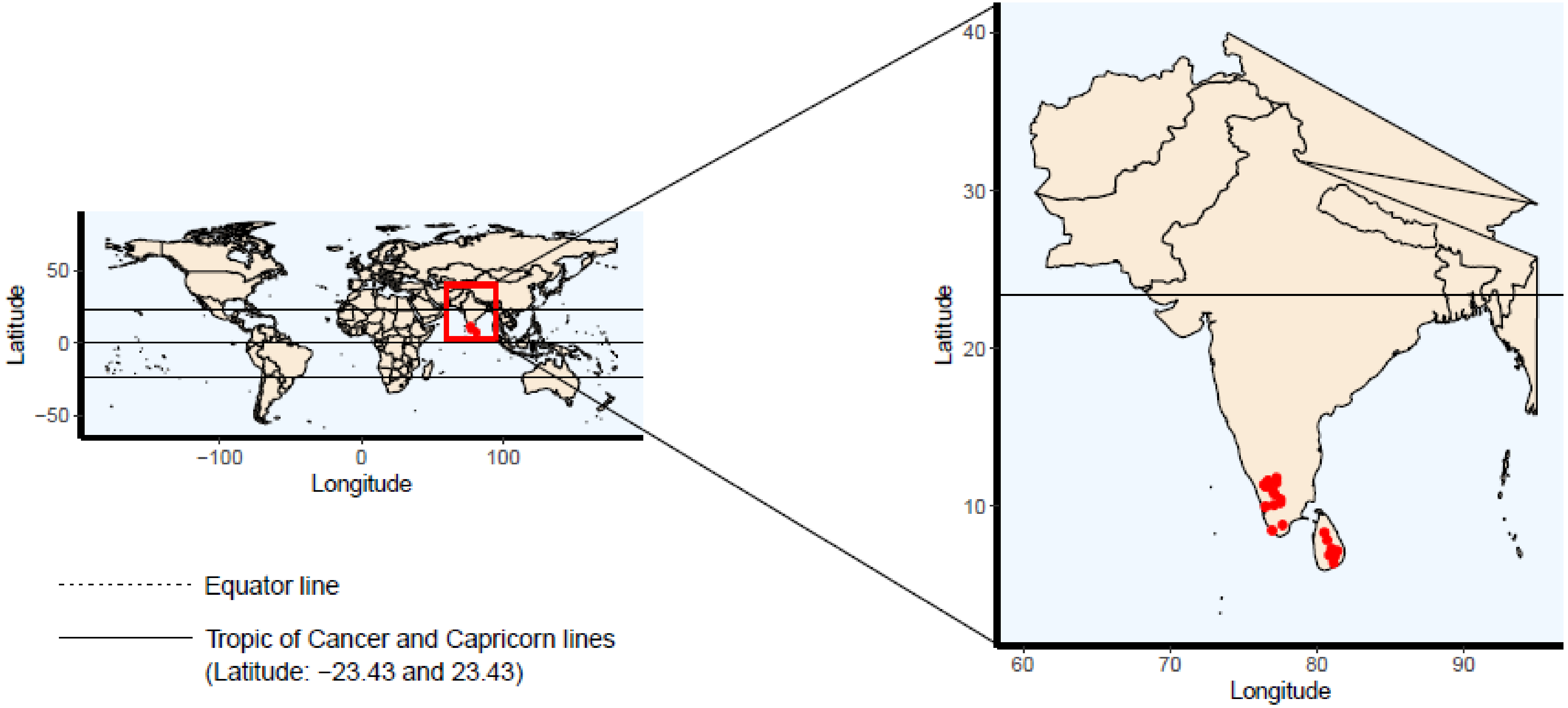
Distribution map of *Themeda avenacea*



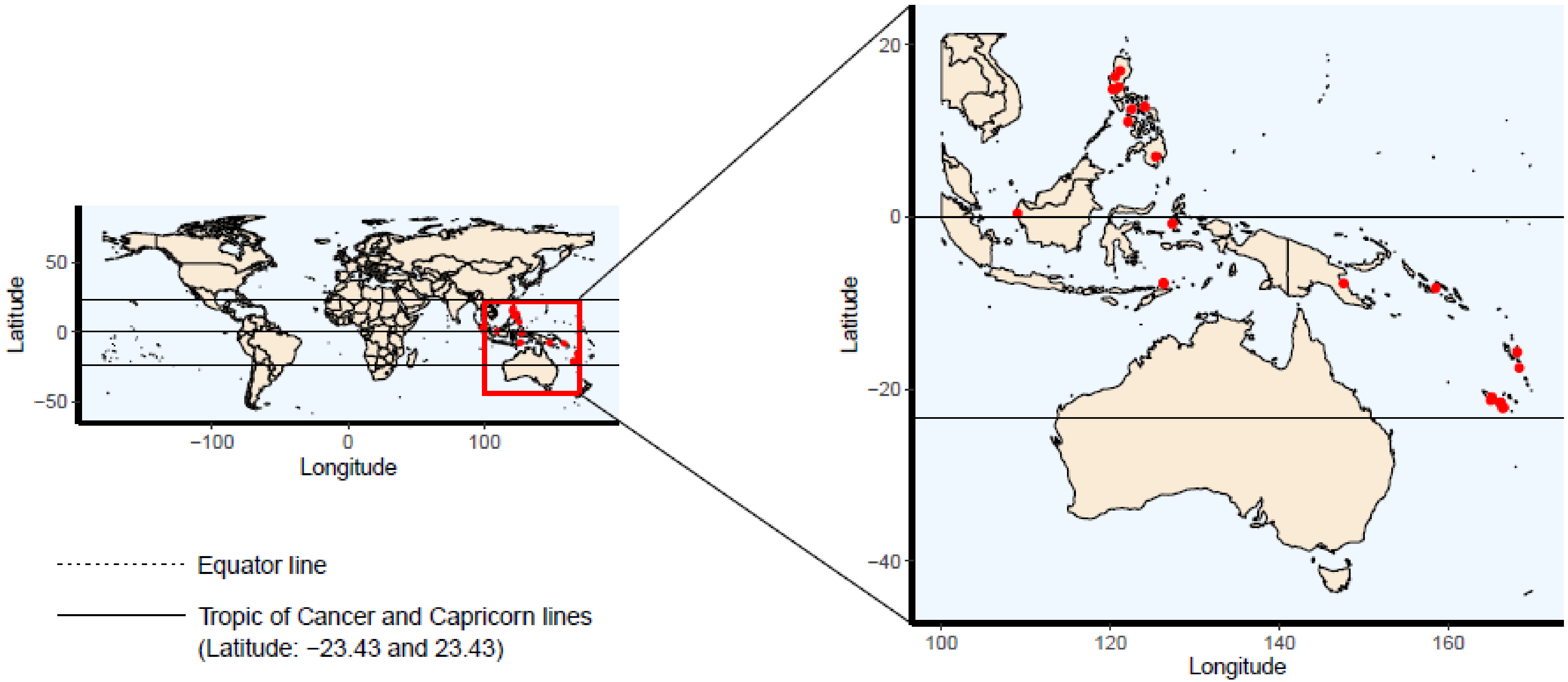
Distribution map of *Themeda caudata*



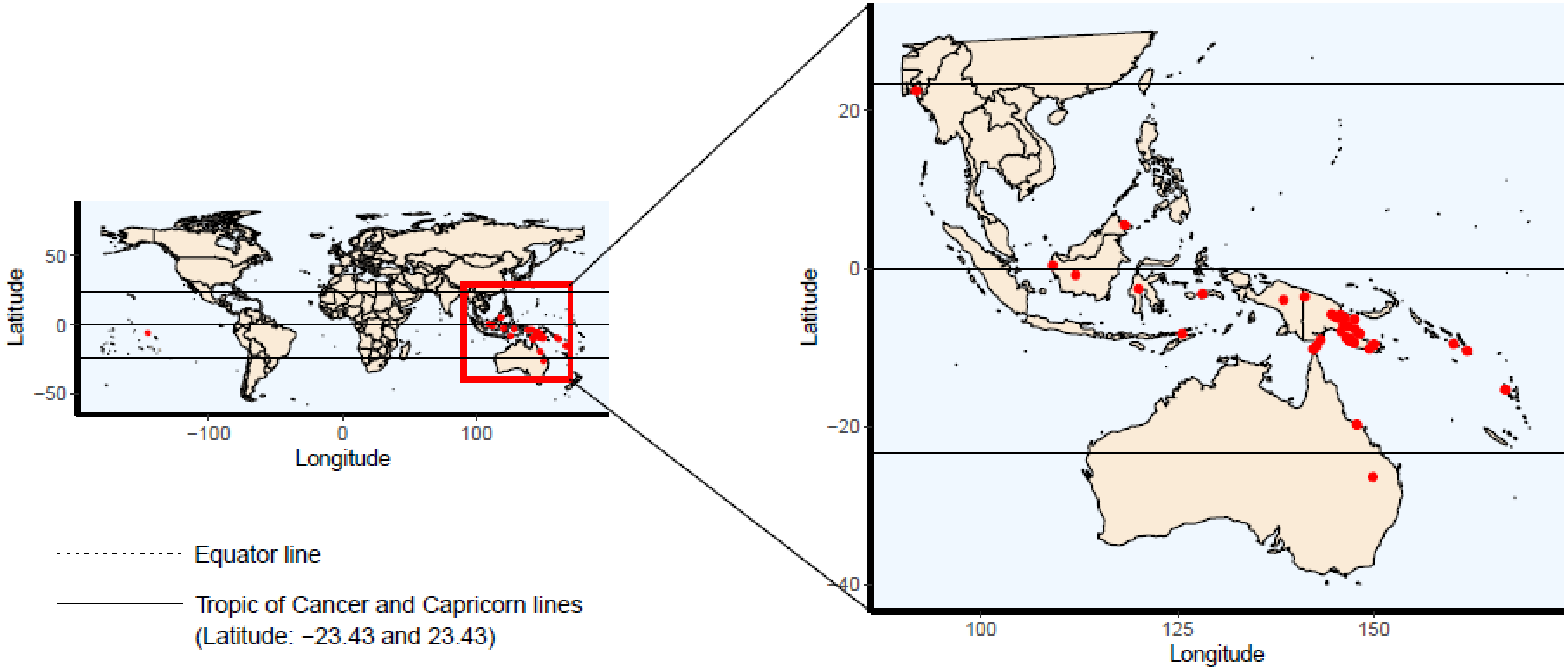
