

## RESEARCH ARTICLE

# Phylogenetics and morphological character evolution in the achyranthoid clade (Amaranthaceae): Evidence to re-circumscribe the genera *Achyranthes* and *Cyathula* and to resurrect a third species of the former genus *Sericocomopsis* in East Africa

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**Abstract** The achyranthoid clade constitutes the second most species-rich lineage of the Amaranthaceae after the gomphrenoid clade. The Achyranthoids are mostly African, in contrast to the largely Neotropical Gomphrenoids, and comprise a large number of genera, many of which were revealed as non-monophyletic. Here we focus on subclade II of the Achyranthoids with the so far accepted genera *Achyranthes*, *Achyropsis*, *Centrostachys*, *Cyathula*, *Nelsia*, *Nototrichium*, *Pandiaka*, *Sericocomopsis*, and *Sericostachys*. Building upon an earlier dataset, we extended taxon and character sampling, both for molecular and morphological characters. Our plastid and nuclear trees converge on several highly supported clades, one comprising most species of *Cyathula*, *Nelsia*, *Pandiaka* and two highly divergent lineages of plants hitherto identified as *Sericocomopsis hildebrandtii*. Morphologically, individuals within these lineages are similar, with one of them matching the type of *Sericocomopsis meruensis*. This name was formerly considered a synonym and is resurrected at species level. Cymous partial florescences are ancestral in this clade, which corresponds to the genus *Cyathula* as re-circumscribed here. To the contrary, sterile flowers and bracteoles or tepals modified to hooks serving dispersal by animals appear multiple times within and outside this clade, indicating how their use as diagnostic characters for genera led to non-monophyletic entities. For the phylogenetically isolated and morphologically distinct *Cyathula orthacantha* the new genus *Sebsebea* is described, and for *Sericocomopsis pallida* the new genus *Evelynastra*. The *Achyranthes* clade is characterized by solitary, fertile flowers including the genera *Achyropsis* and *Nototrichium* both of which are merged to make *Achyranthes* monophyletic. In addition to a treatment to establish all required nomenclatural changes and typifications, we also provide a taxonomic backbone with full synonymy for the achyranthoid subclade II.

**Keywords** Caryophyllales; *Evelynastra*; genus concept; molecular phylogeny; *Pandiaka*; *Sebsebea*; taxonomic backbone

**Supporting Information** may be found online in the Supporting Information section at the end of the article.

## ■ INTRODUCTION

The achyranthoid clade of the Amaranthaceae was newly recovered by Müller & Borsch (2005a,b) and shown to be composed by mainly African taxa. The Achyranthoids were estimated to comprise c. 140 species (Di Vincenzo & al., 2018) in 31 genera and form the second most speciose clade in the Amaranthaceae s.str. (c. 800 species in total) after the Neotropical Gomphrenoids (c. 380 species; Sánchez-del Pino & al., 2009). Based on the currently accepted genus concepts, the achyranthoid clade represents nearly 40% of the genera of the family: Hernández-Ledesma & al. (2015) recognized 79 genera, but included *Gossypianthus* Hook.,

*Lithophila* Sw. and *Philoxerus* R.Br., which were recently merged with *Gomphrena* (Ortuño Limarino & Borsch, 2020). On the other hand, *Ouret* Adans., *Paraerva* T.Hammer and *Wadithamnus* T.Hammer & R.W.Davis were newly described or resurrected (Hammer & al., 2017, 2019). According to Townsend (1993), who derived his classification mainly from Schinz (1893, 1934), all taxa of the achyranthoid clade had been assigned to the subtribe Aervinae of the tribe Amaranthaceae. However, this subtribe was found as non-monophyletic (Müller & Borsch, 2005a,b; Di Vincenzo & al., 2018) because *Aerva* Forssk., *Nothosaerva* Wight, *Ptilotus* R.Br. (Hammer & al., 2017, 2019) and allies constitute an independent clade that branches earlier than the divergence of the Achyranthoids

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from the unilocular Gomphrenoideae. The clade comprising *Aerva* and related genera was informally called aervoid clade (Müller & Borsch, 2005a).

Di Vincenzo & al. (2018) implemented a more extensive phylogenetic analysis of the achyranthoid clade, both in terms of sequence data (*trnK/matK*, *rpl16*, *trnL-F*, nrITS) and taxon sampling (inclusion of nine additional achyranthoid genera and c. 60 additional species). As a result, an increased support for the achyranthoid clade (1 PP, 97% MP-JK, 100% ML-BS) itself was found. Di Vincenzo & al. (2018) discovered two main subclades within the Achyranthoid clade (informally called achyranthoid subclade I and II) whereas genera such as *Arthraerua* (Kuntze) Schinz, *Chionothrix* Hook.f. and *Volkensinia* Schinz were placed as early diverging outside the two. Subclade I has 12 genera, including *Calicorema* Hook.f., *Centemopsis* Schinz, *Psilotrichum* Blume and *Pupalia* Juss. Achyranthoid subclade II was considered to comprise nine genera: *Cyathula* Blume, *Nelsia* Schinz, *Pandiaka* Hook.f., *Sericocomopsis* Schinz, *Sericostachys* Gilg & Lopr. ex Lopr., and then *Achyranthes* L., *Achyropsis* (Moq.) Hook.f., *Centrostachys* Wall. and *Nototrichium* Hillebr. The first five and the latter four genera are found in sister clades. *Achyranthes* was recovered as paraphyletic to *Achyropsis* and *Nototrichium*, and sister to the monotypic *Centrostachys aquatica* L., whereas *Cyathula* and *Sericocomopsis* were polyphyletic (Di Vincenzo & al., 2018). Here we focus on the Achyranthoid subclade II.

The plastid and nrITS trees of Di Vincenzo & al. (2018) further indicated that not all currently applied taxon concepts at species level reflect monophyletic entities. The most striking case became evident for the genus *Sericocomopsis* with three different lineages for only two currently accepted species. One of these lineages comprises all samples of *S. pallida* (S. Moore) Schinz and was found in a polytomy with *Sericostachys scandens* L. Samples of *Sericocomopsis hildebrandtii* Schinz constituted the other two clades, one of which (AC0955, AC1084, AC1094, all from Ethiopia) was sister to *Cyathula cylindrica* Moq., whereas two other individuals (AC0961, from Ethiopia, Sidamo region; AC1130, from Kenya, Mwingi District) were recovered as a clade in a more isolated position as sister to the whole clade of *C. cylindrica* plus *S. hildebrandtii* (AC0955, AC1084, AC1094), *C. uncinulata* (Schrad.) Schinz, *C. polycephala* Baker, *C. capitata* Moq., and *C. tomentosa* (Roth) Moq. Individuals of the two *S. hildebrandtii* clades showed differences in the density of hairs within inflorescences and in leaf morphology, underscoring the need for a closer examination of morphological characters in comparison with other members of the achyranthoid subclade II but also the sampling of further individuals to test species limits. Current Flora treatments (Townsend, 1985, *Flora of Tropical East Africa*; Townsend, 2000, *Flora of Ethiopia and Eritrea*) distinguish only two species of *Sericocomopsis* by simple hairs in *S. hildebrandtii* and stellate hairs in *S. pallida*. As a further consequence of this high level of polyphyly, the whole achyranthoid subclade II had to be included into a detailed analysis of genus concepts to provide

the basis for a taxonomic treatment of biologically meaningful entities.

Most Achyranthoids are dispersed by animals. For that reason, many of the species exhibit adaptations such as hooks and spines which originated multiple times within the achyranthoid clade by modifications of sterile flowers and other inflorescence parts (Di Vincenzo & al., 2018). The reconstruction of ancestral character states for modified sterile flowers suggested at least 14 independent origins in early-branching achyranthoid lineages and within subclades I and II since the Miocene (Di Vincenzo & al., 2018). Considering that the genera in Amaranthoideae were historically defined to a large extent on the basis of inflorescence characters including the presence and absence of modified sterile flowers (Schinz, 1893, 1934; Cavaco, 1962; Townsend, 1993), it is not surprising that several of these genera are now found as non-monophyletic.

The earliest genus described from the achyranthoid clade is *Achyranthes* (Linnaeus, 1753). Generic circumscriptions considerably varied over time, and some of this was due to diverging interpretations of the Linnaean genus concept. Linnaeus classified *Achyranthes* into the class “Pentandria” and order “Monogynia” based on the presence of five stamens and one pistil and included five species in the genus (*A. aspera* L., *A. lappacea* L., *A. lanata* L., *A. repens* L., *A. corymbosa* L.). These are today in the genera *Achyranthes*, *Pupalia* Juss. (segregated by Jussieu, 1803 with *A. lappacea* as type), *Aerva* Forssk. and *Alternanthera* Forssk., as well as *Polycarpaea* Lam. (Caryophyllaceae). Except *Achyranthes*, only *Pupalia* belongs to the Achyranthoids, but to subclade I. Endlicher (1837), who established a classification system for the Amaranthaceae with three tribes, accepted the four genera *Achyranthes*, *Aerva*, *Alternanthera* and *Pupalia*. Moquin-Tandon (1849) further subdivided the now more narrowly defined genus *Achyranthes* into the sections *A. sect. Cadeleri* Adans., *sect. Achyropsis* Moq., and *sect. Pandiaka* Moq., of which the latter two were raised to generic rank by Hooker (1880). Schinz (1893) divided *Achyranthes* into three subgenera, of which one was further split into two sections (*A. sect. Aspera* Boerl. and *sect. Centrostachys* Wall. of his subg. “*Euachyranthes*”). In the second edition of *Die natürlichen Pflanzenfamilien*, Schinz (1934) shifted to accepting generic rank for *Achyropsis* and *Pandiaka*, as for *Achyranthes*. His concepts for these three genera from 1934 have been used until now (Townsend, 1993; Hernández-Ledesma & al., 2015).

To complete the picture, it may be noted that Standley (1915) reported the nomenclatural type of *Achyranthes* to be *A. repens* (L.) Link (= *Alternanthera pungens* Kunth, in tribe Gomphreneae), although the name *Achyranthes* commonly had been applied to a different group of species (tribe Achyrantheae) at that time. Standley implemented various new combinations according to his genus concept. Later, a proposal to conserve the genus name *Achyranthes* L. with its type *A. aspera* L. selected by Hitchcock & Green (1929) was accepted (Jarvis, 1992).

*Cyathula* Blume (non Lour.; *Cyathula* Lour. has been shown to be synonym of *Achyranthes* L. and thus was rejected vs. *Cyathula* Blume nom. cons.; compare Appendix III of the Code, Wiersema & al., 2018–) also suffered a complex nomenclatural history since its publication in 1826. Moquin-Tandon (1849) split *Cyathula* into the two sections, *C.* sect. *Polyscalis* Moq. and sect. *Telostachys* Moq. Schinz (1893) classified *Cyathula* into *C.* sect. “*Eucyathula*” Schinz with cylindrical or capitate inflorescences (to which he assigned *C. cylindrica* (Bojer) Moq., *C. schimperiana* (Hochst.) Moq., *C. globulifera* (Bojer) Moq., *C. capitata* (Wall.) Moq., *C. ceylanica* Hook.) and *C.* sect. *Achyranthoideae* Schinz with slender inflorescences (to which he assigned *C. achyranthoides* (Kunth) Moq., *C. geminata* Moq., *C. prostrata* (L.) Blume, *C. triuncinata* Moq.). In contrast, Standley (1917) accepted *Cyathula* in the sense of Loureiro (1790) with the type *C. geniculata* Lour., which was rated as conspecific with *Achyranthes aspera* by different authors (e.g., Hiern, 1900; Moore, 1925; Hokche & al., 2008). Schinz (1934) did not accept the classification of Standley (1917) and maintained his classification from 1893. He later also described the monotypic genus *Nelsia* (Schinz, 1911) based on *Sericocoma quadrangula* Engl. as type. Cavaco (1962) accepted the sections of Schinz and described the additional section “*Nelsioideae*” Cavaco (not validly published) with the sole species (and type) *C. pobeguinii* Jac.-Fel.

The genus *Sericocomopsis* was described by Schinz (1895) as characterized by plumose or sericeous inflorescences which are either globose or spicate, with flowers arranged in 3-flowered cymes, in which sterile flowers are completely missing, interstaminal appendages (“pseudostaminodes”) are fimbriate or missing, and the ovary is glabrous or pilose. Within the new genus, he described a new species, *S. hildebrandtii*, and further transferred two species from the genus *Sericocoma* Fenzl ex Endl. to *Sericocomopsis*, namely *S. bainesii* (Hook.f.) Schinz and *S. pallida*. *Sericocomopsis pallida* was included in the dichotomous key and Schinz indirectly referred to its basionym by citing its author in brackets, which was sufficient for the valid publication of new combinations before 1 January 1953 according to the *International Code of Nomenclature for algae, fungi, and plants* (Turland & al., 2018; Art. 41.3). In a later publication, Schinz (1911) referred to the basionym and added a detailed species description of *S. pallida*.

Two years after Schinz transferred *Sericocoma bainesii* Hook.f. to his genus *Sericocomopsis*, Gilg (1897) transferred this species to a new genus *Leucosphaera* Gilg. He characterized the genus by sericeous, globose inflorescences, with partial florescences constituted of two fertile flowers only, in which so-called “pseudostaminodes” are missing. Phylogenetic results showed *L. bainesii* (Hook.f.) Gilg to be distantly related to species of both *Sericocomopsis* and *Sericocoma* (Di Vincenzo & al., 2018). The transfer of *Sericocomopsis pallida* and *S. hildebrandtii* to the genus *Kyphocarpa* (Fenzl) Schinz (Baker & Clarke, 1909) was not accepted by other authors.

The specific objectives of this investigation are to further test relationships within subclade II of the Achyranthoids and to evaluate currently used genus concepts in a phylogenetic context and by studying morphological characters. We further aim at clarifying species limits of *Sericocomopsis hildebrandtii*, which requires a closer examination of the genus *Cyathula* as a whole, considering that the two groups of individuals currently identified as *S. hildebrandtii* were found nested in different parts of *Cyathula*. Due to the complex classification history of this group of Amaranthaceae, and the need to closely evaluate previously published taxon concepts at genus and also species level, another goal was to develop a comprehensive checklist of the achyranthoid subclade II to form part of the ongoing work on an Amaranthaceae species-level taxonomic backbone in the monographic synthesis of the order Caryophyllales (Borsch & al., 2015). We aimed at integrating all names for the achyranthoid subclade II to complement a new treatment at the genus level.

## ■ MATERIALS AND METHODS

**Field work and specimen information.** — The sample set presented in Di Vincenzo & al. (2018), which was largely achieved by field work in Ethiopia and Kenya in 2012 and 2013, was complemented by further material available at B and ETH (partially collected in the frame of a DFG-funded Amaranthaceae project from 2001 onwards by different researchers). Additional specimens for molecular analyses came from the Botanic Garden Meise (BR), and for physical examination of (type-) specimens, material was available on loan from the herbaria BM, BR, C, GH, GOET, HBG, K, M, NYS, P, and PRE. Detailed information on samples used is provided in Appendix 1.

**Composition of molecular datasets.** — We generated a plastid dataset (dataset A), which consisted of the regions *trnK/matK*, *rpl16*, *rpl32-trnL<sub>UAG</sub>*, *rps4-trnT-trnL<sub>UAA</sub>*, and *trnL-F*, and a nuclear ribosomal dataset, which consisted of internal transcribed spacer (nrITS) sequences (hereafter referred to as dataset B). Both have a dense taxon sampling of the Achyranthoids II but also include a representation of genera from Achyranthoids I and early branching achyranthoid lineages. A part of the ITS, *trnK/matK*, *rpl16* and *trnL-F* sequences came from Di Vincenzo & al. (2018), and these markers were also sequenced for all new samples. To improve tree resolution and node support, we complemented data from all samples with sequences of the plastid intergenic spacer between *rpl32-trnL<sub>UAG</sub>* and the two spacers in the *rps4-trnT-trnL<sub>UAA</sub>* region. These regions rank among the most variable plastid regions (Shaw & al., 2007; Korotkova & al., 2014), showed fragments of approx. 1000 and 1200 nt that promised efficient lab work, and yielded good hierarchical phylogenetic signal in other analyses of Caryophyllales lineages (e.g., Fassou & al., 2022). We added further species of *Pandiaka* not analysed in phylogenetic studies before, including the type species of the genus, *P. involucrata*. In order to test



species limits within *Sericocomopsis*, we extended the sampling of *S. pallida* and *S. hildebrandtii*, to better represent the geographic range and morphological variation of putative species.