Distribution map of *Themeda cymbaria*



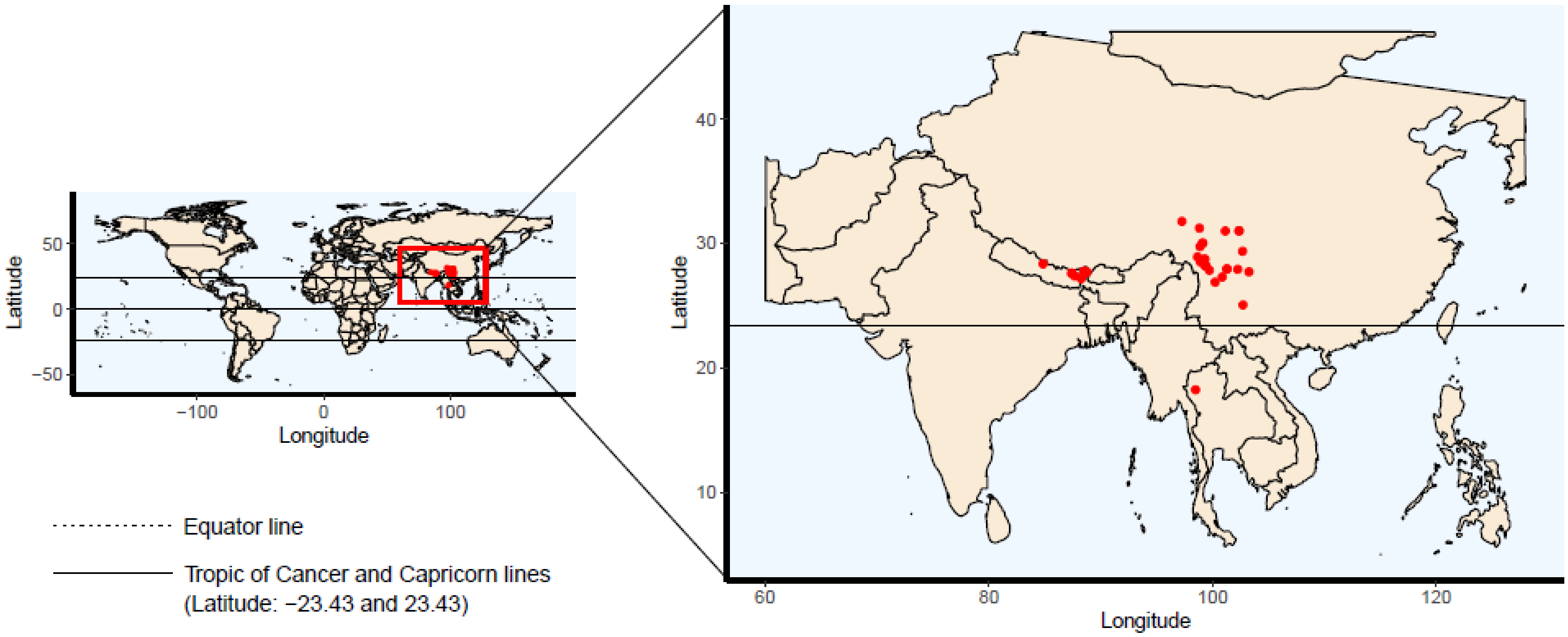
Distribution map of *Themeda gigantea* var. *gigantea*



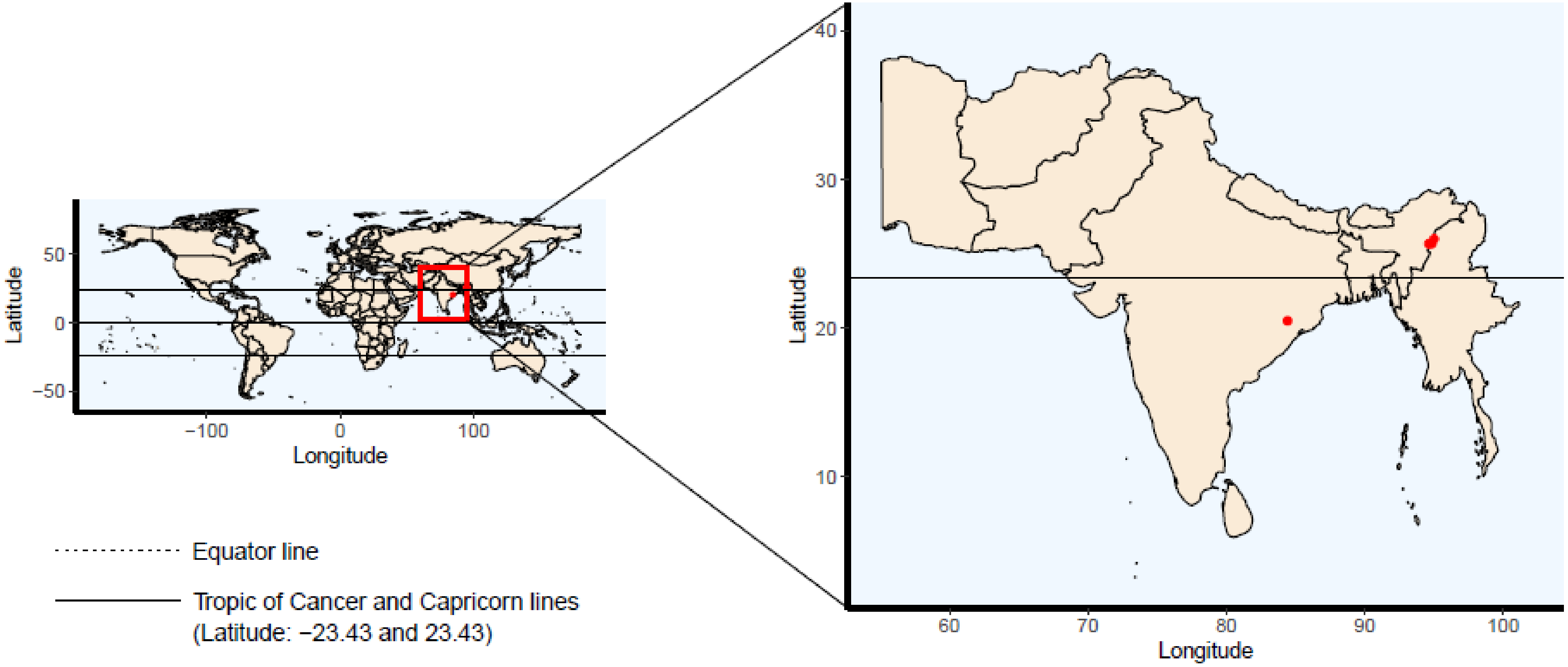
Distribution map of *Themeda gigantea* var. *intermedia*