**Processing of DNA samples and generation of molecular datasets.** — For DNA isolation and sequencing, we followed the same procedures as described in Di Vincenzo & al. (2018). Additional primers were designed for herbarium samples to completely amplify *rpl16* (AMARrpl16-700F 5'-GATTCCAATATGTAAGGTTTTTG-3' and AMARrpl16-950R 5'-ATCGCCTCTTGATTAATGGTTAG-3') and *trnL-F* (AMARtrnL-F-400F 5'-CTGTGCTGTGTTGTTCTAAG-3', AMARtrnL-F-900F 5'-CGGACGAGAATAAAGATAGAGT C-3', AMARtrnL-F-500R 5'-GGTGTCATTAATCATTTG-3', AMARtrnL-F-1000R 5'-GGATAGAGGGACTTGAACC-3'). The *trnL-F* region was extended upstream to cover the *trnT-trnL<sub>UAA</sub>* and *rps4-trnT* spacers using primers AMARrps4-5F (5'-ACGAGGTCCTCGGTAACGTG-3', AMARtrnT-360F 5'-CAGAGTTGSAAGTTTCTATGAC-3', AMARtrnT-L-50F 5'-CGTCGAGAACAATTAGATTC-3', AMARtrnT-L-370F 5'-TTCTTCGGCTTTCATTCATAG-3', AMARtrnT-520R 5'-GCTTAGCTCAGAGTTAGAG-3' and AMARtrnT-L-550R 5'-GTTTCATCTCTATCGGAARTC-3'). We also added the *rpl32-trnL<sub>UAG</sub>* spacer using primers rpl32-F (Shaw & al., 2007) and the newly designed AMARrpl32-trnL\_420F (5'-TAACAACCTTAYGCCAACCC-3'), trnL-UAG-46R (5'-ACTGCTTCCTAAGAGCAGCG-3'), trnL-UAG-90R (5'-GATACCATGCCCACTC-3') and AMARrpl32-trnL-500R (5'-AGAAGGGTGATAAAATAKTTTC-3'). Sanger sequencing was carried out at Macrogen Europe (Amsterdam, The Netherlands). Chromatograms were inspected by eye and corrected for erroneous nucleotide calls. Assembly and a motif-based alignment (as outlined in Löhne & Borsch, 2005) was conducted using PhyDE v.0.9971 (Müller & al., 2010), building upon the multiple sequence alignments of Di Vincenzo & al. (2018). Areas of uncertain homology were excluded from matrices and inversions were reverse-complemented and coded as presence-absence data. For coding insertions and deletions, we applied “simple indel coding” (Simmons & Ochoterena, 2000) as implemented in SeqState v.1.4.1 (Müller, 2005). Final DNA sequences were submitted to ENA (<http://www.ebi.ac.uk/ena/>) upon conversion to checklist files with custom Python scripts (<https://github.com/michaelgruenstaedl/annonex2embl>). ENA/GenBank accession numbers are given in Appendix 1 along with the voucher data. Alignments and corresponding matrices are available from suppl. Appendices S2A,B and S3A,B.

**Model selection and phylogenetic analysis.** — Phylogenetic inference was obtained with maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI). For the latter two analyses, datasets were partitioned to allow for independent parameter estimation. Best-fitting models of nucleotide substitution were selected via the Akaike information criterion corrected for small sample sizes (AICc; Akaike, 1974) for each partition with ModelTest-NG v.0.1.7 (Darriba & al., 2020), which is

implemented in raxmlGUI v.2.0.5 (Edler & al., 2021). Parsimony analyses were conducted in PAUP\* v.4.0b10 (Swofford, 2002) with all characters having equal weight, gaps treated as missing characters and tree bisection-reconnection (TBR) branch swapping; node support was calculated via 10,000 jackknife (JK) replicates deleting 36.788% of characters and maxtrees set to 1. Final ML analyses were conducted, by application of the MULTIGAMMA model for dataset A (tree search and evaluation of final trees under the GAMMA model) and MULTICAT model for dataset B (tree search under the CAT model, evaluation of final trees under the GAMMA model), and with node support calculated via 1000 rapid bootstrap (BS) replicates, using the raxmlGUI v.2.0.4 (Silvestro & Michalak, 2012) as input interface for RAXML (Stamatakis, 2014). BI was performed in MrBayes v.3.2.7a (Ronquist & al., 2012) available from the CIPRES Science Gateway (Miller & al., 2010). Node support was calculated as posterior probabilities from four independent Markov chain Monte Carlo (MCMC) runs with four chains and 5 million generations each. Trees were sampled every 1000th generation resulting in 20,004 trees. The burn-in was set to 25%, resulting in a combined posterior tree distribution of 15,004 trees out of which a majority-rule consensus tree was calculated. Convergence of each independent run was assessed based on the standard deviation of split frequencies and the effective sample size (ESS) using Tracer v.1.6 (Rambaut & al., 2014).

**Dynamic editing of the taxonomic backbone in the EDIT platform.** — All names and taxa included in the achyranthoid subclade II were compiled using the EDIT Platform for Cybertaxonomy, which comprises tools for editing, managing and publishing of taxonomic data (BGBM, 2008–; Ciarrelli & al., 2009; Berendsohn, 2010; Berendsohn & al., 2011). The Platform is used, inter alia, by the Caryophyllales Network (Borsch & al., 2015; Hernández-Ledesma & al., 2015; Berendsohn & al., 2018; Korotkova & al., 2021), and the taxonomic treatment here published was directly generated from that database. Initially, names were imported from the WFO (2019) taxonomic backbone, including their WFO IDs and taxonomic status (thus essentially mirroring the treatment in The Plant List v.1.1; TPL, 2013). Names and protologues were checked against available online resources such as the International Plant Name Index (IPNI, 2000–), Index Nominum Genericorum (Farr & Zijlstra, 1996–) and Tropicos (1986–). Original publications were ascertained using the Biodiversity Heritage Library (BHL, 2007–; Gwinn & Rinaldo, 2009) and where still necessary in the BGBM library. Additionally, this dataset was matched with the dataset of the World Checklist of Vascular Plants (WCVP) received from Royal Botanic Gardens, Kew in December 2019 (WCVP, 2019), and subsequently cross-checked with relevant taxonomic treatments as cited in the introduction. Morphological descriptions from these sources were compared with data from own examination of type material in several cases and original publications. If present at the Berlin herbarium or available on loan, type specimens were examined physically (as indicated by “!”),

otherwise they were checked in a digital form (“[image!]”) if available on JSTOR Global Plants (2004–) or the respective virtual herbaria. We provide type specimen data for accepted species and their synonyms when their generic assignment was changed, their status as synonym or accepted name was altered, or a lectotypification is made. This information is then included into the taxonomic treatment in the main body of this paper. The complete taxonomic backbone of the Achyranthoid II clade is presented in suppl. Appendix S1. For more details on data import and processing of data in the EDIT Platform, see Fassou & al. (2022). All nomenclatural changes are presented in the taxonomic treatment, whereas in the phylogenetic trees hitherto used accepted names are annotated.

**Assessment of morphological characters and ancestral character state reconstruction.** — In order to reconstruct the evolution of morphological characters and evaluate in how far they are diagnostic for genus concepts to be applied in the achyranthoid subclade II, we defined a set of 24 characters covering habit and vegetative morphology, inflorescences and floral morphology, similar to Ortuño Limarino & Borsch (2020). Character states were mainly assessed through examination of herbarium specimens corresponding to the samples also analysed for the molecular data. Regarding the characters “life cycle” and “life form”, the label information from specimens was sometimes incomplete, and states needed to be assessed from morphological descriptions from original publications or Flora treatments. Definitions of characters and their states and the corresponding character matrix are given in Appendix 2. An overview of the morphological diversity is shown in Fig. 1.

BayesTraits v.2 (Pagel & al., 2004) was used to infer ancestral character states. Ancestral character state reconstruction was calculated over 1000 random samples which were extracted from the post-burn-in tree distribution of the Bayesian analyses of dataset A using Mesquite v.3.70 (Maddison & Maddison, 2021). BayesTraits input was generated with TreeGraph2 v.2.14.0-771 (Stöver & Müller, 2010). We selected a multistate analysis under MCMC tree optimization, using the Reverse Jump Hyper-prior. The BayesTraits output files were imported to TreeGraph2 where probabilities of ancestral states were visualized on the maximum clade credibility (MCC) tree.

**Testing species limits in *Sericocomopsis hildebrandtii*.** — For further evaluation of species limits in *Sericocomopsis hildebrandtii*, all individuals of the two lineages found in the molecular trees were examined. Here, we focused on features that varied among specimens of the two lineages such as the hairiness of the inflorescence (“less hairy” and “densely hairy”), the shape of the leaves (corresponds to character 4 in the ancestral character state reconstruction), the shape of paracladia (corresponds to character 6), and the curvature of bracteoles at anthesis (corresponds to character 21), the indumentum of bracts and bracteoles, and the stiffness of the midvein of tepals. Individuals of both groups were then compared to the type specimen of *S. hildebrandtii*, as well as to the

type specimens of names presently considered synonyms. The examined characters were photographed for each individual and one representative per lineage was selected for illustration of character states.

## RESULTS

**Molecular phylogeny.** — We generated the following new sequences: 26 for *trnK/matK*, 24 for *rpl16*, 64 for *rpl32-trnL<sub>UAG</sub>*, 70 for *rps4-trnT-trnL<sub>UAA</sub>*, 21 for *trnL-F* and 19 for ITS. Dataset A included 75 samples and resulted in a multiple sequence alignment of 8932 aligned positions including hotspots. The final matrix (excluding hotspots) comprised 7390 positions, and simple indel coding yielded an additional matrix of 417 characters. For detailed alignment statistics, see suppl. Table S1. Dataset B included 63 samples and resulted in a multiple sequence alignment of 834 aligned positions including hotspots. The final matrix (excluding hotspots) comprised 704 aligned positions, and simple indel coding yielded an additional matrix of 116 characters. For detailed alignment statistics, see suppl. Table S2. The data for the respective models inferred are included in suppl. Table S3.

The phylogeny inferred from the concatenated plastid regions (dataset A; Fig. 2, suppl. Fig. S1) and the tree from nrITS (dataset B; Fig. 3, suppl. Fig. S2) depicts two principal subclades of Achyranthoids II consisting of *Achyranthes* plus allies and *Cyathula* plus allies. In the plastid tree these appear as sisters (1 BI PP, 100 ML-BS, 100 MP-JK) to which a maximum-supported isolated lineage comprising all individuals of *Cyathula orthacantha* (Hochst. ex Asch.) Schinz appears as sister (Fig. 2, suppl. Fig. S1). Based on nrITS we found *C. orthacantha* as moderately supported sister to the clade comprising *Achyranthes* and allies (Fig. 3, suppl. Fig. S2).

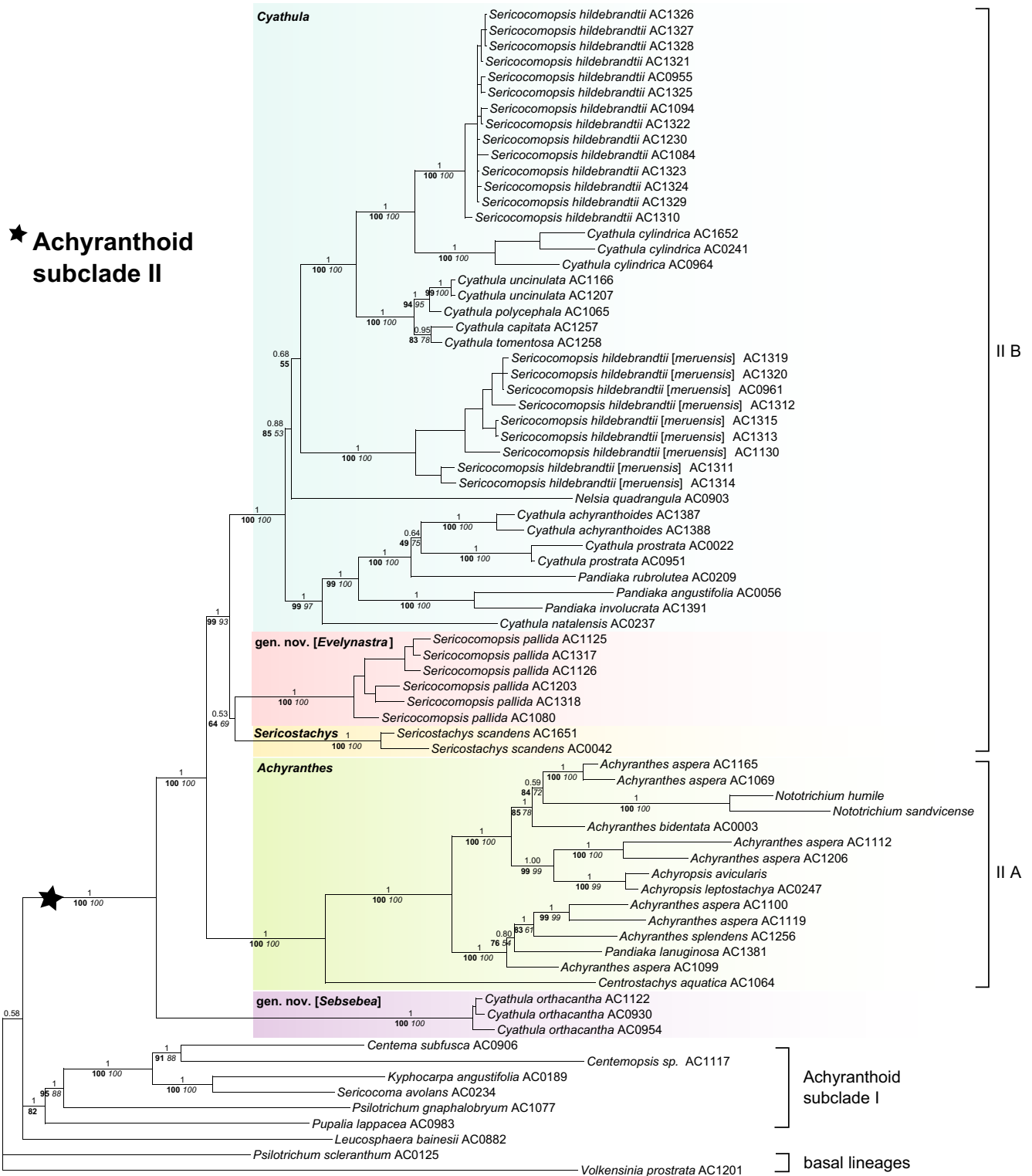
All trees converge on three lineages of *Sericocomopsis*, all of which are nested within subclade II B: one lineage of *S. hildebrandtii* occurring as sister to *Cyathula cylindrica* and another lineage being sister to the whole of *Cyathula cylindrica*, *C. uncinulata* (Schrud.) Schinz, *C. polycephala* Baker, *C. tomentosa* (Roth) Moq., *C. capitata*, and the first lineage of *S. hildebrandtii*. All accessions of *S. pallida* were found as sister to *Sericostachys scandens* in the BI, ML and MP analyses of dataset A but this relationship remained weakly supported. In the BI, ML and MP analyses of dataset B, *S. pallida* alone is highly supported as belonging to subclade II B but its position to all remaining taxa is weakly supported. The following four species of *Pandiaka* and two species of *Cyathula* had never been included in any molecular analyses before: *P. involucreta* (Moq.) B.D.Jacks., which is the type of the genus, *P. lanuginosa* Schinz, *P. rubrolutea* (Lopr.) C.C.Towns., *P. welwitschii* (Schinz) Hiern, *Cyathula divulsa* Suess. (only ITS could be sequenced for the latter two species) and *C. achyranthoides*. In all analyses, *P. lanuginosa* was resolved as a member of subclade II A





**Fig. 1.** Morphological diversity in the achyranthoid subclade II: **A & E**, Synflorescence of *Cyathula uncinulata* (Bale Mountains, Ethiopia), which can become very dense in some individuals (E); **B**, Leafless synflorescence of *C. polycephala*; **C**, Pendant narrow inflorescence of *C. cylindrica* (both Bale Mountains, Ethiopia); **D**, Upper part of inflorescence of *Sericostachys scandens* with the plumose hairs serving dispersal (tree-tops in Yayu forest, Ethiopia); **F**, *Sebsebea orthacantha* (M. Wondafrash 3461, Sidamo, Ethiopia); **G**, *Cyathula meruensis* (M. Wondafrash 3500, Sidamo, Ethiopia); **H**, *C. hildebrandtii* growing up to a 2 m tall shrub (M. Wondafrash 3822; Ogaden region, Ethiopia). — Photos: A–E by T. Borsch, F–H by M. Wondafrash.