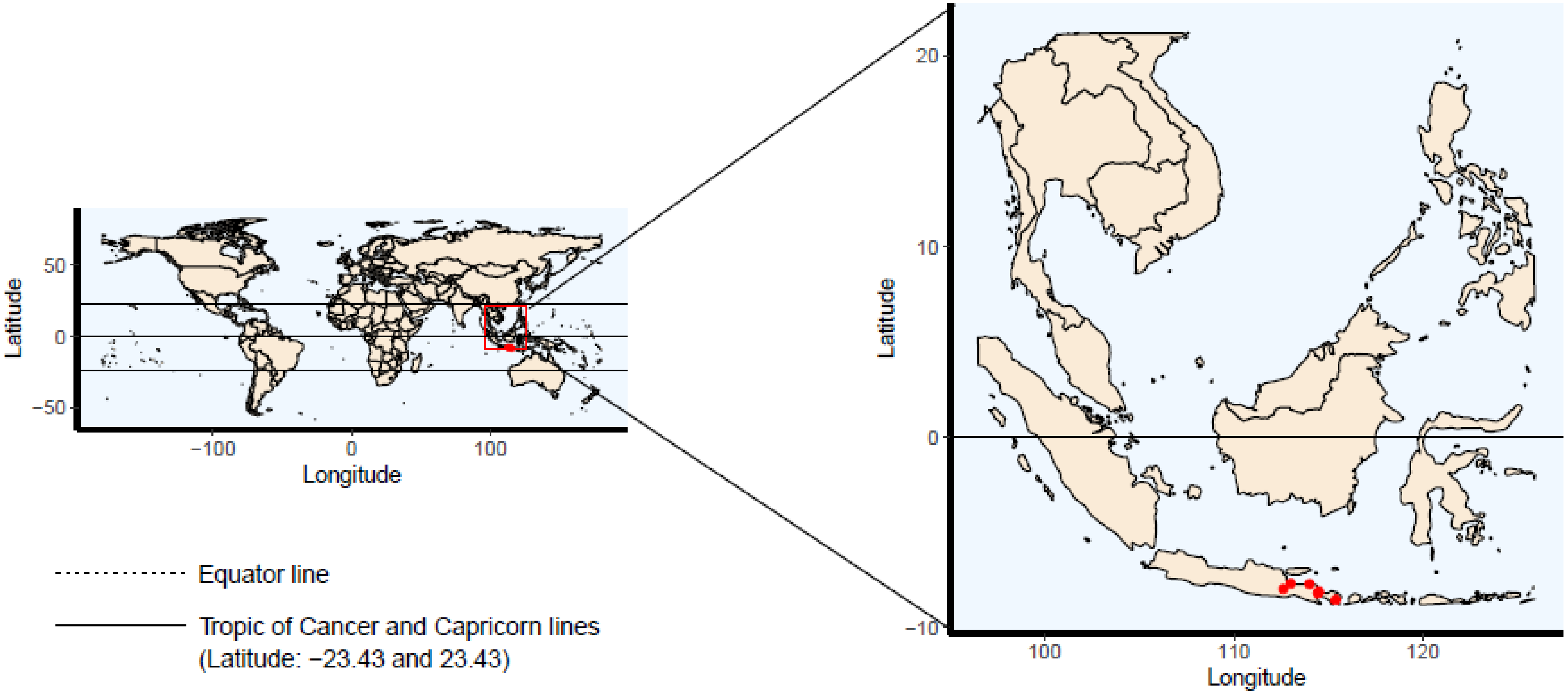
Distribution map of *Themeda hookeri*



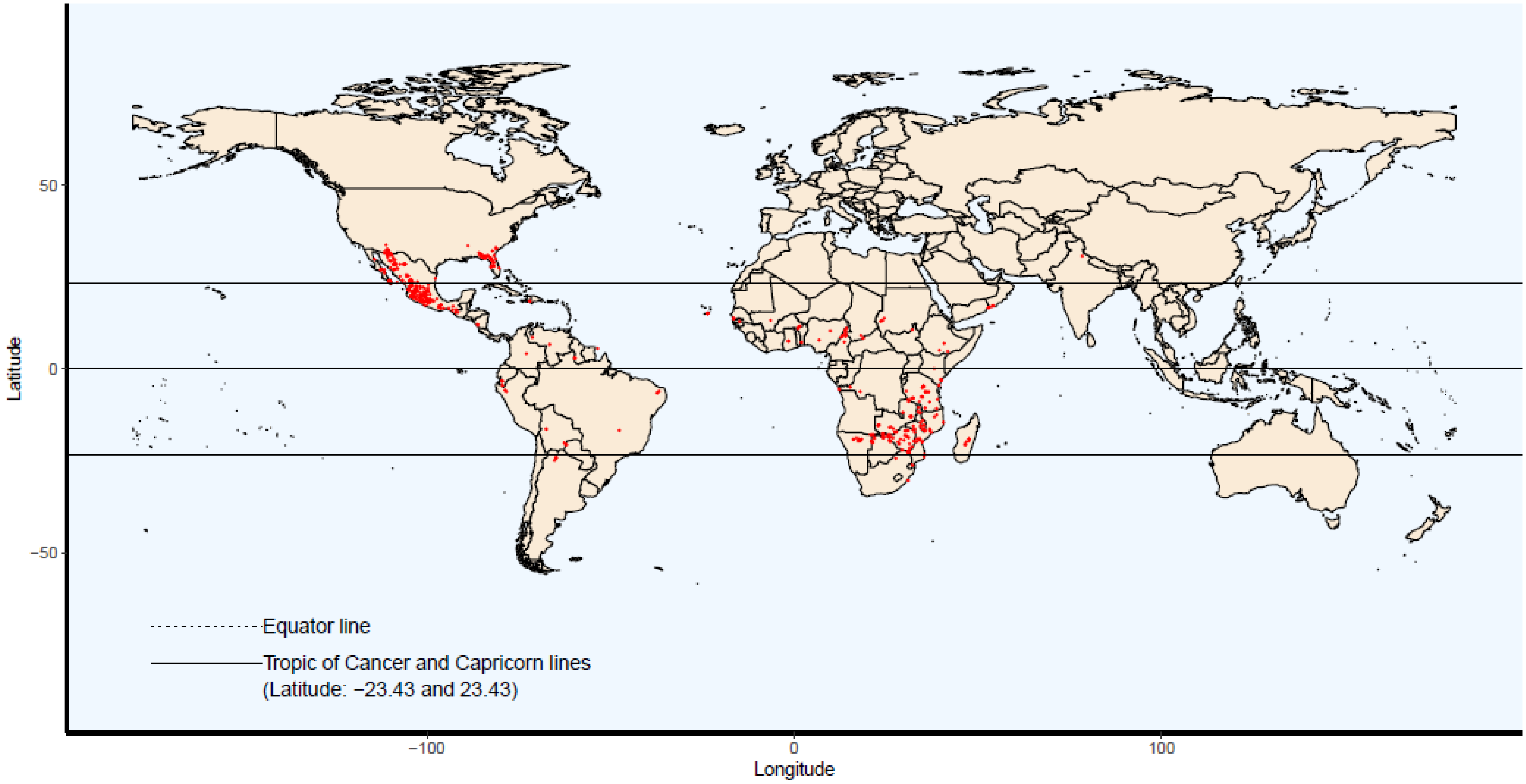
Distribution map of *Themeda huttonensis*



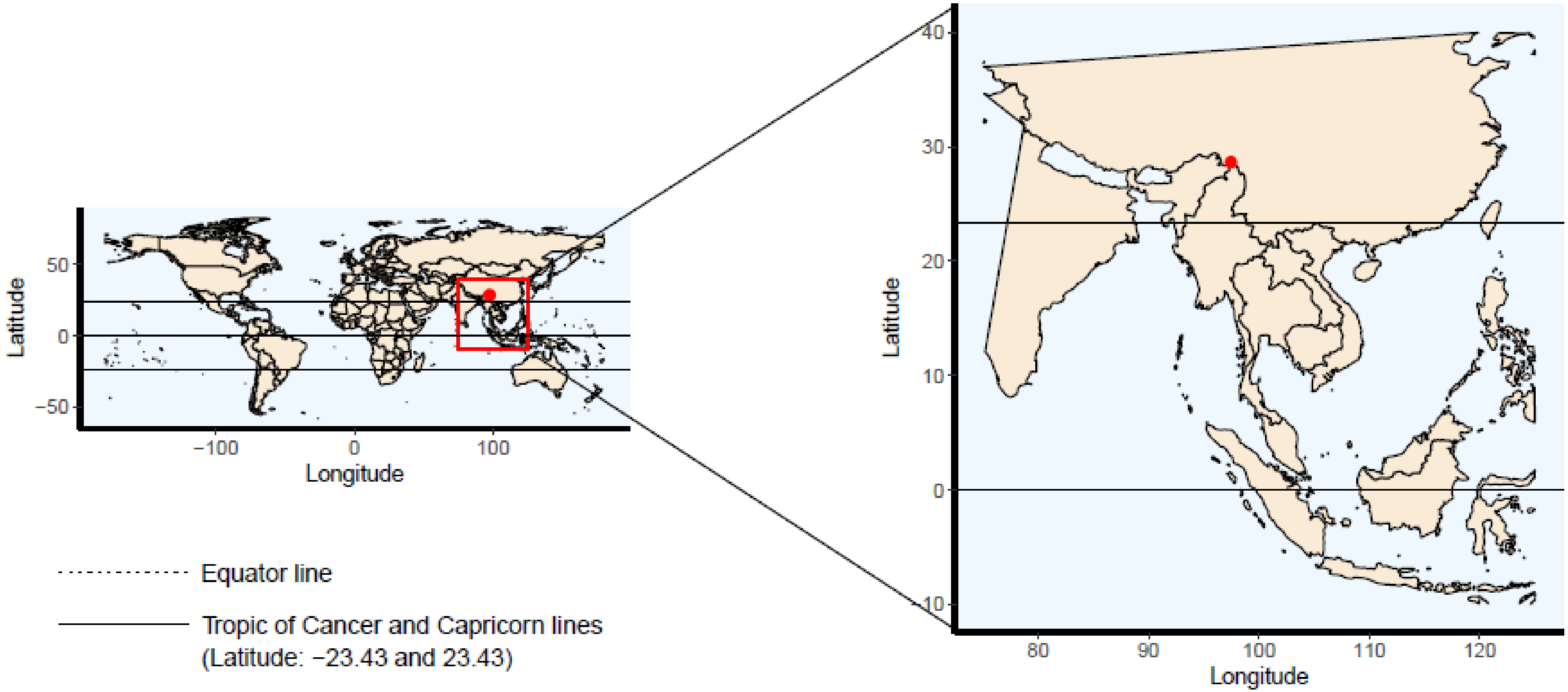
Distribution map of *Themeda idjenensis*



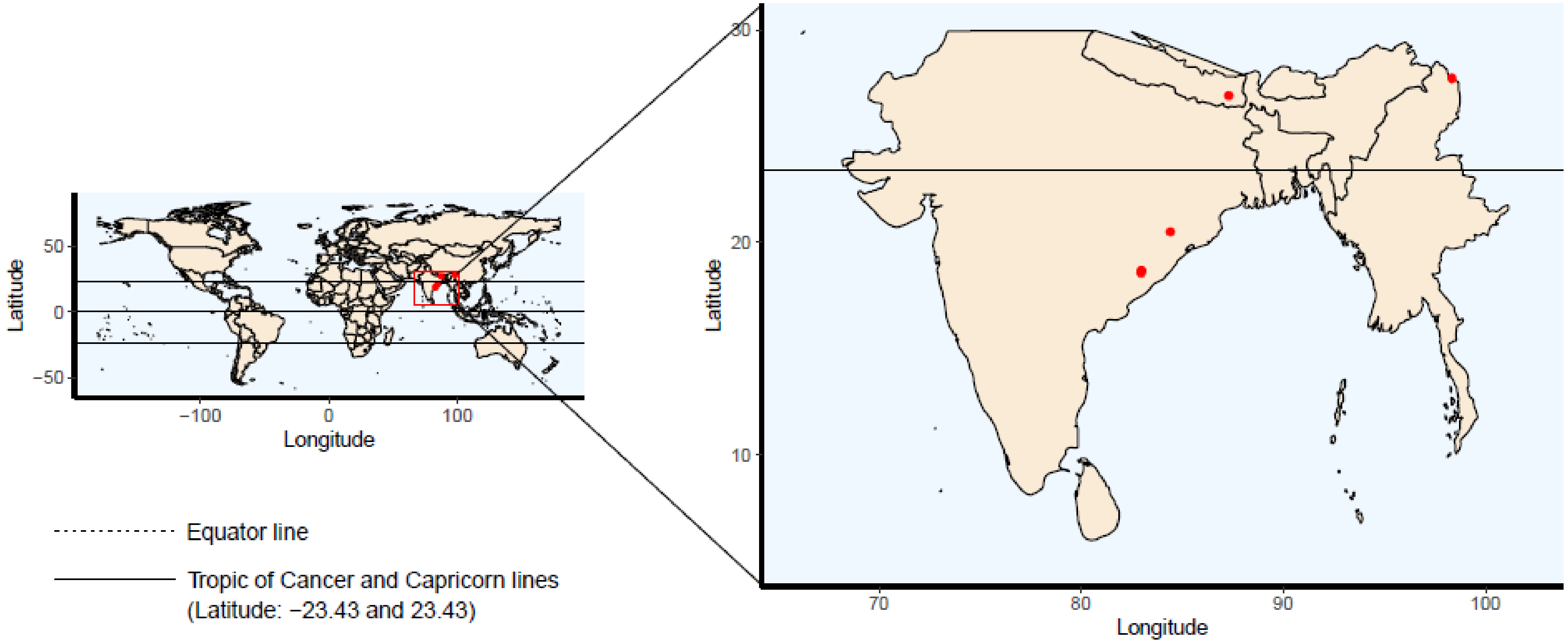
Distribution map of *Themeda melanocarpa*