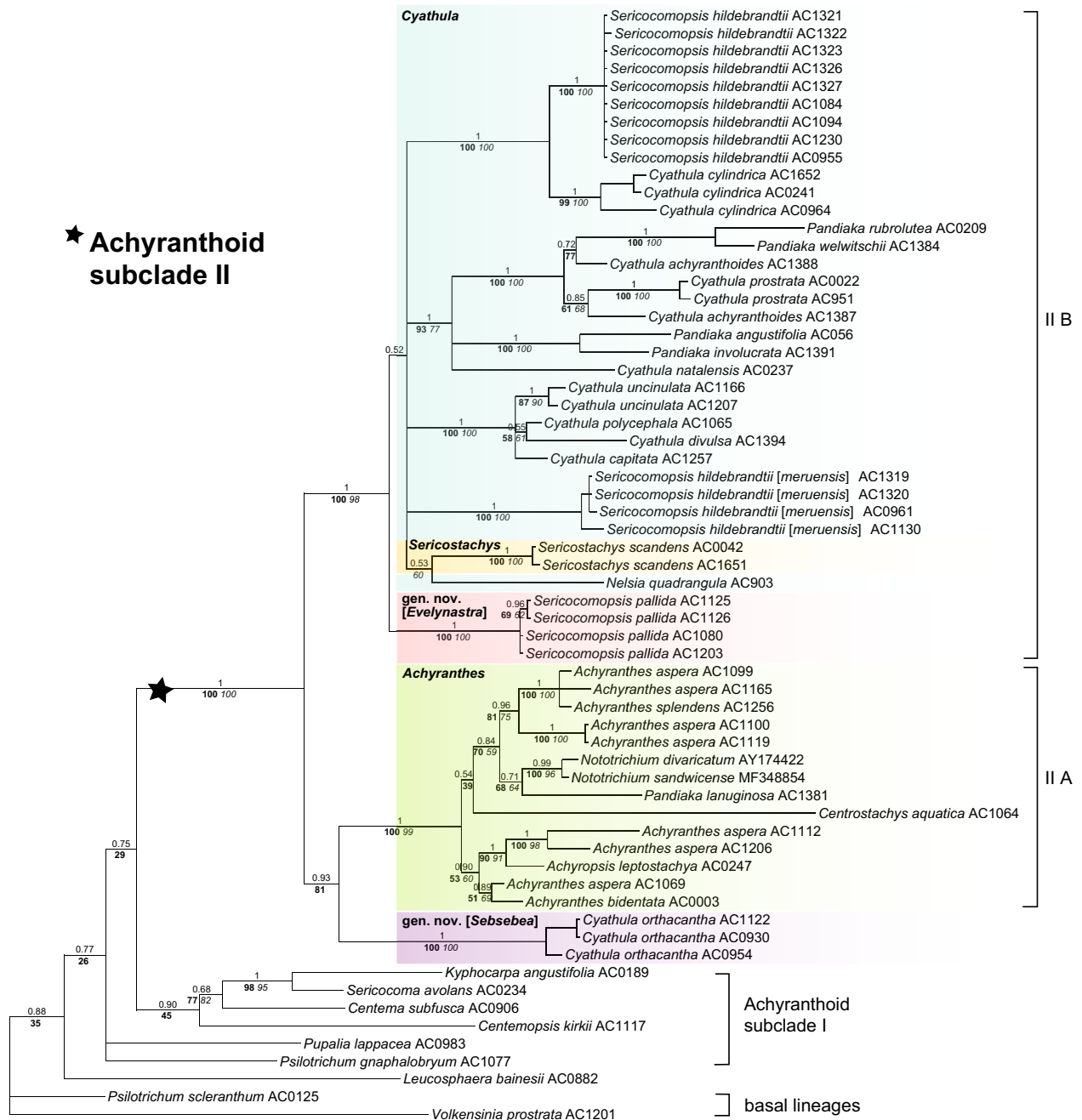




**Fig 2.** Phylogeny of the achyranthoid clade of Amaranthaceae with a focus on subclade II inferred by Bayesian inference on dataset A (combined plastid regions). Posterior probabilities of the Bayesian inference are given above branches, bootstrap percentages of the maximum likelihood analyses in bold letters (left) and jackknife percentages of the maximum parsimony analyses in italics (right) are given below branches. Posterior probabilities below 0.5 and bootstrap as well as jackknife values below 50% are not shown. Genera within subclade II are shaded in different colours according to our new genus concepts with the respective genus names written in bold italics in the upper left side of each clade.

together with *Achyranthes*, *Nototrichium* and *Centrostachys*, while the other five species were found as members of subclade II B. *Cyathula divulsa* depicts a maximum-supported clade together with *C. uncinulata*, *C. polycephala* and *C. capitata* in all analyses of dataset B. *Pandiaka involucreta*

was generally found as sister to *P. angustifolia*, whereas *P. rubrolutea* appears in a subclade together with *C. achyranthoides* and *C. prostrata*, which is the generic type, to which again *C. natalensis* is resolved as sister with high support in the plastid tree (Fig. 2). However, ITS does not



**Fig 3.** Phylogeny of the achyranthoid clade of Amaranthaceae with a focus on subclade II inferred by Bayesian inference on dataset B (nuclear ITS). Posterior probabilities of the Bayesian inference are given above branches, bootstrap percentages of the maximum likelihood analyses in bold letters (left) and jackknife percentages of the maximum parsimony analyses in italics (right) are given below branches. Posterior probabilities below 0.5 and bootstrap as well as jackknife values below 50% are not shown. Genera within subclade II are shaded in different colours according to our new genus concepts with the respective genus names written in bold italics in the upper left side of each clade. Resolution of ITS within clade II B is much lower than in the plastid tree, leaving most species groups in a polytomy, but *Sericocomopsis pallida* is also depicted as an early branch.



resolve the latter node but shows maximum support for a close relationship of *C. achyranthoides*, *C. prostrata* with *P. rubrolutea* and *P. welwitschii* (Fig. 3), the latter two with maximum support as sisters. In contrast, *P. lanuginosa* was resolved in a lineage together with *Achyranthes*, *Nototrichium* and *Centrostachys* by datasets A and B (Figs. 2, 3, suppl. Figs. S1, S2).

**Polyphyly of *Sericocomopsis hildebrandtii* Schinz.** —

The individuals identified as *Sericocomopsis hildebrandtii* according to the currently accepted classification appear in two distant lineages, in both the plastid and nuclear trees depicting well-supported crown groups on a rather long branch (Figs. 2, 3).

We found clear differences in the inflorescences and in the shape of cauline leaves (character 4) between the individuals of either lineage: Hairs on stems and inflorescence parts are much longer and denser in individuals assigned to *Sericocomopsis hildebrandtii* that are related to *Cyathula cylindrica* than in those appearing in the other lineage, especially on bracts and bracteoles where hairs are mainly located on the midrib. Also, on the outer tepals this difference is clearly visible (Fig. 4). Furthermore, we discovered differences regarding the shape of paracladia (character 6), with cymes arranged much denser on the main inflorescence axis in individuals assigned to *S. hildebrandtii* that are related to *C. cylindrica* than in those appearing in the other lineage. The texture of tepals at maturity (character 18) is herbaceous or scarious in specimens assigned to *S. hildebrandtii* that are related to *C. cylindrica*, while tepals were found indurate at the base in individuals appearing in the other lineage. The bracteoles were found strongly recurved in all fertile flowers at anthesis in the individuals assigned to *S. hildebrandtii* that are related to *C. cylindrica*, whereas they were not or only slightly recurved in those appearing in the other lineage (character 21). The cauline leaf shape (character 4) varied within single individuals, but in the lineage that is sister to *C. cylindrica* the broadest portion was observed in the lower half, while in the other lineage the widest part was observed in the upper half of the leaf (see paragraphs on morphology and ancestral character state reconstructions). All specimens resolved in the two different lineages of *S. hildebrandtii* consistently showed the same deviant morphological features, indicating the existence of another species in addition to *S. hildebrandtii*.

**Distribution and ancestral states of morphological characters.** — The ancestral state probabilities for the most relevant characters are illustrated as pie charts in Figs. 5–8 starting with habit and inflorescence morphology (characters 1, 2, 6, 7; Fig. 5), structure and position of cymes as well as presence and shape of sterile flowers (characters 8, 9, 10, 11; Fig. 6), tepal morphology (characters 13, 15, 16, 17, 18; Fig. 7), and morphology of the androecium and the bracteoles (characters 12, 19, 20, 21; Fig. 8). Ancestral states for the remaining characters (characters 3, 4, 5, 14, 22, 23, 24) are presented in suppl. Fig. S3.

Annuals are derived several times (character 1, state 0) from plants with a perennial life cycle, whereas multiple shifts

between woody shrubs, subshrubs and herbs (life form, character 2) were inferred. The habit of *Sericostachys scandens*, being a woody liana (character 2, state 4) is an autapomorphy for the genus within the Achyranthoids, as are treelets of the Hawaiian island endemic *Nototrichium*, which derived from herbs (Fig. 5). The stellate indumentum of stems and cauline leaves is a derived feature of all individuals of *Sericocomopsis pallida* (suppl. Fig. S3).

Paracladia within Achyranthoids II are mostly spiciform with cymes or solitary flowers (reduced cymes) clearly separated during anthesis. This is also the ancestral state (character 6, state 0; Fig. 5) whereas denser inflorescences (states 1, 2) derived several times. Paracladia are usually solitary on main axes and lateral branches, whereas the arrangement in a complex thyrsoid structure derived twice, once in *Sericostachys* and once in *Psilotrichum gnaphalobryum* outside the Achyranthoids II (character 7; Fig. 5). Cymes commonly have more than one order of branches in Achyranthoids, which is also the plesiomorphic state. Our ancestral state reconstruction shows that they were reduced to single flowers in the whole *Achyranthes* subclade (clade “B” in Figs. 2, 3) but also in *Pandiaka* (character 8; Fig. 6). Cymes with first-order branches are rare and within Achyranthoids II autapomorphic for *Sericostachys* (character 8, state 1; Fig. 6). The common ancestor of *Achyranthes* and *Centrostachys* evolved cymes which are deflexed and appressed to the inflorescence axis at maturity (character 9). This conspicuous feature apparently has been lost in the lineages nested within *Achyranthes* that are currently classified under *Achyropsis*, *Nototrichium*, and *Pandiaka lanuginosa*. The presence of sterile flowers is a plesiomorphic condition in Achyranthoids (character 10, state 1), and sterile flowers became lost in conjunction with the evolution of single-flowered cymes. Sterile flowers also became lost in the two lineages of *Sericocomopsis hildebrandtii*, but not in *S. pallida* (Fig. 6). The latter species further deviates from the rest in that it retained unmodified sterile flowers which became modified into hooks in those species currently classified as *Cyathula* (character 11, state 1), except *C. orthacantha*, in which they evolved into straight spines. In the liana *Sericostachys*, filiform, feathery hairs serving dispersal develop from the midribs of the tepals of sterile flowers, being an autapomorphic feature in Amaranthaceae. Androecial tube appendages (character 12) derived multiple times, once in the common ancestor of Achyranthoids II but were lost in *Nototrichium* (Fig. 8). The ovary in Achyranthoids II is always glabrous, whereas it can be pilose or lanate within Achyranthoids I (character 14, suppl. Fig. S3).

Tepals with equal size and shape (character 13, state 0) are the most common feature in the Achyranthoids II. In their clade A, unequal tepals, gradually decreasing in length from outer to inner are derived, and from this state *Cyathula polycephala* and close relatives have further developed flowers with the three inner tepals smaller than the two outer ones (Fig. 7). This group of species also stands out by excurrent and uncinate hooked midribs as a derived state of character 15 (Fig. 7), contributing to the function of attaching diaspores



**Fig. 4.** Floral morphology and leaf indumentum of *Sericocomopsis* Schinz: **A**, Partial florescence of *S. pallida* (*V. Di Vincenzo & M. Wondafrash* 42, AC1203); **B**, Inflorescence of *S. hildebrandtii* (*M. Wondafrash* 2213, AC1094) with several partial florescences; **C**, Inflorescence of *S. hildebrandtii* ['*meruensis*'] (*M. Wondafrash* 3500, AC0961); **D**, Stellate indumentum on leaves of *S. hildebrandtii*; **E**, Simple trichomes of *S. hildebrandtii* (AC1094); **F**, Simple trichomes of *S. hildebrandtii* ['*meruensis*'] (AC0961); **G & I**, Flower with bract and bracteoles and tepal of *S. hildebrandtii* (*V. Di Vincenzo & A. Hailu* 204, AC1325); **H & J**, Flower with bract and bracteoles and tepal of *S. hildebrandtii* ['*meruensis*'] (AC0961).



to large animals in addition to the hooks in modified sterile flowers. The number of veins in outer and inner tepals is homoplastic (characters 16, 17; Fig. 7) with reductions in vein number appearing correlated to the very dense inflorescences in *C. polycephala* and relatives on the one hand, but derived many-veined tepals in lineages with rather isolated flowers like *Sericostachys* and *Centrostachys*. Different degrees of induration of tepals at maturity (character 18) are also derived in particular in species with less dense inflorescences, including a noteworthy difference in the two lineages of *Sericocomopsis hildebrandtii* (Fig. 7) but a trend to stronger induration in achyranthoid subclade I. The morphology of bracteoles (characters 19–21) also appears homoplastic and orbicular bracteoles with an emarginate tip (character 19, state 4), are present in taxa currently classified within *Achyranthes* and *Centrostachys*, which is shown to be plesiomorphic in clade B (Fig. 8).

■ DISCUSSION

**Phylogenetic relationships with a focus on the achyranthoid subclade II.** — Compared to the phylogenetic analysis of the achyranthoid clade by Di Vincenzo & al. (2018) three further plastid intergenic spacers (*rps4-trnT-trnL<sub>UAA</sub>*, *rpl32-trnL<sub>UAG</sub>*), and further species of the genera *Cyathula* and *Pandiaka* were added for this investigation. Since *Cyathula* had earlier been shown as polyphyletic (Di Vincenzo & al., 2018), it was crucial to represent its morphological and geographical diversity at species level. Our increased character sampling of the plastid genome resulted in increased statistical confidence for most backbone nodes (maximum support throughout all three inference methods: Bayesian inference, maximum parsimony and maximum likelihood, Fig. 2). *Cyathula orthacantha* is now established as an isolated lineage as is an *Achyranthes* subclade including

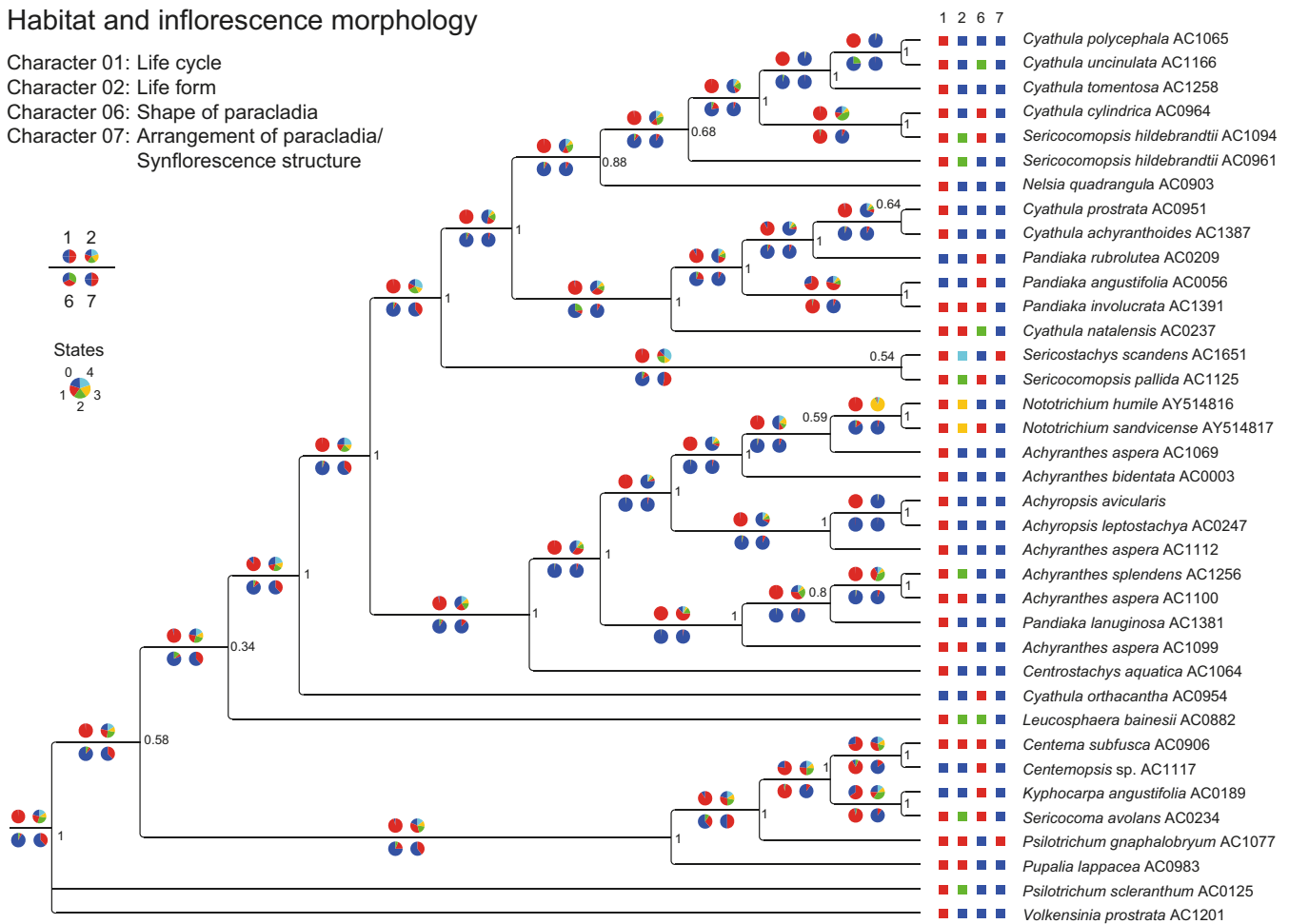
Habitat and inflorescence morphology

Character 01: Life cycle

Character 02: Life form

Character 06: Shape of paracladia

Character 07: Arrangement of paracladia/  
Synflorescence structure



**Fig. 5.** Evolution of habit and inflorescence morphology using the maximum clade credibility tree inferred from the plastid dataset. Pie charts correspond to probabilities of ancestral character states reconstructed with MrBayes for habit (life cycle is character 1 and life form is character 2) and inflorescence morphology (shape of paracladia is character 6, arrangement of paracladia in the synflorescence is character 7). For character and state definitions, see Appendix 2. Support values next to nodes are Bayesian posterior probabilities.



*Achyropsis*, *Centrostachys*, *Nototrichium* and *Pandiaka lanuginosa* (clade II A in Figs. 2 and 3; clade annotation consistent with Di Vincenzo & al., 2018) that is sister to a clade comprising all the other genera including the majority of species of *Cyathula* and *Pandiaka* (clade II B in Figs. 2 and 3). The nrITS trees (Fig. 3) largely agree on the plastid backbone and the composition of the subclades, although there is weak support for *C. orthacantha* as sister (0.93 PP, 81 ML-BS) to the also here well-supported Achyranthes subclade (1.0 PP, 100 ML-BS, 99 MP-JK, clade B in Figs. 2 and 3). Internally, relationships in the *Achyranthes* subclade are less clear and the nrITS topology (Fig. 3) deviates in the position of some samples of *A. aspera* (such as AC1099) in comparison to the mostly well-supported plastid tree. Species limits of *A. aspera* appear to be largely unclear as evidenced by our molecular data, which is also reflected by its high number of infraspecific taxa (suppl. Appendix S1). Further research with a much greater taxon sampling is needed to clarify this. Since taxonomic decisions made in this study are not affected, such research was beyond the scope of this paper. *Centrostachys*

*aquatica* appears inside the clade in the BI and ML trees of nrITS (Fig. 3) but on a very short and hardly supported internal node and depicts a long branch itself. In the plastid tree (Fig. 2), it is sister to the remainder of the species in the *Achyranthes* subclade. Resolving such inconsistencies will not only require multiple samples of *Centrostachys* and a thorough representation of *Achyranthes*, but also nuclear loci which other than nrITS, allow for well-resolved and statistically supported gene trees to effectively test for possible reticulations as well as complete plastid genomes to examine if the short internal branches within subclade II B in the plastid tree (Fig. 2) represent the signal of the whole genome. Nevertheless, all phylogenetic evidence converges on the fact that the members of the morphologically rather homogeneous genus *Achyranthes* as currently circumscribed, gave rise to entities currently recognized at genus level as *Achyropsis* and *Nototrichium*.

Our plastid tree based on extended character sampling now provides maximum support for a core of the clade comprising most species of *Cyathula* and *Pandiaka* (clade II B),

### Floral morphology

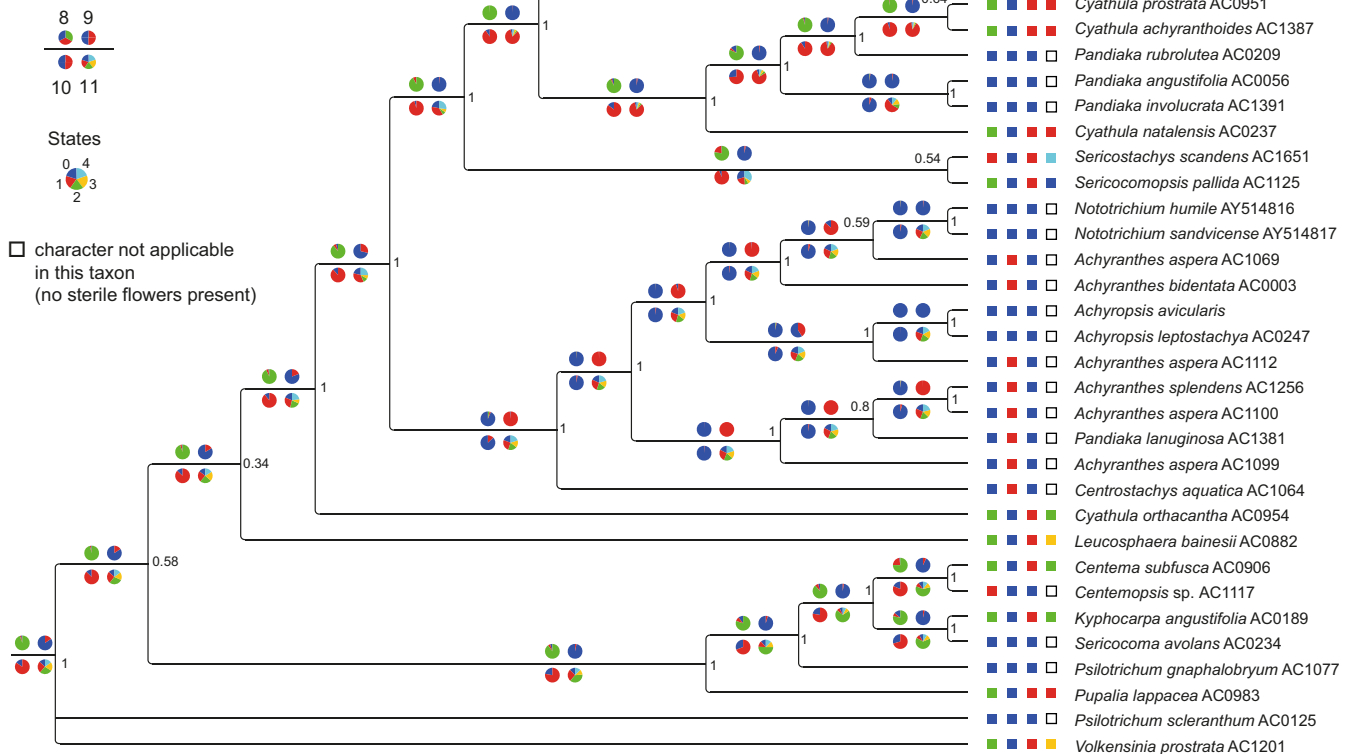
Character 08: Structure of cymes

Character 09: Position (angle) of cymes

in relation to the inflorescence axis

Character 10: Presence / absence of sterile flowers

Character 11: Shape of sterile flowers



**Fig. 6.** Evolution of floral morphology using the maximum clade credibility tree inferred from the plastid dataset. Pie charts correspond to probabilities of ancestral character states reconstructed with MrBayes for the structure of cymes (character 8), the position of cymes in relation to the inflorescence axis (character 9), the presence or absence of sterile flowers (character 10) and the shape of sterile flowers (character 11). For character and state definitions, see Appendix 2. Support values next to nodes are Bayesian posterior probabilities.

that was initially found by Di Vincenzo & al. (2018) and also includes *Nelsia* and the two different lineages of *Sericocomopsis hildebrandtii* (Fig. 2), whereas *Sericocomopsis pallida* and *Sericostachys scandens* appear outside. Their sister-group relationship as suggested in the plastid tree (Fig. 2) needs further testing with additional sequence data. The nuclear tree (Fig. 3) congruently depicts a sister-group relationship of *Cyathula cylindrica* to one of the lineages of *Sericocomopsis hildebrandtii* as well as two lineages of *Cyathula*, one comprising *C. polycephala* and allies, and the other *C. achyranthoides* and *C. prostrata* appearing as sister species, *C. natalensis* and all species of *Pandiaka* except *P. lanuginosa* (Figs. 2, 3). *Nelsia quadrangula* is not part of any of these four species groups. Albeit with low support, the ITS tree depicts *Sericocomopsis pallida* as first branch of clade II B, outside the *Cyathula* clade, whereas ITS otherwise does not provide any resolution among the species groups of the *Cyathula* clade, including the unresolved position of *Sericostachys* (Fig. 3). The short internal branches among the sublineages, in both plastid and nuclear trees

(Figs. 2, 3) are in line with their suggested rapid diversification in the late Miocene (Di Vincenzo & al., 2018).

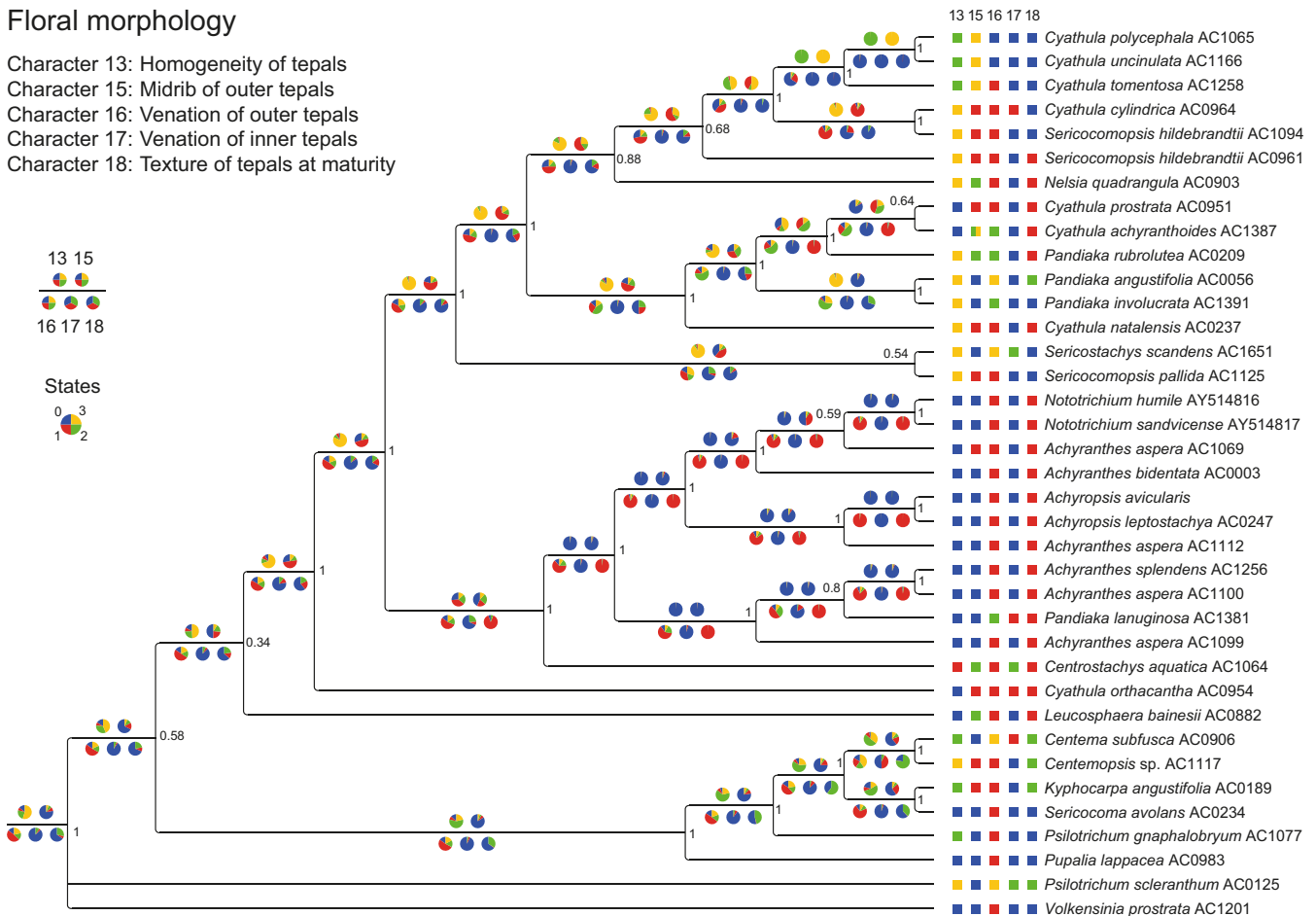
As indicated by results from BayesTraits, *Sericostachys* is morphologically outstanding with several characters autapomorphic within Achyranthoids II, such as the life form, the arrangement of paracladia, the structure of cymes, and the shape of sterile flowers (characters 2, 7, 8, and 11) or at least rare within Achyranthoids II (e.g., the venation of outer tepals; character 16). Additionally, stamens in *Sericostachys* are free and alternate with short, triangular interstaminal appendages (Townsend, 1985, 2000).

#### Evolution of habit and vegetative morphology. —

Taxa with annual life cycle (character 1, state 0) evolved several times from perennials in different lineages of the Achyranthoids (Fig. 5). These results are in line with Ortuño Limarino & Borsch (2020), who also found several independent transitions from perennials to annuals in *Gomphrena* and relatives (core Gomphrenoid clade of Amaranthaceae) in line with the observation that vegetative characters tend to be homoplastic rather than to exhibit synapomorphies for

#### Floral morphology

Character 13: Homogeneity of tepals  
 Character 15: Midrib of outer tepals  
 Character 16: Venation of outer tepals  
 Character 17: Venation of inner tepals  
 Character 18: Texture of tepals at maturity



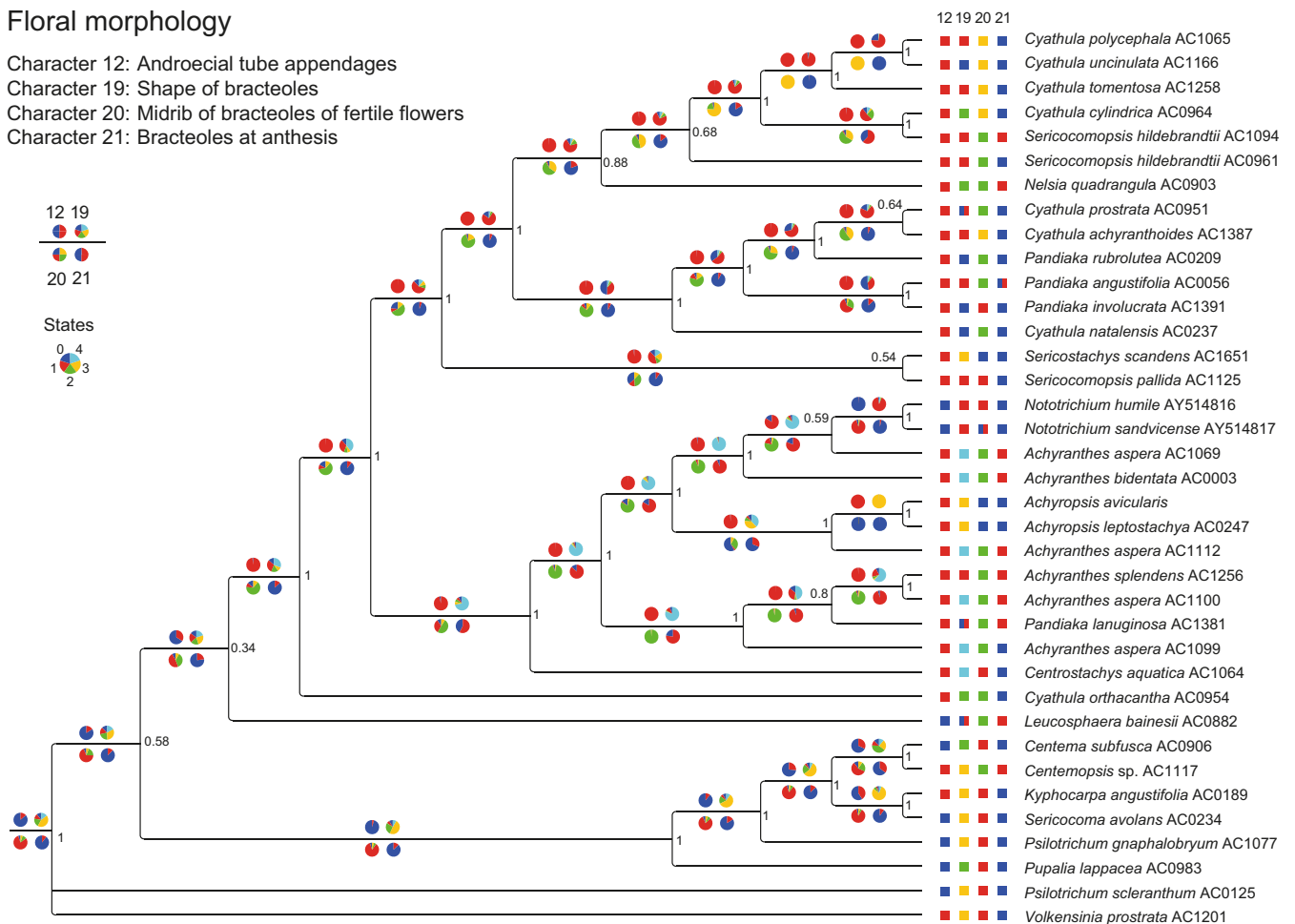
**Fig. 7.** Evolution of floral morphology (variation of the tepals) using the maximum clade credibility tree inferred from the plastid dataset. Pie charts correspond to probabilities of ancestral character states reconstructed with MrBayes for homogeneity of tepals (character 13), midrib of outer tepals (character 15), venation of outer and inner tepals (characters 16 and 17) and the texture of tepals at maturity (character 18). For character and state definitions, see Appendix 2. Support values next to nodes are Bayesian posterior probabilities.

individual lineages. In the case of *Gomphrena* the transition to an annual life cycle is connected to an adaptation to seasonally dry Inner-Andean valleys, where these plants survive the dry season as seeds. In the Achyranthoids such contrasts in habitat humidity are less evident. *Cyathula orthacantha*, for example, is a plant of overgrazed and disturbed places (Townsend, 1985, 2000), indicating that the annual life cycle has evolved fostering the ability to rapidly colonize open soils. The life form (character 2) shows multiple transitions between woody shrubs, subshrubs and herbaceous perennials. Interestingly, shrubs seem derived in species growing in dry bushland to semideserts like *Sericocomopsis pallida* (Fig. 5). The treelets of *Nototrichium* clearly originated from herbs, and exhibit an example of island gigantism and island woodiness in the Hawaiian archipelago. This result fits to the general pattern of the evolution of island woodiness in various other flowering plant lineages, as documented, e.g., by Lens & al. (2013). The habit of a woody liana in *Sericostachys scandens* is an autapomorphy within the Achyranthoids. *Sericostachys* is a rain forest

plant that grows over tree tops and shows various adaptations as a liana (including diaspores that can be distributed by air, see below). In a broader context of the Amaranthaceae, lianas evolved in several distant lineages with species growing in tropical forests such as *Chamissoa* (Sohmer, 1977), *Hebanthe* (Borsch & Pedersen, 1997) or *Pedersenia* (Borsch & al., 2011). Also, the stellate indumentum of stem and leaves (character 3, state 1) is a derived apomorphy in *Sericocomopsis pallida* at the level of the core Achyranthoids but independently evolved in dry-adapted *Chionothis latifolia* that is an early branch of the achyranthoid clade (Di Vincenzo & al., 2018) not included in this investigation, and within various genera of the Neotropical Gomphrenoideae such as *Alternanthera* (Sánchez-del Pino & al., 2012) or *Hebanthe* (Borsch & Pedersen, 1997). The cauline leaf shape (character 4) is highly homoplastic but provides a useful feature for differentiating the two *Sericocomopsis hildebrandtii* lineages (suppl. Fig. S3). The petiole length (character 5) is highly homoplastic within genera as is within single individuals (suppl. Fig. S3).