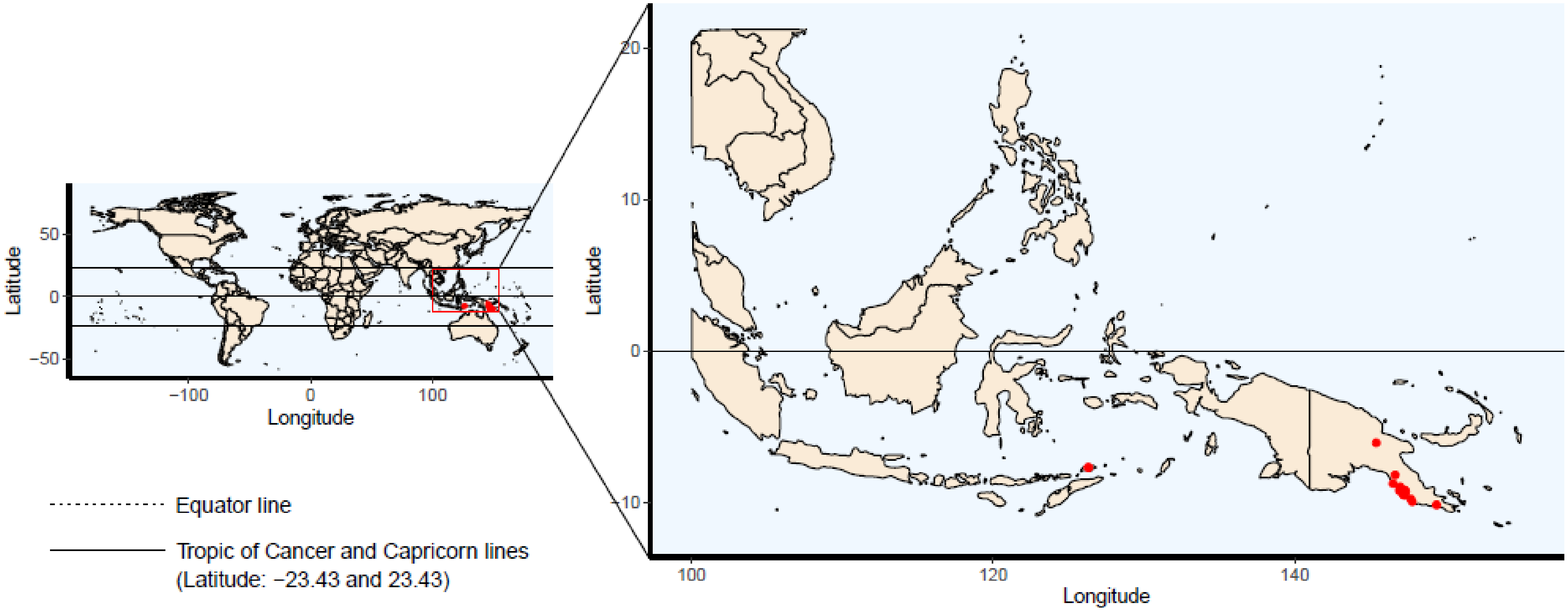
Distribution map of *Themeda minor*



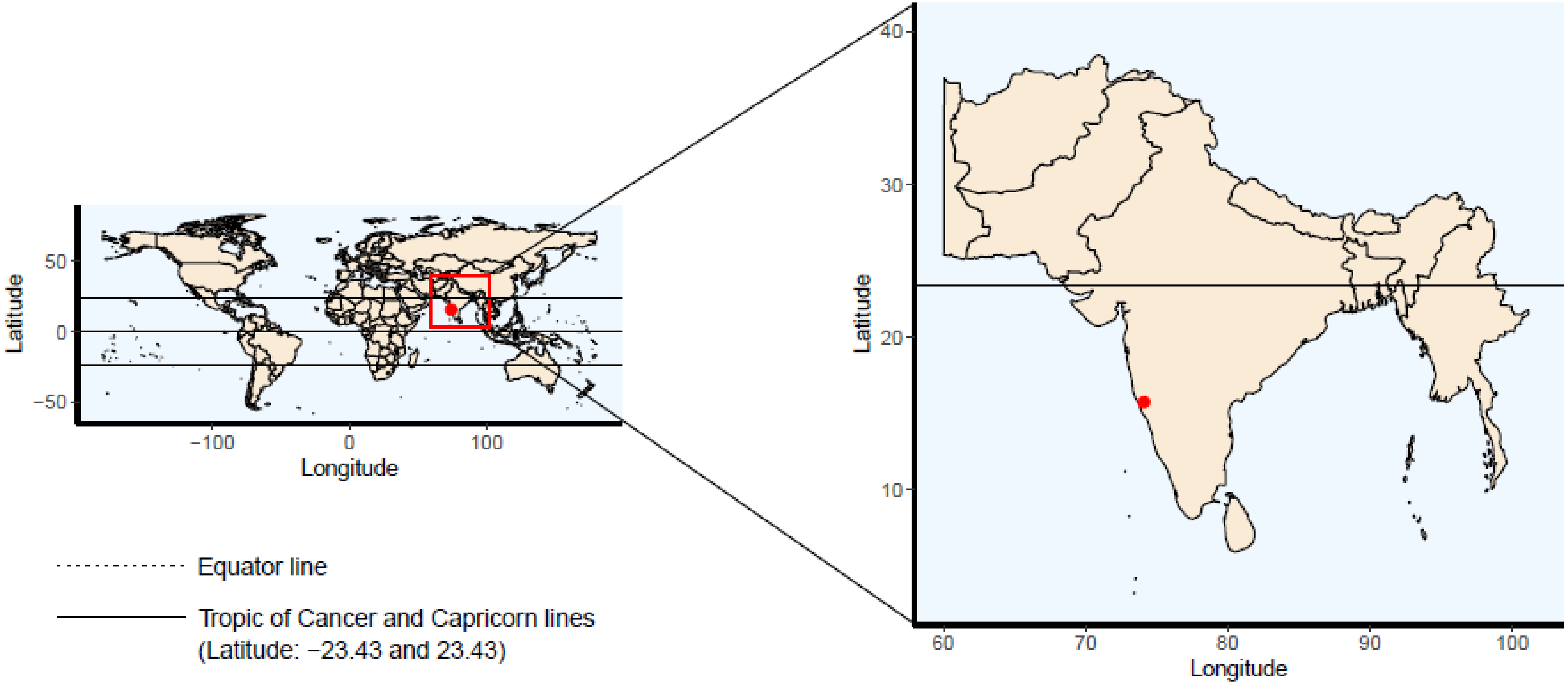
Distribution map of *Themeda mooneyi*



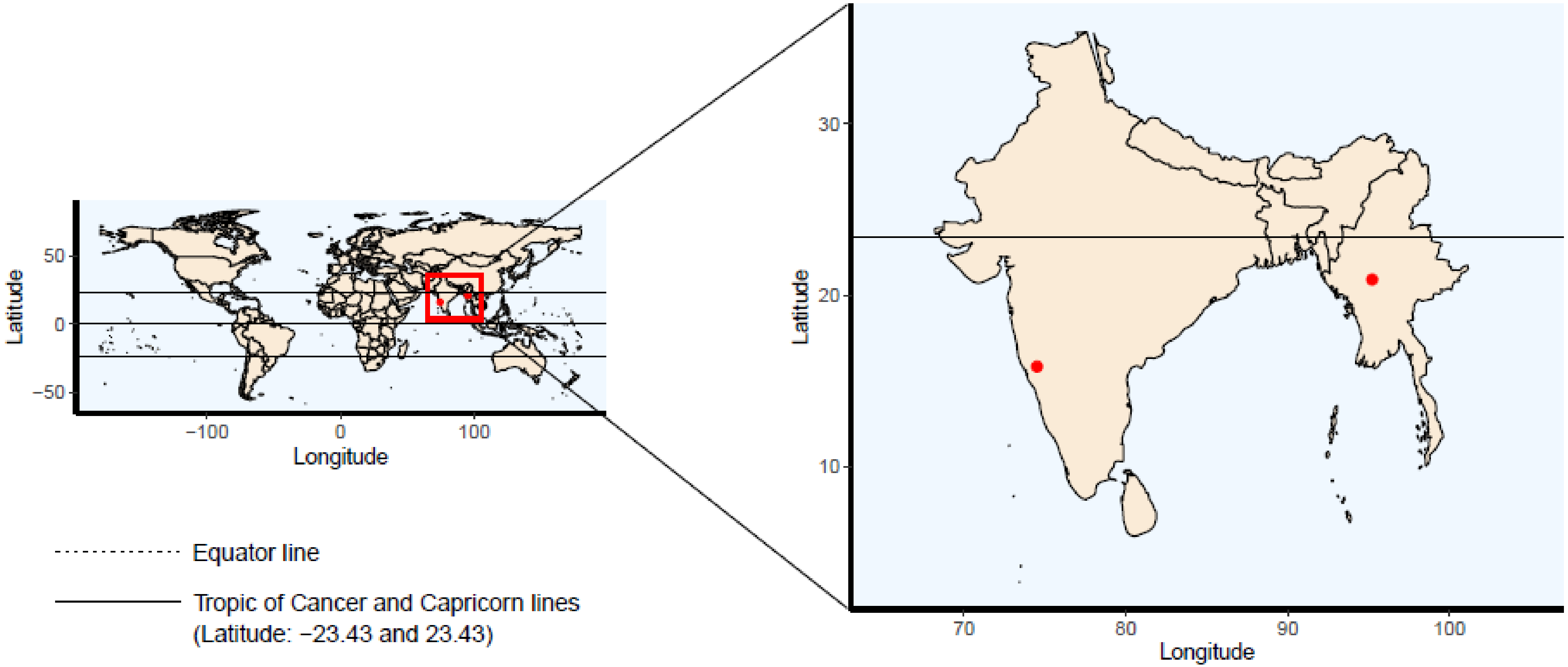
Distribution map of *Themeda novoguineensis*