Floral morphology

Character 12: Androecial tube appendages  
 Character 19: Shape of bracteoles  
 Character 20: Midrib of bracteoles of fertile flowers  
 Character 21: Bracteoles at anthesis



**Fig. 8.** Evolution of floral morphology using the maximum clade credibility tree inferred from the plastid dataset. Pie charts correspond to probabilities of ancestral character states reconstructed with MrBayes for the variation of androecial tube appendages (character 12), the shape of bracteoles (character 19), midrib of bracteoles of fertile flowers (character 20) and bracteoles at anthesis of (character 21). For character and state definitions, see Appendix 2. Support values next to nodes are Bayesian posterior probabilities.



### Evolution of inflorescence and floral morphology. —

We found several character states for Achyranthoids II which differentiate it from Achyranthoids I or early-branching lineages of Achyranthoids: All taxa of Achyranthoids II (except *Nototrichium*) possess androecial tube appendages which presumably derived once in the common ancestor of subclade II but additionally within early-branching lineages of Achyranthoids and in *Centemopsis* and *Kyphocarpa* of subclade I. To the contrary, androecial tube appendages are missing in most genera outside subclade II (character 12; Fig 8), also in genera not sampled here such as *Chionothis*, *Dasyphaera*, *Lopriorea*, and *Marcelliopsis*, but which belong to the Achyranthoids (Di Vincenzo & al., 2018). The ovary in all taxa of Achyranthoids II is glabrous, whereas it can be pilose or lanate in genera outside this clade, such as *Centemopsis*, *Kyphocarpa*, *Leucosphaera* and *Sericocoma* (character 24; suppl. Fig. S3), as well as in *Marcelliopsis*, and *Mechowia* (both Achyranthoids I; Di Vincenzo & al., 2018).

Morphological differences between Achyranthoid II subclades A and B were found mainly in inflorescence and floral morphology, e.g., in the structure of cymes (character 8; Fig. 6). We earlier reported that sterile flowers appeared multiple times and were overrated so far as diagnostic characters supporting the circumscription of genera and tribes (Di Vincenzo & al., 2018). In this investigation, we defined a set of inflorescence characters (characters 8–11; see Appendix 2 for a detailed discussion on character definitions) that are largely based on paracladia as basic units of the inflorescences (Acosta & al., 2009), and using a reductive morphological character coding approach (Torres Montúfar & al., 2018). Our results indicate that cymes with more than one order of branches (character 8, state 2) are the ancestral state for achyranthoid subclade II (Fig. 6). These were reduced to cymes with first-order branches or to single flowers several times (character 8, states 0, 1). One of these reductions occurred in the ancestor of subclade II A, which only includes taxa with solitary flowers (*Achyranthes*, *Achyropsis*, *Centrostachys*, *Nototrichium*). Additionally, deflexed cymes which are appressed to the inflorescence axis in maturity (character 9, state 1) depict the ancestral state for subclade II A and constitute a conspicuous feature of the genera *Achyranthes* and *Centrostachys* as currently circumscribed. However, our ancestral state reconstruction also shows that state 1 is plesiomorphic, and probably was reversed in plants no longer dispersed by large animals such as *Nototrichium* on the Hawaiian islands, which also lost the spine-like excurrent midribs of bracteoles. Sterile flowers are completely missing in subclade II A, whereas they are present in most taxa of subclade II B (character 10; Fig. 6). In our ancestral state reconstruction (Fig. 6) there is a high probability that the common ancestor of subclade II A had no sterile flowers, implying a character state transformation (= loss of sterile flowers on the branch of the common ancestor of subclade II A) along with the reduction in flower number in the cymes. Di Vincenzo & al. (2018) found almost equal state probabilities for the presence (59%) and absence (41%) of sterile

flowers as ancestral state in Achyranthoids under an unconstrained model, whereas best-fit BiSSE models favoured independent gains of sterile flowers (i) in a core of subclade II with a subsequent loss in the lineage of *Sericocomopsis hildebrandtii* sister to *C. cylindrica*, (ii) in *C. orthacantha*, and (iii) within Achyranthoids I in the terminal clades of *Pupalia* and relatives as well as (iv) in *Kyphocarpa* and relatives in Achyranthoids I. The latter terminal clades are just represented by a single individual in this investigation as we focus on Achyranthoids II but future research will also address this in the other Amaranthaceae as well as the influence of models for better understanding the evolution of morphological diversity. For the purpose of exploring possible synapomorphies to circumscribe taxa and of evaluating hitherto used diagnostic characters in a phylogenetic context we believe that the use of MCMC tree optimization as implemented in BayesTraits is providing adequate results. For example, our ancestral character state reconstruction unambiguously shows that the genus *Achyranthes* as currently understood was basically circumscribed with plesiomorphic character states.

Another difference between subclades II A and II B is observed in the homogeneity of tepals (character 13; Fig. 7). Tepals are all equal in the taxa of subclade II A (except in *Centrostachys aquatica*, in which the outermost tepal is different in shape and size, which depicts an autapomorphy for the species). In subclade II B most taxa exhibit two outer and three inner tepals, which are smaller but similar in shape, which is also the ancestral state for subclade II B (character 13, state 3).

### Monophyletic circumscription of *Cyathula* and status of *Sericocomopsis*. —

Most of the analysed species of *Cyathula* appear within the core of clade B including the type species of the genus – *C. prostrata*. *Cyathula* is the oldest generic name present within subclade II B. According to the genus concept of *Cyathula* applied by Schinz (1893, 1934) and Townsend (1993, 2000), all species have cymes with sterile flowers with more or less excurrent midribs of bracteoles or tepals that are often forming hooks. Species of *Cyathula* have more or less quadrangular androecial tube appendages with a dentate or fringed distal margin. The presence of sterile flowers also applies to the genus *Nelsia*, which has quadrangular fimbriate androecial tube appendages (Schinz, 1911). *Nelsia* therefore falls well into the range of morphological variation of *Cyathula*, although the discussion on the diagnostic characters in Schinz (1911) rather focused on a comparison with the genera *Sericocoma* and *Kyphocarpa* since he separated *Nelsia quadrangula* (Engl.) Schinz as an own genus from *Sericocoma*, which was transferred to *Kyphocarpa* by Baker & Clarke (1909). However, none of the historical authors, including Suessenguth (1952) employed a comprehensive morphological comparison of all putatively related taxa as it was undertaken for this investigation, also applying a phylogenetic perspective. According to our phylogenetic results, *Sericocoma* and *Kyphocarpa* are closely related, but do not belong to Achyranthoids II (Figs. 2, 3). Among its next relatives in clade B of Achyranthoids II, *Nelsia quadrangula* stands out by sterile flowers with bracteoles modified to conspicuous

hairy, stiff and spine-like structures (character 11, state 3; Fig. 6). However, this is a single specific feature in a series of modifications that convergently led to increased adhesive ability in diaspores serving zoochory in the Achyranthoids. Morphological analysis shows that the core of clade B corresponding to the *Cyathula* clade in Fig. 2 is characterized by cymous partial florescences, with cymes of more than one order of branches and with sterile flowers in most cases present and modified into hooks (characters 8, 10, 11 in Fig. 6). Although the remaining species of *Pandiaka* (approx. 8 additional species) and *Nelsia* (1 additional species) were not included in this phylogenetic analysis, it is clear that their generic names cannot be maintained since their type species (*P. involucrata* and *N. quadrangula*) are nested within *Cyathula* (Figs. 2, 3).

*Sericocomopsis* was described by Schinz (1895) as having only fertile flowers and broadly obovate to quadrangular androecial tube appendages with a fringed upper margin, a glabrous ovary with elongated style and an inconspicuous stigma otherwise only present in *Achyranthes*, *Centrostachys* and *Pandiaka* (but these have solitary flowers) and in *Nelsia* (but this has sterile flowers). *Sericocomopsis pallida* remains in a phylogenetically distant position from the other two lineages of *Sericocomopsis* and from the core of *Cyathula*. However, since the type species of the genus, *S. hildebrandtii* must be included into *Cyathula* to make this genus monophyletic, a new genus has to be described for this lineage (see taxonomic treatment, below). Morphologically, this new genus is easily recognized within Achyranthoids by the stellate hairs of the indumentum of stem and leaves, and the unmodified sterile flowers. In order to make *Cyathula* monophyletic we further suggest to merge the genera *Sericocomopsis* (*S. hildebrandtii*, *S. meruensis*), *Nelsia*, and *Pandiaka* (except *P. lanuginosa*) with *Cyathula*, also considering that the inflorescence and floral characters originally used to define the first three genera turned out to be homoplastic. In this circumscription *Cyathula* now contains 40 species (see suppl. Appendix S1). An alternative classification scheme to extend the genus *Cyathula* to the complete clade II B would have meant to merge the well-established genus *Sericostachys* against robust phylogenetic evidence from the plastid genome (Fig. 2) and morphology in the absence of contradicting signal from the nuclear genome.

*Cyathula orthacantha* is clearly established as a separate lineage constituting an early branch of subclade II of Achyranthoids and therefore must be excluded from *Cyathula*. It is therefore described as a genus of its own as part of the treatment in our study. *Cyathula lanceolata* was resolved as one of the basally branching lineages of the Achyranthoids (Müller & Borsch, 2005b; Di Vincenzo & al., 2018) and therefore is not part of *Cyathula* according to our new genus circumscription. Considering its distant phylogenetic position, it was not included in this investigation and the name is listed under “excluded names” in our taxonomic backbone for *Cyathula*. The further treatment of *C. lanceolata* is going to be part of a different publication.

### Species limits of *Sericocomopsis hildebrandtii*. —

According to the widely used taxonomic accounts in *Flora of Tropical East Africa* and *Flora of Ethiopia and Eritrea* (Townsend, 1985, 2000) only two species of *Sericocomopsis* occur in East Africa: *S. pallida* is native to Kenya, Tanzania, Djibouti, Somalia and Ethiopia and *S. hildebrandtii* to Uganda, Kenya, Tanzania and Ethiopia. This view has been accepted in genus-level treatments of the Amaranthaceae s. str. (Townsend, 1993; Hernández-Ledesma & al., 2015). In contrast, Di Vincenzo & al. (2018) found specimens identified as *S. hildebrandtii* to belong to two distant lineages in phylogenetic analyses or plastid and nuclear trees. In this investigation we broadened the sampling of individuals from *Sericocomopsis*, and added further regions from the plastid genome, which resulted in a corroboration of the distant position of these two lineages of *S. hildebrandtii* (Figs. 2, 3) with further increased node support in the plastid tree compared to our previous study (Di Vincenzo & al., 2018). Notably, all sequenced individuals were resolved in two highly supported terminal clades, one sister to *Cyathula cylindrica*, and the other appearing in an isolated position among different sublineages of *Cyathula*, suggesting the existence of two different, monophyletic species instead of one.

Morphologically, the individuals are very similar within these two lineages, but differ strongly between them in indumentum (nearly glabrous in the more isolated lineage) and tepal morphology (indurate with thickened midvein in the more isolated lineage; Fig. 4). Further differences are in the distances between cymes on the main inflorescence axis (character 6 – shape of paracladia) and the shape of cauline leaves (character 4) and leaf size. In order to find the right name for the second, more isolated lineage, which morphologically is not corresponding to the type material of *Sericocomopsis hildebrandtii*, we considered all synonyms cited for *S. hildebrandtii* (Townsend, 1985, 2000). In his description of *S. meruensis* Suess., Suessenguth (1950) already recognized the difference in the hairiness of the inflorescences between *S. hildebrandtii* and *S. meruensis* and stated that “pili multo minores et nimius densi quam in *S. Hildebrandtii*, quare inflorescentia tota sine lente in hac specie glabra videtur” indicating that the hairs are less dense and shorter in *S. meruensis* compared *S. hildebrandtii* and that observed without a lens, *S. meruensis* appears glabrous. We agree to this statement. During our field work, specimens collected as “*S. hildebrandtii*” could already be noticed to belong to two groups differing in the hairiness of inflorescences. However, Suessenguth (1950) did not recognize the differences in leaf shape and considered leaves to be similar in both species. By examining multiple specimens from each lineage, we found that leaves in the hairy specimens matching the type of *S. hildebrandtii* have a more ovate shape whereas leaves in the other lineage are obovate in shape. To the contrary, the type specimen of *S. grisea* Suess. shares the same states of the morphological characters with the type specimen of *S. hildebrandtii*. We therefore confirm the name *S. grisea* as a synonym of *S. hildebrandtii* as treated by Townsend (1985, 2000).

The specimen on which “*Sericocomopsis lindaviana* Peter” was based resembles the type of *S. meruensis* and not that of *S. hildebrandtii*. However, “*S. lindaviana*” is not validly published according to Art. 39.1 of the *Code* (Turland & al., 2018).

We therefore propose to resurrect *Sericocomopsis meruensis* Suess. as this provides the oldest valid name for the second, more isolated lineage of *S. hildebrandtii*. In summary, the morphological distinctness between *S. hildebrandtii* and *S. meruensis* reported by Suessenguth (1950) is confirmed here in a phylogenetic context. These results underscore the need to carefully evaluate entities put into synonymy using a morpho-species approach.

**Monophyletic circumscription of *Achyranthes*.** — This study confirms the earlier results from Di Vincenzo & al. (2018) in that *Achyranthes* is paraphyletic to *Achyropsis* and *Nototrichium*, and altogether they are strongly supported as sister to the monotypic *Centrostachys aquatica*, which is branching first within subclade II A (plastid tree, Fig. 2). Whereas the nrITS trees inconsistently show *Centrostachys* nested within the *Achyranthes* clade, there are strong morphological similarities of *Achyranthes* species and *Centrostachys*. The fact that our molecular trees from both genomic compartments revealed *Pandiaka lanuginosa* as part of the *Achyranthes* clade is also supported by morphological characters, which clearly distinguish it from other species of *Pandiaka*, e.g., the conspicuously deflexed cymes at maturity (character 9, state 1; Fig. 6), but also the life cycle (character 1; Fig. 5) and the petiole length (character 5, suppl. Fig. S3). The deviant morphology of *P. lanuginosa* was also noted by Townsend (1980), who, while maintaining *P. lanuginosa* within *Pandiaka*, described it as “morphologically transitional” between *Achyranthes* and *Pandiaka*. As a result of our investigation of nomenclature and typification it turned out that *Achyranthes schinzii* (Standl.) Cufod. is the correct name for this species, which is cited as synonym of *Pandiaka lanuginosa* in the widely used account in *Flora of Tropical East Africa* (Townsend, 1985). This entity is therefore also dealt with in the taxonomic treatment part in the main body of this paper.

Even though there are some characters making *Nototrichium* unique compared to the remaining genera of subclade II A, the phylogeny clearly shows *Nototrichium* nested within *Achyranthes*, and in order to make this genus monophyletic the species of *Nototrichium* need to be included. Flowers in *Nototrichium* are described as 4-parted, while in all remaining genera of subclade II A they are 5-parted. Furthermore, *Nototrichium* is a Hawaiian endemic geographically separated from the remaining genera and its species grow as treelets (character 2 – life form), which is a derived feature associated to island gigantism, which also appeared convergently in single species being endemics on islands within many other genera.

*Centrostachys* is the only genus within subclade II A and within the entire Achyranthoids which is adapted to an aquatic or subaquatic habitat, such as shore areas and marshy places but this alone is not a sufficient criterion to maintain it as a

separated monotypic genus. *Centrostachys* was transferred to the genus *Achyranthes* many times in the history of classification by different authors (or vice versa, as suggested by Standley, 1915) due to its morphological similarities (e.g., Hooker, 1880; Schinz, 1893; Cavaco, 1962). As shown in our BayesTraits analyses, *Centrostachys aquatica* shares several morphological characters with *Achyranthes* such as the absence of sterile flowers (character 10), the shape of paraclydia (character 6), the structure of cymes (character 8), and, in particular the position/angle of cymes related to the inflorescence axis (character 9), a unique feature within Achyranthoids. Overall, there is more evidence to include *Centrostachys* in *Achyranthes* than to retain it as a separate genus, regardless of a sister-group or nested position with respect to the other species.

The status of *Achyropsis* was also discussed controversially by several authors and it was sometimes included into *Achyranthes* (e.g., Moquin-Tandon, 1849; Schinz, 1893). Townsend (1980) mentioned that both genera are very close morphologically but considered their species as unlikely to be confused. According to him, flowers of *Achyropsis* are much smaller than in most species of *Achyranthes*, bracteoles are not long-aristate and the fruiting perianth is not deflexed in *Achyropsis*. However, these are rather pragmatic arguments for maintaining a genus *Achyranthes* whereas phylogenetic evidence clearly shows that *Achyranthes* is paraphyletic to *Achyropsis*. Within subclade II A we therefore propose to maintain only one monophyletic genus, which has to be called *Achyranthes* L. as this is the oldest available generic name and comprises 27 currently accepted species.

## ■ TAXONOMIC TREATMENT

A comprehensive taxonomic backbone of all genera and species within subclade II of the achyranthoid clade of Amaranthaceae is presented in this paper, following the style adopted earlier for *Iresine* (Borsch & al., 2018). In addition, the World Flora Online identifiers (WFO-IDs) have already been included for each name and will facilitate the ingestion of the taxonomic backbone through the Caryophyllales Taxonomic Expert Network into the WFO (see Borsch & al., 2020). Due to the large number of names the full taxonomic backbone is provided in suppl. Appendix S1, whereas newly established genera, new combinations, new names required to avoid generating later homonyms, and new lectotypifications are presented in the following section. Relevant provisions of the *International Code of Nomenclature for algae, fungi, and plants* (Turland & al., 2018), were applied and cited after the nomenclatural status (e.g., “nom. illeg. [Art. 53.1]”).

In total, we accept five genera within achyranthoid subclade II. The genus *Achyranthes* is considerably extended, now including also the species of the former genera *Achyropsis*, *Nototrichium* and *Centrostachys* plus *Pandiaka lanuginosa*. The latter was formerly treated as a species of



*Pandiaka* but the combination into this genus (Schinz, 1934) was based on an illegitimate basionym. Cufodontis (1953) already made a combination under *Achyranthes* for a conspecific entity originally described in *Centrostachys*, so the name *Achyranthes schinzii* (Standl.) Cufod. must be applied to this species. The second genus which is also largely extended is *Cyathula*, now also comprises two species of *Sericocomopsis* (one of which is resurrected belonging here), and the genera *Pandiaka* and *Nelsia*. The genus *Sericostachys* continues to be accepted. In addition, two easily recognizable monotypic genera are newly described to accommodate phylogenetically isolated and morphologically distinct species formerly included in *Cyathula* and *Sericocomopsis*, respectively. We favour a treatment that maintains the morphologically very distinct genus *Sericostachys*, which is also widely accepted in African botany, over further expanding the circumscription of *Cyathula* to a deeper node, so it would comprise the complete subclade II B.

The complete taxonomic backbone in suppl. Appendix S1 contains the already validated new names, and therefore provides a comprehensive and complete species-level treatment for the Achyranthoids II. However, type information has not yet been added for names not treated here in the main section of this paper; these are being added during ongoing work for a complete species list of the Amaranthaceae. The complete taxonomic backbone also includes secundum references for synonyms.

*Achyranthes* L., Sp. Pl.: 204. 1753, nom. cons. ≡ *Stachyarpagophora* Vaill. ex M.Gómez in Anales Inst. Segunda Enseñ. 2: 312. 1896 – Type: *Achyranthes aspera* L., nom. cons. (typ. cons.) (≡ *Stachyarpagophora aspera* (L.) M.Gómez).

= *Centrostachys* Wall. in Roxburgh, Fl. Ind. 2: 497. 1824 – Type: *Centrostachys aquatica* (R.Br.) Wall., **syn. nov.**

= *Amorgine* Raf., New Fl. 4: 44. 1838 (“1836”) – Type: *Amorgine albescens* Raf.

= *Achyranthes* sect. *Achyropsis* Moq. in Candolle, Prodr. 13(2): 310. 1849 ≡ *Achyropsis* (Moq.) Hook.f. in Bentham & Hooker, Gen. Pl. 3(1): 36. 1880 – Type (designated by Cavaco in Mém. Mus. Natl. Hist. Nat., B, Bot. 13: 149. 1962): *Achyropsis leptostachya* (E.Mey. ex Meisn.) Hook.f., **syn. nov.**

= *Nototrichium* Hillebr., Fl. Hawaiian Isl.: 372. 1888 – Type (designated by Iamónico in Phytotaxa 350(2): 150. 2018): *Nototrichium viride* Hillebr., **syn. nov.**

*Emended genus description.* – Perennial herbs, subshrubs, shrubs or treelets (one species, *Achyranthes aquatica*, occurring in subaquatic or aquatic habitats). Leaves always entire and opposite; shortly to distinctly petiolate and variable in shape (ranging from ovate, elliptic, or lanceolate to obovate-spathulate-oblancheolate) and size within the genus and within single species or individuals. Indumentum of stem and leaves constituted of simple hairs (hairs never stellate). Paracladia solitary on main axes as well as on lateral branches and normally spiciform with solitary flowers (reduced cymes) clearly

separated during anthesis or rarely elongate to cylindrical with flowers densely aggregated as in *A. sandwicensis*. Cymes always reduced to single flowers and modified sterile flowers never present. In many species the reduced cymes are deflexed and closely appressed to the inflorescence axis in fruit ripening (e.g., in *Achyranthes aquatica*, *A. aspera*). Bracts always persistent, lanceolate or ovate (rarely broadly ovate as in *Achyranthes bidentata*) with acuminate tip, rarely ovate with blunt tip (as in *A. humile*); midrib of bracts either not excurrent or mucronate/shortly excurrent to long excurrent. Bracteoles not persistent and falling with the perianth and fruit. In some taxa bracteoles become strongly recurved during anthesis (e.g., in *Achyranthes aspera*, *A. bidentata*, *A. schinzii*, *A. splendens*). Bracteoles (lanceolate-) ovate with acuminate tip, ovate to broadly ovate with obtuse tip or orbicular with an emarginate/retuse tip (e.g., in *Achyranthes aquatica*, *A. aspera*, *A. bidentata*); midrib of bracteoles normally distinctly/long excurrent, sometimes not or only shortly excurrent or mucronate. Perianth segments (4–)5; tepals all equal (except in *A. aquatica*, in which the outermost tepal is different in size and shape) and becoming slightly indurate at base at maturity, outer and inner tepals 1–3-nerved (and max. 5-nerved in *A. schinzii*), inner tepals of *A. aquatica* with more than 5 veins; tepals are narrowly lanceolate with an acute or acuminate tip; the midrib of the outer tepals is not excurrent in the majority of species and rarely shortly or distinctly excurrent. Stamens 2–5; anthers bilocular; filaments filiform, delicate or stout; androecial tube appendages present between the filaments and triangular to (broadly) quadrate-spathulate, rarely absent as in *A. humile* and *A. sandwicensis*. Style very short to slender; stigma capitate. Ovary uniovulate and always glabrous.

*Note.* – In his description of the genus *Nototrichium*, Hillebrand (1888) mentions that it is based on “*Ptilotus*, sect. *Nototrichium* Gray, in Bot. U. S. E. E. ined.” We are not aware of any valid publication of this name. Therefore, there is no basionym author in parenthesis for the genus *Nototrichium*, although this is sometimes cited.

*Achyranthes divaricata* (Lorence) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, **comb. nov.** ≡ *Nototrichium divaricatum* Lorence in Novon 6(1): 64, fig. 1. 1996 – Holotype: U.S.A. Hawaiian Islands, Kaua‘i: Hanalei District, Kalalau rim, 320° NW-facing cliffs below and E of first Kalalau lookout, diverse montane precipitous slopes with small pockets of forest and vertical cliffs, alt. 1000–1100 m, 15 Sep 1991, K. Wood 1227, M. Query & D. Boynton (PTBG barcode PTBG100000023 [image!]; isotypes: BISH barcode BISH1005539 [image!], F No. 2166403 [barcode V00475286F, image!], MO No. 05036867 [barcode MO-215356; image!], NY barcode 00074031 [image!], US barcode 00512723 [image!]).

*Achyranthes fruticulosa* (C.B.Clarke) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, **comb. nov.** ≡ *Achyropsis*

*fruticulosa* C.B. Clarke in Thiselton-Dyer, Fl. Trop. Afr. [Oliver] 6(1): 66. 1909 – Holotype: KENYA. Kiambu District, Kukui, 12 Jun 1902, *Kässner 1011* (K barcode K000243763 [image!]; isotypes: BM barcode BM000910336 [image!], MO No. 1649307 [barcode MO-255165; image!]).

= *Achyropsis greenwayi* Suess. in Kew Bull. 4(4): 475. 1949 – Holotype: TANZANIA. *Greenway 6740* (K barcode K000243764 [image!]; isotypes: EA barcode EA0000 02196 [image!], K barcode K000243765 [image!], PRE barcode PRE0824155-0 [image!]).

– “*Achyranthes fischeri* Schinz ex R.E. Fr.” in Notizbl. Bot. Gart. Berlin-Dahlem 9(85): 319. 1925, nom. nud.

– “*Pandiaka fischeri* (Schinz) Peter” in Repert. Spec. Nov. Regni Veg. Beih. 40(2.3): 242. 1938, combination not validly published.

*Note.* – Fries & Fries (1925) report a specimen annotated by Schinz in 1911 with the name “*Achyranthes fischeri* Schinz” which according to them does not differ from *Achyropsis fruticulosa*. However, Schinz never published the name, a fact already mentioned by Fries & Fries (1925) who effectively published this herbarium name. There is a specimen *Fischer 48* in HBG (barcode HBG-503186) annotated by Schinz in 1916 as “*Achyranthes Fischeri* Schinz = *Achyropsis fruticulosa* C.B. Clarke?” which indicates that Schinz himself was not sure about the distinctness of this entity, what is consistent with his later treatment (Schinz, 1934) in which he listed it as “ined.” following *Achyropsis fruticulosa*, also citing “R.E. Fries 1925” whose opinion he seemed to have accepted.

*Achyranthes graminiformis* Di Vincenzo, Berendsohn, M. Wondafrash & Borsch, **comb. nov.** ≡ *Achyropsis filifolia* C.C. Towns. in Kew Bull. 34(3): 431. 1980, non *Achyranthes filifolia* Willd. ex Schult. – Holotype: TANZANIA. Mbeya District, Ruaha National Park, Magangwe Hill, 20 Mar 1973, *A. Bjørnstad AB 2687* (O barcode V-201402; isotypes: DSM n.v., K barcode K000243770 [image!]).

*Note.* – *Achyranthes filifolia* Willd. ex Schult. [in Roemer & Schultes, Syst. Veg. 5: 549. 1819 – Type: *Humboldt A. s.n.* (HAL barcode HAL-0117856)] is validly published, so a new name is needed to avoid creating a later homonym. *Achyranthes filifolia* has so far been an unresolved name but an examination of the specimen shows that it is not an Amaranthaceae but belongs to the Caryophyllaceae (*Polycarpea corymbosa* (L.) Lam.) to which this name will be a new synonym. We agree with Townsend (1985) in that *Achyropsis filifolia* C.C. Towns. represents an entity different from *Achyropsis gracilis* C.C. Towns. and also from other species in the genus *Achyranthes*.

*Etymology.* – The specific epithet reflects the slender, grass-like morphology of this species.

*Achyranthes humilis* (Hillebr.) Di Vincenzo, Berendsohn, M. Wondafrash & Borsch, **comb. nov.** ≡ *Nototrichium*

*humile* Hillebr., Fl. Hawaiian Isl.: 373. 1888 ≡ *Psilotrichum humile* (Hillebr.) Drake, Ill. Fl. Ins. Pacif.: 270. 1892 – Holotype: U.S.A. Hawaii – O’ahu: Waianae [Cape Ka’ena, near the coast], 1851–1871, *W. Hillebrand s.n.* (B barcode B 10 0699421!; isotype: K barcode K000814963 [image!]).

= *Nototrichium humile* var. *parvifolium* O. Deg. & Sherff in Bot. Leafl. 1: 4. 1950 – Holotype: U.S.A. Hawaii – O’ahu: W branch of Wai’anae Valley, not far from Kolekole Pass, dry cliff, *O. Degener 8665* (F [image!]; isotypes: CAS barcode 0007265 [image!], MASS barcode 00312959 [image!], NY barcode 00324549 [image!], US barcode 00102706 [image!]).

= *Nototrichium humile* var. *subrhomboideum* Sherff in Bot. Leafl. 1: 4. 1950 – Holotype: U.S.A. Hawaii – O’ahu: Wai’anae Mts., Mt. Ka’ala Trail from Schofield Barracks, dry slope. 1300 ft, 14 Aug 1927, *L. MacDaniels 933* (BISH No. 49833 [barcode BISH1005541; image!]; isotype: BISH No. 498332 [barcode BISH1005542; image!]).

*Note.* – We follow Wagner & al. (1990) for the circumscription of the species.

*Achyranthes laniceps* (C.B. Clarke) Di Vincenzo, Berendsohn, M. Wondafrash & Borsch, **comb. nov.** ≡ *Achyropsis laniceps* C.B. Clarke in Thiselton-Dyer, Fl. Trop. Afr. [Oliver] 6(1): 66. 1909 – Holotype: MALAWI, Nyasaland, Yort Hill [Chitipa], Tanganyika Plateau, alt. 3500–4000 ft, 1816, *A. Whyte s.n.* (K barcode K000243766 [image!]).

= *Achyropsis robynsii* Schinz in Vierteljahrsschr. Naturf. Ges. Zürich 76: 143. 1931 ≡ *Achyropsis laniceps* f. *robynsii* (Schinz) Cavaco in Mém. Mus. Natl. Hist. Nat., B, Bot. 13(1): 153. 1962 – Holotype: CONGO (D.R.C.). *W. Robyns 1812* (BR barcode 0000008819482 [image!]; Isotype: BR barcode 0000008819499 [image!]).

*Achyranthes sandwicensis* (A. Gray ex H. Mann) Di Vincenzo, Berendsohn, M. Wondafrash & Borsch, **comb. nov.** ≡ *Ptilotus sandwicensis* A. Gray ex H. Mann in Proc. Amer. Acad. Arts 7: 200. Jul 1867 ≡ *Psilotrichum sandwicense* (A. Gray ex H. Mann) Seem., Fl. Vit.: 198. 1 Oct 1867 ≡ *Nototrichium sandwicense* (A. Gray ex H. Mann) Hillebr., Fl. Hawaiian Isl.: 373. 1888 – Lectotype (designated by Sherff in Bot. Leafl. 4: 6. 1951): U.S.A. Hawaii, Oahu, near the coast, *J. Rémy 207* (GH barcode 00037133 [image!]; isolectotypes: BISH barcode BISH1005572 [image!], NY barcode 00341968 [image!]).

= *Ptilotus sandwicensis* var. *kawaiensis* A. Gray ex H. Mann in Proc. Amer. Acad. Arts 7: 200. 1867 ≡ *Nototrichium sandwicense* var. *kauaiense* (A. Gray ex H. Mann) Hillebr., Fl. Hawaiian Isl.: 373. 1888 – Holotype: U.S.A. Hawaii, Coast of Kauai, 1838–1842, *U.S. South Pacific Exploring Expedition under the command of Capt. Wilkes, U.S.N., s.n.* (US barcode 00462185 [image!]).