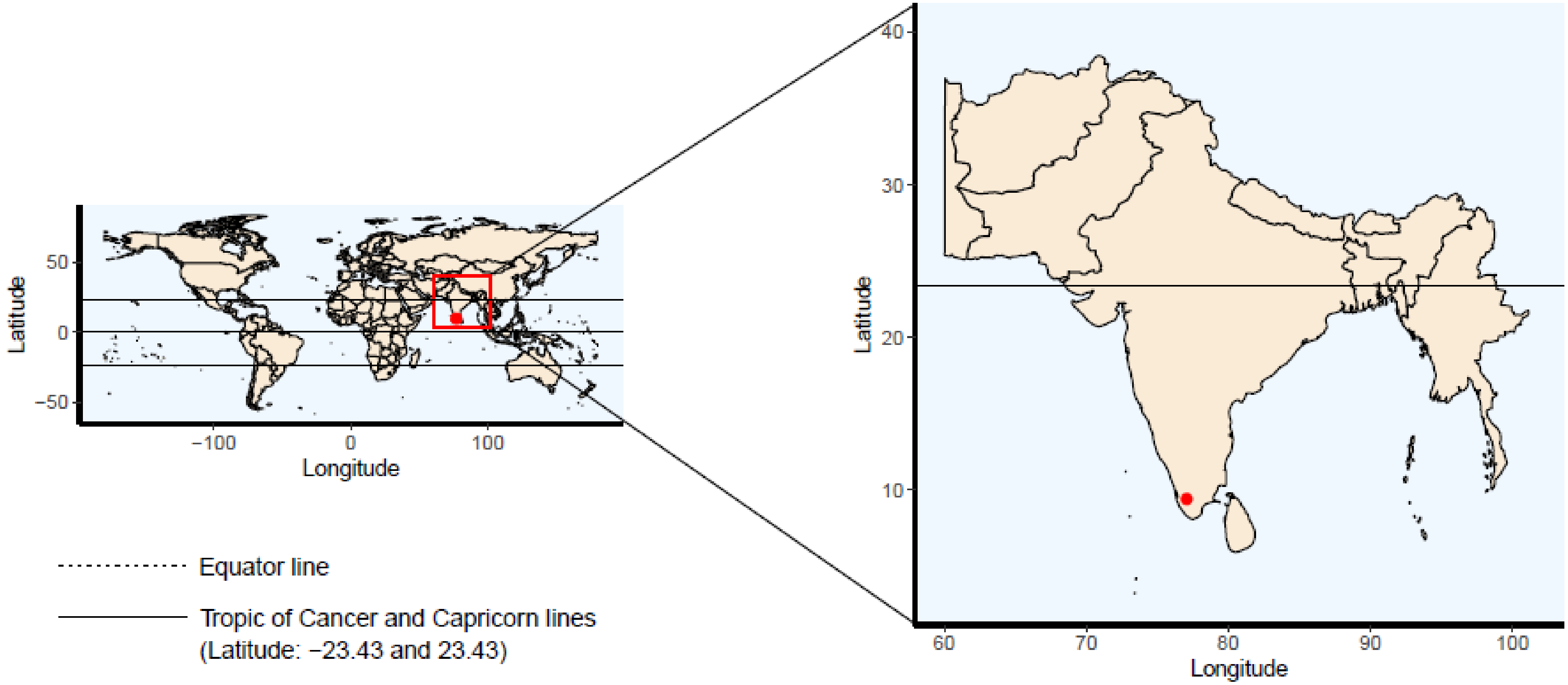
Distribution map of *Themeda pseudotremula*



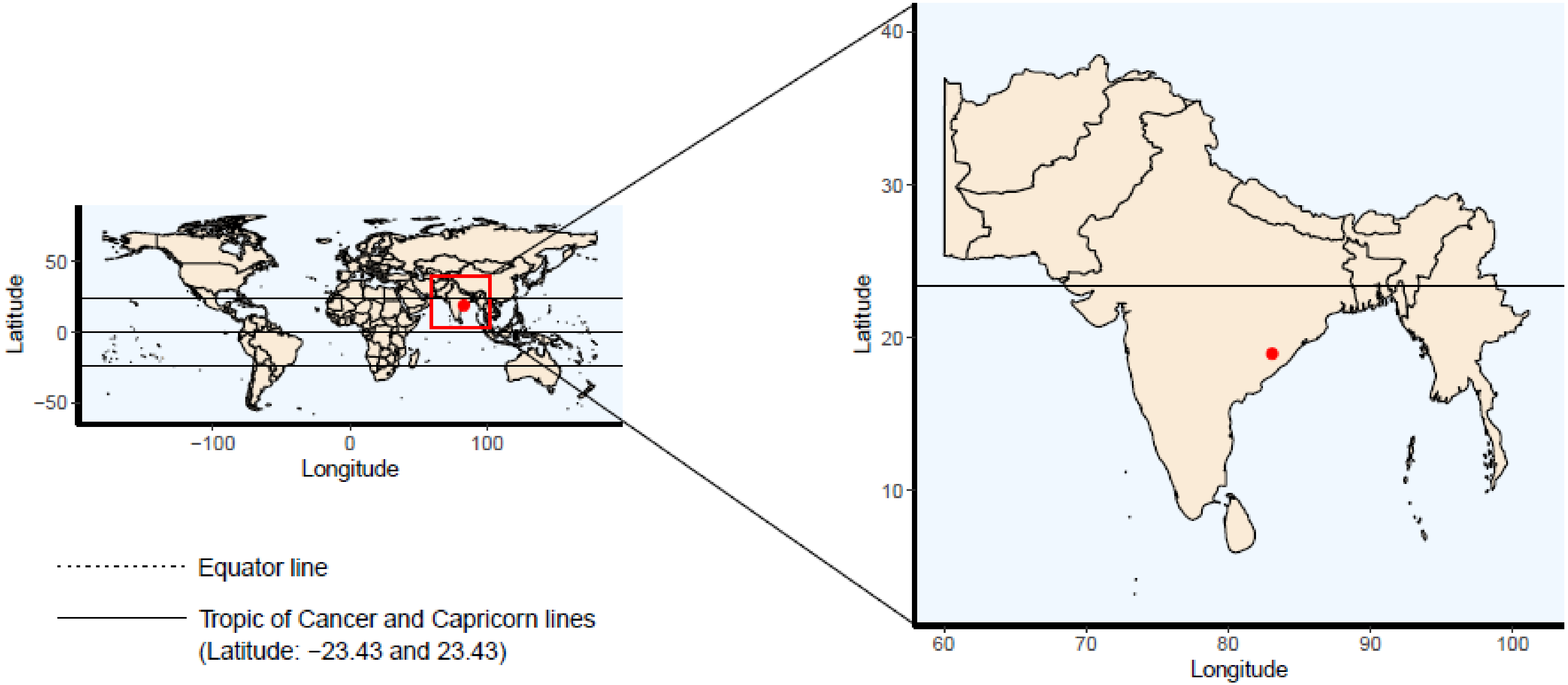
Distribution map of *Themeda ritchiei*



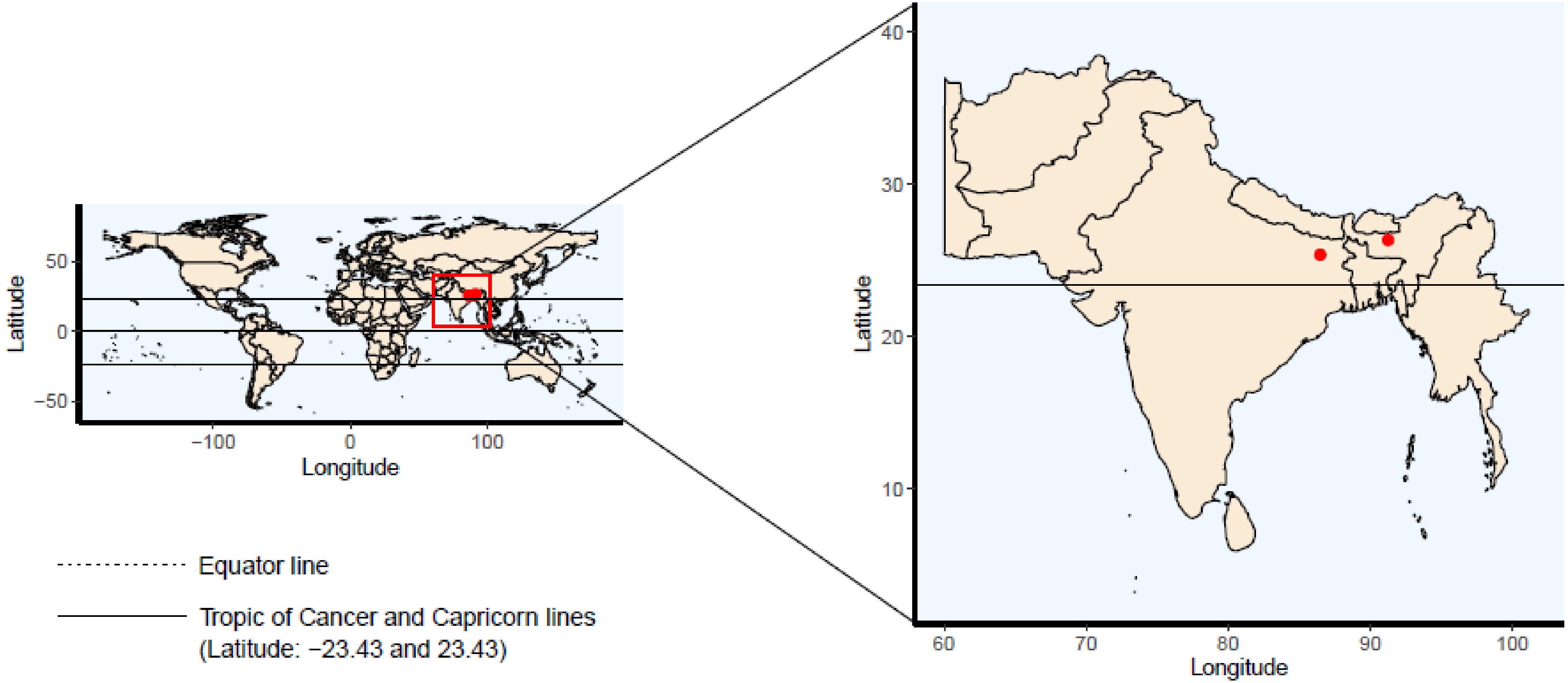
Distribution map of *Themeda sabarimalayana*