- = *Nototrichium sandwicense* var. *longe-spicatum* Hillebr., Fl. Hawaiian Isl.: 373. 1888 ≡ *Psilotrichum sandwicense* var. *longespicatum* (Hillebr.) Drake, Ill. Fl. Ins. Pacif.: 270. 1892 – Neotype (designated by St. John in Phytologia 42: 27. 1979): U.S.A. Hawaiian Islands, Molokai, Settlement Trail, Jun 1912, *C. Forbes* 43.Mo. (BISH barcode BISH1005560 [image!]; isoneotypes: BISH barcodes BISH1005558 [image!], BISH1005559 n.v., US barcode 00462171 [image!]).
- = *Nototrichium viride* Hillebr., Fl. Hawaiian Isl.: 373. 1888 ≡ *Psilotrichum viride* (Hillebr.) Drake, Ill. Fl. Ins. Pacif.: 270. 1892 – Holotype: U.S.A. Hawaii, Kauai, Hanapepe, *H. Mann & W. Brigham* 590 (CU, incorporated in BH in 1977, n.v.; isotypes: BISH barcodes BISH1005567 [image!], BISH1005568 [image!], GH barcode 00037128 [image!], K barcode K000814959 [image!], US barcode 00102713 [image!]).
- = *Nototrichium fulvum* Schinz in Vierteljahrsschr. Naturf. Ges. Zürich 76: 142. 1931 – Holotype: U.S.A. Hawaii – Kauai: Kaholuamanu, above Waimea, between forks of Waimea River [on exposed slope on ridge up to Kaholuamanu at 2500 ft], 24–30 Sep 1895, *A. Heller* 2831 pro parte (Z+ZT barcode Z-000000320 [image!]; isotypes: BISH n.v., MO No. 37457 [barcode MO-216273; image!], NY barcode 00324551, US barcode 00102707 [image!]). Note: See Wagner & Shannon (1999) for a discussion of the mixed collection *A. Heller* 2831 and the typification of *N. fulvum*, *N. sandwicense* var. *decipiens* and *N. sandwicense* var. *helleri*.
- = *Nototrichium sandwicense* var. *decipiens* Sherff in Bot. Leaf. 2: 2. 1950 – Holotype: U.S.A. Hawaiian Islands, Kauai: on ridge leading up to Kaholuamanu, between forks of Waimea River, 24 Sep 1895, *A. Heller* 2831 pro parte (US barcode 00102707 [image!]; isotypes: AC barcode 00312958 [image!], MO No. 37457 [barcode MO-216373; image!], NY barcode 00341951 [image!]).
- = *Nototrichium sandwicense* var. *dubium* Sherff in Bot. Leaf. 2: 2. 1950 – Holotype: U.S.A. Hawaiian Islands, Maui: southeastern East Maui, Manawainui, south slope of Haleakala, on side of a gulch, 3 Mar 1920, *C. Forbes* 1816.M. (BISH barcode BISH1005543 [image!]; isotypes: A barcode 00037121 [image!], BISH barcodes BISH1005544 [image!], BISH1005545 [image!], K barcode K000814958 [image!], L barcode L 0038796 [image!], PTBG barcode PTBG 1000000022 [image!], US barcodes 00102708 [image!], 00516918 [image!]).
- = *Nototrichium sandwicense* var. *forbesii* Sherff in Bot. Leaf. 2: 2. 1950 – Holotype: U.S.A. Hawaiian Islands, Molokai: Mauna Loa, Jun 1912, *C. Forbes* 3.Mo. (NY barcode 00341952 [image!]; isotypes: BISH barcodes BISH1005546 [image!], BISH1005547 [image!], BISH 1005548 [image!], BISH1005549 [image!], K barcode K000814957 [image!], MO No. 788105 [barcode MO-247247; image!]).
- = *Nototrichium sandwicense* var. *helleri* Sherff in Bot. Leaf. 1: 3. 1950 – Holotype: U.S.A. Hawaiian Islands, Kauai: on ridge leading up to Kaholuamanu, between forks of Waimea River, 24 Sep 1895, *A. Heller* 2831 pro parte (F No. 429251 [barcode V0047630F; image!]; isotypes: GH barcode 00037122 [image!]).
- = *Nototrichium sandwicense* var. *kolekolense* Sherff in Bot. Leaf. 1: 3. 1950 – Holotype: U.S.A. Hawaiian Islands, Molokai: on slopes of Puu Kolekole, Jul 1912, *C. Forbes* 179.Mo. (F No. 485227 [barcode V0047631F; image!]; isotypes: BISH barcodes BISH1005550 [image!], BISH1005551 [image!], MO No. 786771 [barcode MO-216355; image!]).
- = *Nototrichium sandwicense* var. *lanaiense* Sherff in Bot. Leaf. 1: 3. 1950 – Holotype: U.S.A. Hawaiian Islands, Lanai: W end [of island], in dry forests, Jun 1913, *C. Forbes* 155.L. (BISH barcode BISH1005552 [image!]; isotypes: BISH barcode BISH1005553 [image!], CAS barcodes 0007266 [image!], 0007267 [image!], US barcode 00102711 [image!]).
- = *Nototrichium sandwicense* var. *lanceolatum* Sherff in Bot. Leaf. 1: 3. 1950 – Holotype: U.S.A. Hawaiian Islands, Hawaii: Kona, Puuwaawaa, Aug 1917, *J. Rock* 12973 (BISH barcode BISH1005554 [image!]; isotype: BISH barcode BISH1005555 [image!]).
- = *Nototrichium sandwicense* var. *latifolium* Sherff in Bot. Leaf. 1: 3. 1950 – Holotype: U.S.A. Hawaiian Islands, Lanai: Maunalei Gorge, 30 Jul 1910, *J. Rock & J. Hammond* 8117 (GH barcode 00037124 [image!]; isotypes: BISH barcode BISH1005556 [image!], NY barcode 00341955 [image!]).
- = *Nototrichium sandwicense* var. *leptopodium* O.Deg. & Sherff ex Sherff in Bot. Leaf. 1: 2. 1950 – Holotype: U.S.A. Hawaiian Islands, Maui: Nakaohu, on a lava waste, 23 Dec 1948, *O. Degener* 19341 (F No. 1449387 [barcode V0047632F; image!]; isotypes: BISH barcode BISH1005557 [image!], GH barcode 00037125 [image!], P barcode P00636905 [image!], US barcode 00462159 [image!]).
- = *Nototrichium sandwicense* var. *macrophyllum* Sherff in Bot. Leaf. 1: 2. 1950 – Holotype: U.S.A. Hawaiian Islands, Hawaii: Kau, Hilea, between Hilea & Honuapo, Government Road, alt. 125 ft, *G. Russ* s.n. (BISH barcode BISH1005561 [image!]; isotype: BISH barcode BISH1005562 [image!]).
- = *Nototrichium sandwicense* var. *mauiense* O.Deg. & Sherff ex Sherff in Bot. Leaf. 2: 3. 1950 – Holotype: U.S.A. Hawaiian Islands, Maui: from Papawai Point, toward Puu Anu through Manawainui Gulch, arid region near cliff, *O. Degener & H. Wiebke* 3341 (NY barcode 00341956 [image!]).
- = *Nototrichium sandwicense* var. *olokeleanum* Sherff in Bot. Leaf. 2: 3. 1950 – Holotype: U.S.A. Hawaiian Islands, Kauai: Olokele Canyon, *J. Rock* 5422 (GH barcode 00037126 [image!]; isotypes: BISH barcode BISH 1005536 [image!], US barcode 00102712 [image!]).
- = *Nototrichium sandwicense* var. *pulchellum* Sherff in Bot. Leaf. 2: 3. 1950 – Holotype: U.S.A. Hawaiian Islands,



- Western Molokai, Mahana, Feb 1910, *J. Rock s.n.* (GH barcode 00037127 [image!]; isotypes: BISH barcodes BISH1005565 [image!], BISH1005566 [image!], NY barcode 00341958 [image!]).
- = *Nototrichium sandwicense* var. *subcordatum* O.Deg. & Sherff ex Sherff in Bot. Leaf. 1: 3. 1950 – Holotype: U.S.A. Hawaiian Islands, Hawaii, 17 miles from Kohala toward Waimea, 13 Aug 1926, *O. Degener 9873* (NY barcode 00341959 [image!]).
- = *Nototrichium sandwicense* var. *syringifolium* Sherff in Bot. Leaf. 1: 2. 1950 – Holotype: U.S.A. Hawaiian Islands, *W. Hillebrand s.n.* (K barcode K000814960 [image!]).
- = *Nototrichium viride* var. *oblongifolium* Sherff in Bot. Leaf. 2: 3. 1950 – Holotype: U.S.A. Kaua'i: Waimea, rocky places of mountains, Island Oahu, Hawaiian Islands, Mar 1910, *U. Faurie 1070* (G n.v.; isotype: BISH barcode BISH1005570 [image!]).
- = *Nototrichium viride* var. *subtruncatum* Sherff in Bot. Leaf. 2: 4. 1950 – Holotype: U.S.A. O'ahu: Kawaihapai, Island Oahu, Hawaiian Islands, *G. Russ s.n.* (BISH barcode BISH1005571 [image!]).
- = *Nototrichium sandwicense* var. *pulchelloides* O.Deg. & Sherff ex Sherff in Bot. Leaf. 3: 2. 1951 – Holotype: U.S.A. Hawaiian Islands, West Molokai, near Waiahewa-hewa Gulch, last relic of arid forest, on cliff, 18 Apr 1928, *O. Degener 9869* (NY barcode 00341957 [image!]).
- = *Nototrichium sandwicense* var. *niihauense* H.St.John in Pacific Sci. 13(2): 166. 1959 – Holotype: U.S.A. Hawaii. Ni'ihau: first valley W of Ka'ali Cliff, top of steep basalt talus, 100 ft, 16 Aug 1947, *H. St.John 22830* (BISH barcode BISH1005563 [image!]; isotypes: BISH barcode BISH1005564 [image!], K barcode K000814961 [image!], L 2D-barcode L.3725009 [image!], CANB barcode CBG8100594 [image!], P barcode P00636906 [image!]).
- = *Nototrichium viride* var. *kalaupapae* H.St.John in Phytologia 45: 295. 1980 – Type: U.S.A. Hawaiian Islands, Molokai Island, Kalaupapa, Uau Crater (= Puu Uao), inside crater, 8 Mar 1974, *B. Harrison & W. Gagné s.n.* (BISH barcode BISH1005569 [image!]).
- “*Nototrichium sandwicensis* H.Mann” in Proc. Amer. Acad. Arts 7: 200. Jul 1867, not validly published.
- “*Nototrichium sandwicense* var. *typicum* Sherff” in Bot. Leaf. 1: 2. 1950, not validly published (according to Art. 24.3).
- Note.* – We follow Wagner & al. (1990) for the circumscription of the species.

*Achyranthes schinzii* (Standl.) Cufod. in Bull. Jard. Bot. État Bruxelles 23(3–4): 73. 1953 ≡ *Centrostachys schinzii* Standl. in J. Wash. Acad. Sci. 5(3): 76. 1915 ≡ *Achyranthes lanuginosa* Schinz in Bot. Jahrb. Syst. 21: 186. 1895, nom. illeg., non *Achyranthes lanuginosa* Nutt. in Trans. Amer. Philos. Soc., n.s., 5: 166. 1835 ≡ *Pandiaka lanuginosa* (Schinz) Schinz in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16c: 64. 1934, nom. illeg. –

**Lectotype (designated here):** UGANDA. Unjoro, Seengebiet, *F. Stuhlmann 335* (JE barcode JE00013105 [image!]).

*Notes.* – So far, the name *Pandiaka lanuginosa* Schinz has been widely used for this taxon, as in *Flora of Tropical East Africa* (Townsend, 1985) or the African Plant Database (2007–). The fact that the name *Achyranthes lanuginosa* Schinz is a later homonym for a name already used for an American taxon with the accepted name *Tidestromia lanuginosa* (Nutt.) Standl., and thus illegitimate (Art. 53.1), was recognized by Standley (1915), who consequently published *Centrostachys schinzii* Standl. as a new name for *Achyranthes lanuginosa* Schinz when assigning the respective species to the genera *Achyranthes* and *Centrostachys* in his circumscription. But Standley did not further deal with African taxa, and likewise, Townsend (1985) did apparently not consider the literature on the American Amaranthaceae when working on African species although *Tidestromia lanuginosa* is widespread in the southern U.S.A. and northern Mexico. This may explain why Townsend (1985) noted “The name *Achyranthes lanuginosa* ‘Nutt. (1820)’ stated by Standley to antedate *A. lanuginosa* Schinz, does not appear in the Index Kewensis and I have not been able to trace any description or any work published by Nuttall in 1820 in which it might have appeared. Standley merely quotes the date” and did not further check for the existence of a validly published name by Nuttall. There is a second publication from Standley (1917) in which he gives a full citation as “*Achyranthes lanuginosa* Nutt. Trans. Am. Phil. Soc. II. 5: 166. 1820” but again he cited a wrong date for the publication by Nuttall, as the respective volume was effectively published in 1835 (“1837” is printed on cover). *Pandiaka lanuginosa* is an illegitimate (nomenclaturally superfluous) replacement name for *A. lanuginosa* Schinz, based on the same types as *Centrostachys schinzii* Standl. Schinz (1934) put a small paragraph at the end of his treatment of *Pandiaka* listing several taxa that would probably belong there including “*P. lanuginosa* Schinz (*Achyranthes lanuginosa* Schinz non Nutt.), *Centrostachys schinzii* Standley), in Ostafrika [...]” but commented that they need further checking. Thus, it is evident that Schinz noted the existence of homonyms, but apparently he did not follow the details in the work by Standley. Cufodontis (1953) then correctly inferred that *Centrostachys schinzii* Standl. is the earliest validly published name for this taxon and used it as the basionym for the transfer to the genus *Achyranthes*.

The lectotypification is necessary as the protologue only mentions syntypes from Ostafrika, sine loco (*Fischer 557*) and from Uganda (*Stuhlmann 335*). The only specimen that could be located is from *Stuhlmann 335* at JE, where it came as a duplicate from B.

*Achyranthes viriditepala* Di Vincenzo, Berendsohn, M. Wondafrash & Borsch, **nom. nov.** ≡ *Achyropsis gracilis* C.C. Towns. in Kew Bull. 34(3): 432. 1980, non *Achyranthes gracilis* (M.Martens & Galeotti) Standl. ≡ *Gomphrena gracilis* M.Martens & Galeotti in Bull. Acad. Roy. Sci.

Bruxelles 10: 349. 1843 – Holotype: TANZANIA. Mile 10, Haudeni road, Dist. Khogue, alt. 155 m, 12 Jun 1969, *Faulkner 4235* (K barcode K000243771 [image!]; isotypes: BR barcode 000008819208 [image!], EA barcode EA000002197 [image!]).

*Etymology.* – Compared to other species of former *Achyropsis* and also *Achyranthes* the tepals are glabrous and shiny, appearing in a clear pale green.

**Cyathula** Blume, Bijdr. Fl. Ned. Ind.: 548. 1826, nom. cons. – Type: *Cyathula prostrata* (L.) Blume ( $\equiv$  *Achyranthes prostrata* L.).

= *Achyranthes* sect. *Pandiaka* Moq. in Candolle, Prodr. 13(2): 310. 1849  $\equiv$  *Pandiaka* (Moq.) Hook.f. in Bentham & Hooker, Gen. Pl. 3(1): 35. 1880 – Type: *Pandiaka involu-crata* (Moq.) B.D.Jacks., **syn. nov.**

= *Sericocomopsis* Schinz in Bot. Jahrb. Syst. 21: 184. 1895 – Type (designated by Greuter & al. in Regnum Veg. 129 [NCU-3. Names in Current Use for Extant Plant Genera]: 1095. 1993): *Sericocomopsis hildebrandtii* Schinz, **syn. nov.**

= *Argyrostachys* Lopr. in Bot. Jahrb. Syst. 30(1): 108. 1901 – Type: *Argyrostachys splendens* Lopr.

= *Nelsia* Schinz in Vierteljahrsschr. Naturf. Ges. Zürich 56: 247. 1911 – Type: *Nelsia quadrangula* (Engl.) Schinz, **syn. nov.**

– “*Polyscalis* Wall.”, Numer. List: No. 6939. 1832, not validly published.

*Emended genus description.* – Annual or perennial herbs, subshrubs or shrubs. Leaves always entire and opposite; sessile to distinctly petiolate and variable in shape (ranging from linear or narrowly lanceolate to oblanceolate or obovate) and size within the genus and also within single species or individuals. Indumentum of stem and leaves constituted of simple hairs (hairs never stellate). Paracladia solitary on main axes as well as on lateral branches and spiciform with cymes or solitary flowers clearly separated during anthesis (e.g., in *Cyathula polycephala*, *C. prostrata*), globose or elongate to cylindric with cymes densely aggregated (e.g., in *C. cylindrica*, *C. involu-crata*) or strongly condensed with cymes closely aggregated and paracladia agglomerated, thus synflorescences appear as a single subglobose to irregularly and thickly cylindrical paracladium (e.g., in *C. uncinulata*, *C. natalensis*). Cymes either reduced to single flowers (e.g., in *C. involu-crata*) or with more than one order of branches (e.g., in *C. hildebrandtii*, *C. uncinulata*); sterile flowers normally modified to hooks or rarely with dominating plumose-pilose spine-like bracteoles (only present in *C. quadrangula*) and sometimes missing (e.g., in *C. angustifolia*). Bracts persistent with a mucronate/shortly excurrent midrib (except in a few species where the midrib is long excurrent or not excurrent). Bracteoles not persistent and normally falling with the perianth and fruit. Bracteoles lanceolate to broadly ovate with acuminate tip; midrib of bracteoles distinctly excurrent to uncinately hooked (and mucronate in *C. involu-crata*). Perianth segments 5; tepals feebly to

strongly 1–5(–7)-nerved and either all equal or the 3 inner tepals differ from the 2 outer tepals and are then smaller and sometimes differently shaped; tepal shape is variable among species ranging from (narrow) lanceolate with an acute or acuminate tip in most species to elliptic-oblong with a blunt tip in *C. natalensis*; the midrib of the outer tepals is mucronate to distinctly excurrent in the majority of species, uncinately hooked in *C. polycephala*, *C. tomentosa* and *C. uncinulata*, whereas it is not excurrent in *C. angustifolia* and *C. involu-crata*. Stamens 5; anthers bilocular; filaments filiform or slender, sometimes flattened; androecial tube appendages always present between the filaments and normally quadrate or oblong to cuneate and dentate to fimbriate. Style slender or filiform; stigma always capitate. Ovary uniovulate and always glabrous.