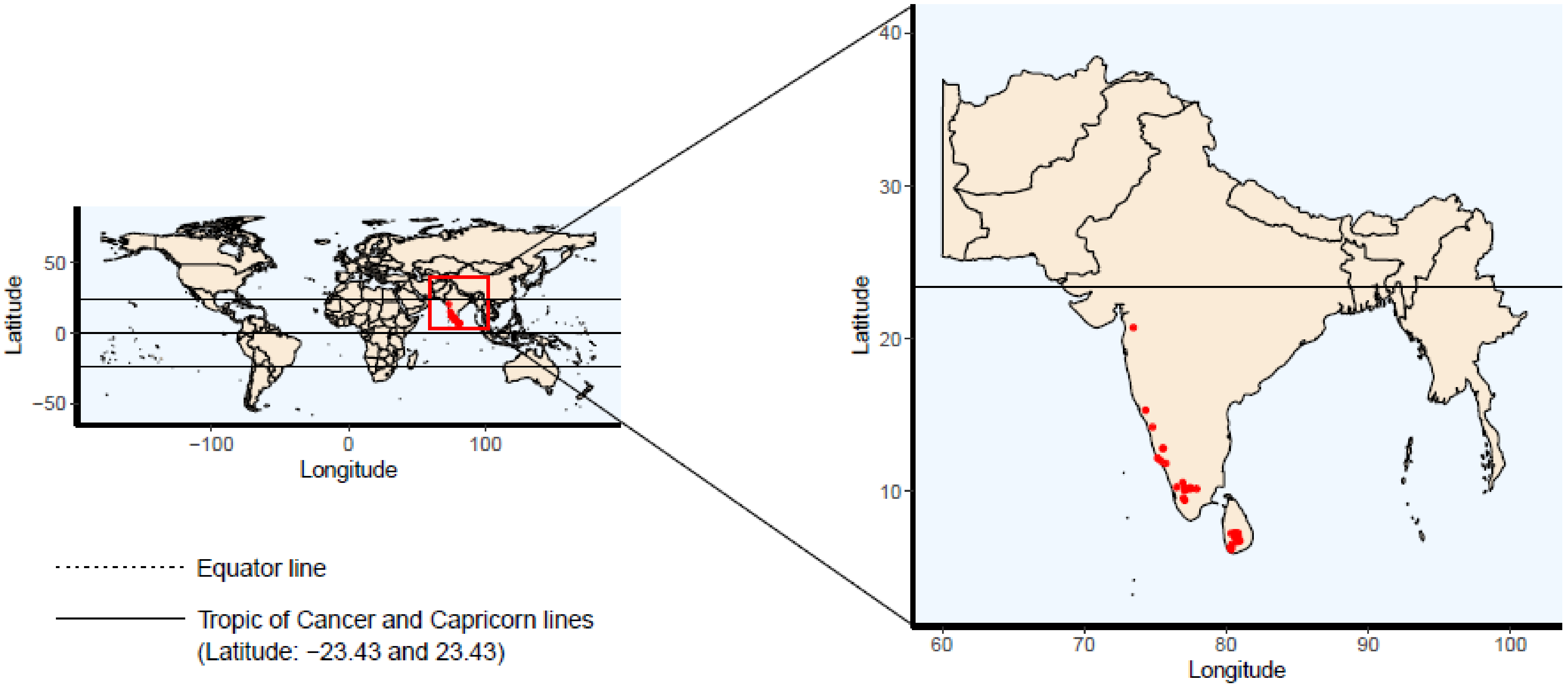
Distribution map of *Themeda saxicola*



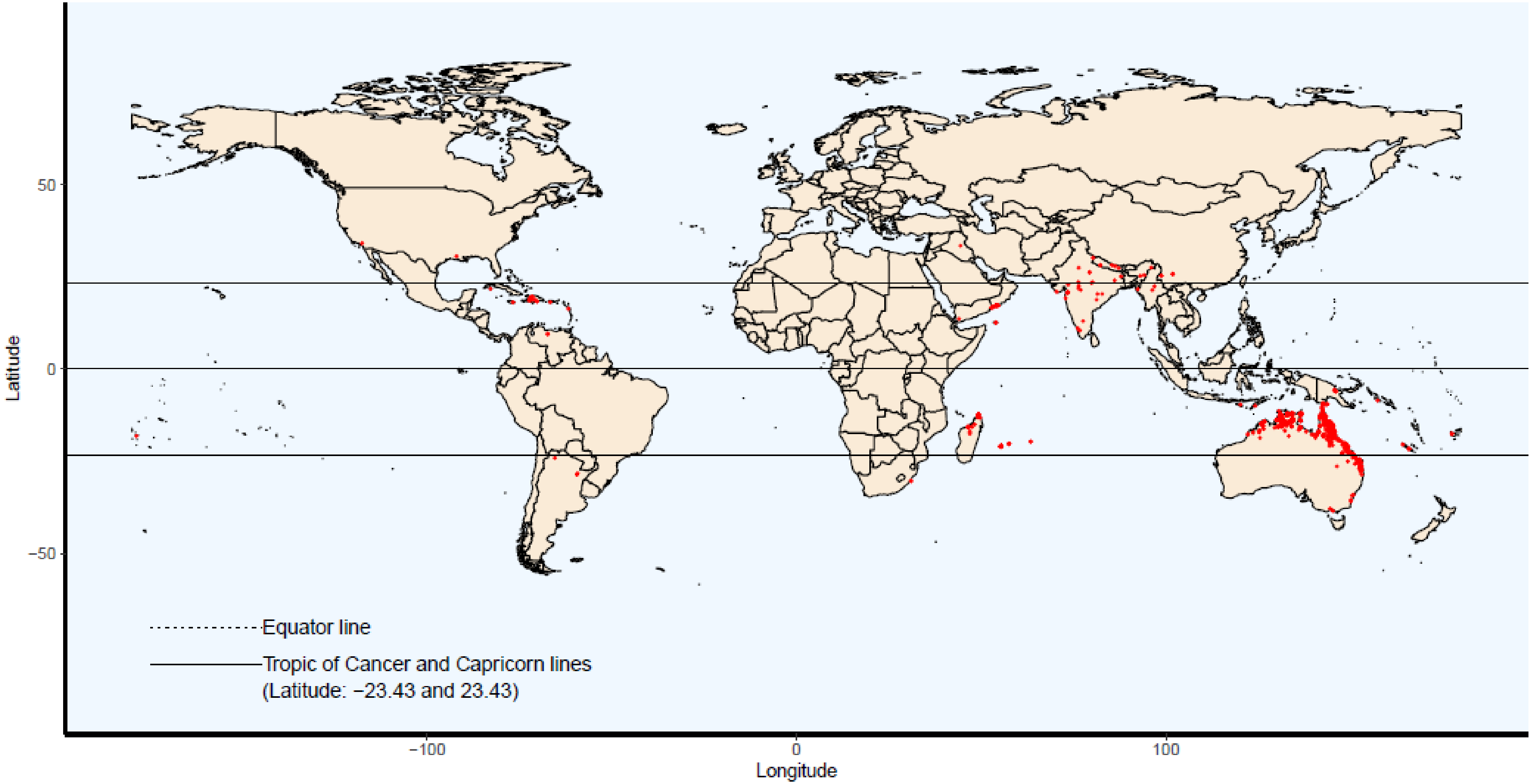
Distribution map of *Themeda strigosa*



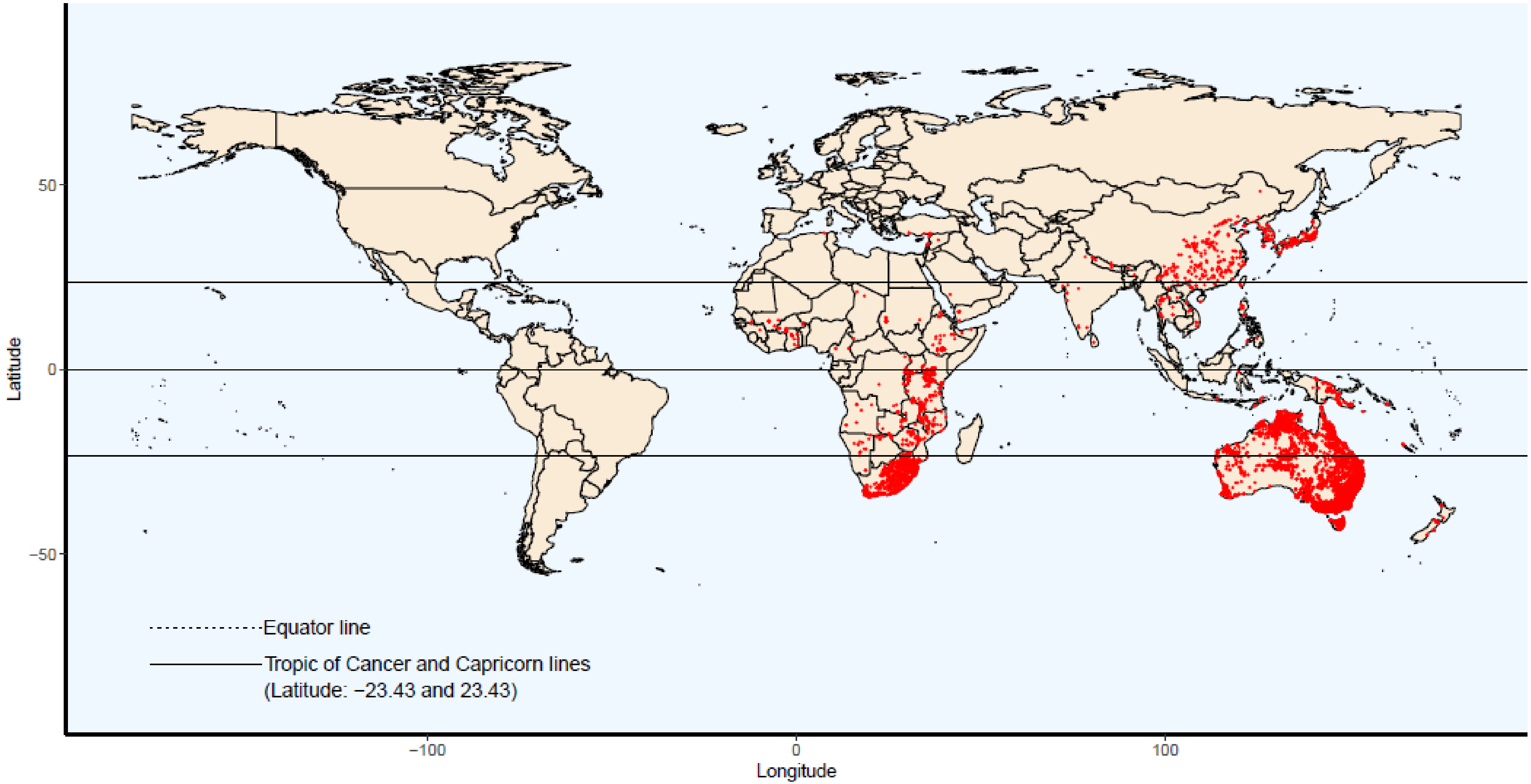
Distribution map of *Themeda tremula*



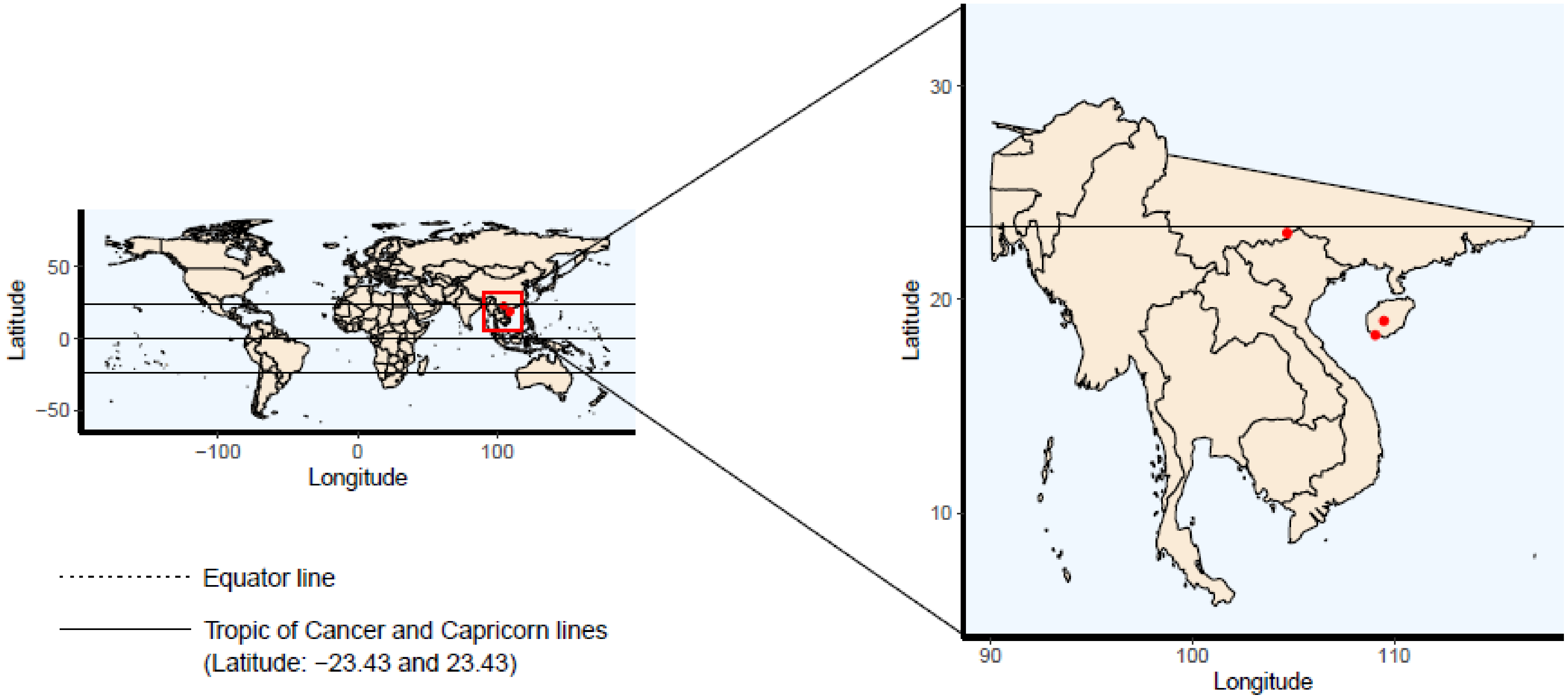
Distribution map of *Themeda triandra* var. *quadrivalvis*



Distribution map of *Themeda triandra* var. *triandra*



Distribution map of *Themeda trichiata*



Distribution map of *Themeda villosa*