**Cyathula angolensis** (Bamps) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, **comb. nov.**  $\equiv$  *Nelsia angolensis* Bamps in Garcia de Orta, Sér. Bot. 2: 71. 1975 – Holotype: ANGOLA. Huíla: Tundavala, au NW de Sá da Bandeira, rocaïles en prairie submontagnarde, alt. 2230 m, 13°22' N, 14°49'59.999"E, 19 Mar, *P. Bamps, Raimundo & Matos 4058* (BR barcode 000008819741 [image!]).

= *Nelsia tropidogyna* C.C.Towns in Kew Bull. 34(2): 235. 1979 – Holotype: ANGOLA. Huíla: Lubango, nos plainos do alto de Tundavala, 12 May 1964, *O. Azancot de Meneses 1109* (K barcode K000975943 [image!]; isotype: PRE barcode PRE0567712-0 [image!]), **syn. nov.**

*Note.* – Townsend placed a handwritten note dated 20.2.1980 on the type specimen of *N. tropidogyna* that this is not a distinct species but should be synonymized with *C. angolensis* but this was never published to our knowledge. Both types come from the same habitat in Angola. To the contrary, the African Plant Database accepts *N. tropidogyna* following Figueiredo & Smith (2008).

**Cyathula carsonii** (Baker) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch var. **carsonii**, **comb. nov.**  $\equiv$  *Achyranthes carsonii* Baker in Bull. Misc. Inform. Kew 1897: 280. 1897  $\equiv$  *Pandiaka carsonii* (Baker) C.B.Clarke in Thiselton-Dyer, Fl. Trop. Afr. [Oliver] 6(1): 70. 1909  $\equiv$  *Centrostachys carsonii* (Baker) Standl. in J. Wash. Acad. Sci. 5(3): 76. 1915 – **Lectotype (designated here):** ZAMBIA. Fwambo: Lake Tanganyika, alt. 5000–6000 ft., 1893, *Carson 8* (K barcode K000243752 [image!]).

= *Argyrostachys splendens* Lopr. in Bot. Jahrb. Syst. 30(1): 109. 1901 – **Lectotype (designated here):** TANZANIA. Unyika beim Dorfe Luembu, auf feuchten Wiesen, alt. 1600 m, Oct 1899, *W. Goetze 1391* (BR barcode 0000008819727 [image!]; isolectotype: E barcode E00193546 [image!]).

= *Achyranthes lanata* Schinz in Vierteljahrsschr. Naturf. Ges. Zürich 76: 141. 1931, nom. illeg.  $\equiv$  *Pandiaka lanata* Hauman in Bull. Jard. Bot. État Bruxelles 18: 113. 1946 – Holotype: CONGO (D.R.C.). Katanga: Sep 1899, *Verdick 204* (BR barcode 000008820075 [image!]).

= *Pandiaka obovata* Suess. in Bull. Jard. Bot. État Bruxelles 15: 67. 1938 – **Lectotype (designated here)**: CONGO (D.R.C.). Distrikt des oberen Katanga: Katuba, Nov 1934, *Quarré 4316* (BR barcode 0000008820020 [image!]; isoelectotypes BR barcode 0000008820037 [image!], M barcode M-0107307 [image!]).

= *Pandiaka schweinfurthii* var. *glabra* Schinz ex Suess. in Bull. Jard. Bot. État Bruxelles 15: 68. 1938 ≡ *Pandiaka glabra* (Suess.) Hauman in Bull. Jard. Bot. État Bruxelles 18: 113. 1946 – Holotype: CONGO (D.R.C.). Distrikt des oberen Katanga: Elisabethville, *Quarré 691* (BR barcode 0000008819963 [image!]), **syn. nov.**

*Note.* – There are two different gatherings by Carson mounted side by side on the same sheet in K. They were consequently given two different specimen IDs. For clarity, we assign lectotype status to the one mentioned in the protologue. For *Achyranthes splendens*, Lopriore just cites the gathering *W. Goetze 1391* obtained during the Nyassa-See and Kinga-Gebirgs-Expedition. This expedition was supported by the Wentzel-Heckmann Foundation, and for these historic circumstances it is very likely that a specimen was also in B but was later destroyed. Duplicates were distributed to BR and E but could still have been at the disposal of Lopriore when he worked on the description, shortly after the expedition. The BR specimen has an original label and is selected as lectotype, whereas the E specimen has a handwritten label that apparently was produced separately.

*Cyathula carsonii* var. *milnei* (Suess. & Overkott) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, **comb. nov.** ≡ *Pandiaka milnei* Suess. & Overkott in Bot. Arch. 41: 76. 1940 ≡ *Pandiaka carsonii* var. *milnei* (Suess. & Overkott) Cavaco in Mém. Mus. Natl. Hist. Nat., B, Bot. 13(1): 139. 1962 – **Lectotype (designated here)**: ZAMBIA. Mwinilunga: Kalenda-Plain auf Laterit; *E. Milne-Redhead 2835* (M barcode M-0107309 [image!]; isoelectotypes BR barcode 0000008820044 [image!], K barcode K000243753 [image!]).

– “*Pandiaka carsonii* var. *linearifolia* Hauman” in Boutique, Fl. Congo Belge Ruanda-Urundi, Spermatoph. 2: 49. 1951, not validly published.

*Note.* – The assignment of *Pandiaka milnei* as a variety to *P. carsonii* goes back to Cavaco (1962). In the absence of any phylogenetic data to evaluate this, we keep this classification. The different leaf widths of the respective type specimens may just be extremes of a gradual variation, but more collections would be needed to judge. Since the M specimen of *E. Milne Redhead 2835* has “n.sp.” in the handwriting of Carl Suessenguth and also pencil illustrations that probably served preparing the description, it is selected as lectotype. The name “*P. carsonii* var. *linearifolia* Hauman” is not validly published because a latin description or diagnosis (Art. 36.1) is missing. That was also not delivered by Townsend (1988), who accepted this variety and synonymized *P. carsonii* var. *milnei* ignoring the invalid status of “*P. carsonii* var. *linearifolia*”. We do cite the “type specimens” of this designation in order to complement the

treatment: CONGO (DRC). Haut-Katanga: mines de Luiswishi, *Quarré 5213* (P barcode P00466161 [image!]; “isotypes”: BR barcodes 0000008819932 [image!], 0000008819949 [image!], K barcode K000243739 [image!]).

*Cyathula confusa* (C.C.Towns.) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, **comb. nov.** ≡ *Pandiaka confusa* C.C.Towns in Kew Bull. 34(3): 427. 1980 – Holotype: ZAMBIA. Mwinilunga District: Just S of Matonchi Farm, 18 Oct 1937, *Milne-Redhead 2841* (K barcode K000243762 [image!]).

= *Pandiaka schweinfurthii* var. *compacta* Suess. & Overkott in Bot. Arch. 41: 78. 1940 – Type: ZAMBIA. Regio Mwinilunga, prope “Matonchi-Farm”, inter *Brachystegias*, *Milne-Redhead 2841b* (K barcode K000243760 [image!]; isotypes: BR barcode 0000008819956 [image!], M barcode M-0107302 [image!]).

= *Pandiaka schweinfurthii* var. *minor* Suess. & Overkott in Bot. Arch. 41: 79. 1940 – Holotype: ZAMBIA. Mwinilunga region: Half a mile N of Mwinilunga, 23 Nov 1937, *Milne-Redhead 3358* (K barcode K000243761 [image!]; isotypes: BR barcode 0000008819970 [image!], M barcode M-0107301 [image!]).

= *Pandiaka schweinfurthii* var. *parvifolia* Suess. & Overkott in Bot. Arch. 41: 78. 1940 – Holotype: ZAMBIA. Mwinilunga District: Just S of Matonchi Farm, 18 Oct 1937, *Milne-Redhead 2841a* (K barcode K000243759 [image!]; isotype: M barcode M-0107303 [image!]).

*Cyathula elegantissima* (Schinz) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, **comb. nov.** ≡ *Achyranthes elegantissima* Schinz in Bot. Jahrb. Syst. 21: 186. 1895 ≡ *Pandiaka cylindrica* Hook.f. ex Baker & C.B. Clarke in Thiselton-Dyer, Fl. Trop. Afr. [Oliver] 6(1): 68. 1909, nom. superfl. ≡ *Centrostachys elegantissima* (Schinz) Standl. in J. Wash. Acad. Sci. 5(3): 76. 1915 ≡ *Pandiaka elegantissima* (Schinz) Dandy, Fl. Pl. Sudan 1: 119. 1950 – **Lectotype (designated here)**: CONGO (D.R.C.). Djur: Majob, 26 Apr 1869, *G. Schweinfurth 1542* (S No. 07-12227 [image!]; isoelectotype: K barcode K000243742 [image!]).

= *Achyranthes oblanceolata* Schinz in Bot. Jahrb. Syst. 21: 187. 1895 ≡ *Pandiaka oblanceolata* (Schinz) C.B. Clarke in Thiselton-Dyer, Fl. Trop. Afr. [Oliver] 6(1): 70. 1909 ≡ *Centrostachys oblanceolata* (Schinz) Standl. in J. Wash. Acad. Sci. 5(3): 76. 1915 – Type: SUDAN. Addai, 28 Jul 1869, *G. Schweinfurth 2185* (K barcode K000243741 [image!]).

– “*Cyathula cylindrica* Hook.f.” in Bentham & Hooker, Gen. Pl. 3(1): 36. 1880, nom. nud.

– “*Pandiaka cylindrica* Schweinf. ex Hook.f.” in Bentham & Hooker, Gen. Pl. 3(1): 36. 1880, nom. nud.

– “*Pandiaka cylindrica* Hook.f. ex B.D.Jacks.”, Index Kew. 2: 409: 1894, nom. nud.

*Note.* – Hooker fil. annotated the K specimen of Schweinfurth’s gathering *1542* with “*Pandiaka cylindrica* Hook. fil.”



ignoring that on the same gathering, probably using a duplicate, Schinz had already described *Achyranthes elegantissima*. When Baker & C.B. Clarke published Hooker fil.'s name in 1909 they further ignored that an earlier homonym already existed, based on *Cyathula cylindrica* Moq., which is a different accepted species. For *Achyranthes elegantissima*, there was probably a specimen at B that Schinz used, and a duplicate with a label from the B herbarium is at S, now chosen as lectotype.

- Cyathula heudelotii*** (Moq.) Di Vincenzo, Berendsohn, M. Wondafrash & Borsch, **comb. nov.** ≡ *Achyranthes heudelotii* Moq. in Candolle, Prodr. 13(2): 310. 1849 ≡ *Pandiaka heudelotii* (Moq.) Benth. & Hook.f. ex B.D. Jacks., Index Kew. 2: 409. 1894 ≡ *Centrostachys heudelotii* (Moq.) Standl. in J. Wash. Acad. Sci. 5(3): 76. 1915 – **Lectotype (designated here):** SENEGAL. *Heudelot 280* (P barcode P00466159 [image!]; isolectotypes: P barcodes P00466160 [image!], P00487011[image!]).
- = *Gomphrena angustifolia* Vahl, Symb. Bot. 3: 45. 1794 ≡ *Achyranthes angustifolia* (Vahl) Lopr. in Malpighia 14: 434. 1901, nom. illeg. ≡ *Pandiaka angustifolia* (Vahl) Hepper in Kew Bull. 25(2): 189. 1971 – **Lectotype (designated here):** probably West Africa, “König s.n.” (C barcode C10005385 [image!]).
- = *Achyranthes angustifolia* Benth. in Hooker, Niger Fl.: 492. 1849 ≡ *Achyranthes benthamii* Lopr. in Bot. Jahrb. Syst. 30(1): 108. 1902, nom. illeg. ≡ *Centrostachys angustifolia* (Benth.) Standl. in J. Wash. Acad. Sci. 5(3): 75. 1915 ≡ *Pandiaka benthamii* Schinz in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16c: 64. 1934, nom. illeg. – Type: NIGERIA. On the Quorra, *Vogel 98* (K barcode K000243734 [image!]).
- = *Pandiaka heudelotii* [var. *subglobosa* Suess.] f. *rubella* Suess. in Bull. Jard. Bot. État Bruxelles 15: 66. 1938 – Holotype: NIGERIA. *Lely 641* (K n.v.) **syn. nov.**
- = *Pandiaka heudelotii* var. *spicata* Suess. in Bull. Jard. Bot. État Bruxelles 15: 65. 1938 – **Lectotype (designated here):** TOGO. Prope Lome, *Warnecke 182* (BR barcode 0000008819734 [image!]).
- = *Pandiaka heudelotii* var. *subglobosa* Suess. in Bull. Jard. Bot. État Bruxelles 15: 66. 1938 – **Lectotype (designated here):** CONGO (D.R.C.). Distrikt de Kasai: Luluabourg, *Vanderyst 20933* (BR barcode BR0000013734022 [image!]).

*Note.* – The protologue of *Gomphrena angustifolia* Vahl explicitly cites the *König* specimen from “Habitat in India Orientali”. Morphologically the specimen belongs to an African taxon which was independently described two times again later using different types from Nigeria (*Vogel 98*) as *Achyranthes angustifolia* Benth. and from Senegal (*Heudelot 280*) as *Achyranthes heudelotii* Moq. Apparently, Vahl (1794) believed the provenance of this specimen to be India, although there are arguments that it could have been confused historically as this taxon only occurs in Africa. In fact the specimen could be material collected by Isert in Guinea (Friis

& Callmänder, 2021). Such a confusion was also suspected by Hepper (1971) when he investigated the taxon and made a combination under *Pandiaka*. Technically, the C specimen with barcode C10005385 is a syntype because it is explicitly cited in the protologue (Art. 9.6). Also the name “*Gomphrena angustifolia*” on the specimen is in the handwriting of Vahl, plus it has the note “HB. VAHLII” indicating that it is from Vahl’s private herbarium (Ib Friis, pers. comm). So it is very likely that Vahl had examined this particular specimen. According to Art. 9.12 this specimen takes precedence over uncited original material in selecting a lectotype, even if the provenance information was wrong. If we assume that specimen was confused, there will also not be a problem for the correct application of the name.

Based on new phylogenetic evidence presented in this investigation, the respective species belongs to the genus *Cyathula*, but the name *C. angustifolia* was already used by Moquin-Tandon (1849) for a member of Achyranthoids subclade I that belongs to the genus *Kyphocarpa* (≡ *K. angustifolia* (Moq.) Lopr.). The next-earliest legitimate name for the taxon at the same rank is therefore *Achyranthes heudelotii* Moq. which has to be used as a basionym (Art. 11.4) for the combination under *Cyathula*. Moreover, Lopriore (1902) made a new combination for *Gomphrena angustifolia* Vahl under *Achyranthes*, ignoring that Bentham (1849) unfortunately had published the name *Achyranthes angustifolia* based on a different type specimen from Nigeria (*Vogel 98*), and thus Lopriore created an illegitimate name and renamed Bentham’s taxon as *Achyranthes benthamii* Lopr., creating a further superfluous name.

The infraspecific taxa proposed by Suessenguth (1938) were based on several syntypes, rendering lectotypifications necessary.

- Cyathula hildebrandtii*** (Schinz) Di Vincenzo, Berendsohn, M. Wondafrash & Borsch, **comb. nov.** ≡ *Sericocomopsis hildebrandtii* Schinz in Bot. Jahrb. Syst. 21: 184. 1895 ≡ *Cyphocarpa hildebrandtii* (Schinz) C.B. Clarke in Thiselton-Dyer, Fl. Trop. Afr. [Oliver] 6(1): 54. 1909 – **Lectotype (designated here):** KENYA. Teita District: Ndi, Jul 1877, *J. Hildebrandt 2584* (Z+ZT barcode Z-000000325 [image!]; isolectotypes: K barcode K000243587!, M barcode M-0107377!).
- = *Sericocomopsis grisea* Suess. in Kew Bull. 4(4): 479. 1949 – Holotype: TANZANIA. Kiruru: Upare, Moshi, alt. 780 m, May 1927, *A. Haarer 499* (K barcode K000243588; isotype: M barcode M-0107376!).
- “*Kyphocarpa hildebrandtii*” is an orthographic variant for *Cyphocarpa hildebrandtii* (Schinz) C.B. Clarke.

***Cyathula involucrata*** (Moq.) Di Vincenzo, Berendsohn, M. Wondafrash & Borsch, **comb. nov.** ≡ *Achyranthes involucrata* Moq. in Candolle, Prodr. 13(2): 310. 1849 ≡ *Pandiaka involucrata* (Moq.) B.D. Jacks., Index Kew. 2: 409. 1894 ≡ *Centrostachys involucrata* (Moq.) Standl. in J. Wash. Acad. Sci. 5(3): 76. 1915 – Holotype:

NIGERIA. Village of Pandiaki, 17 Sep 1841, *Vogel s.n.* (K barcode K000243731 [image!]; isotype: K barcode K000243732 [image!]).

- = *Pandiaka involucrata* var. *megastachya* Suess. in Repert. Spec. Nov. Regni Veg. 44: 46. 1938 – Holotype: NIGERIA. Naraguta, *H.V. Lely 239* (K barcode K000243733 [image!]).
- “*Achyranthes capitata* Moq.” in Candolle, Prodr. 13(2): 310. 1849, pro syn.
- “*Pandiaka involucrata* (Moq.) Hook.f.” in Bentham & Hooker, Gen. Pl. 3(1): 35. 1880, combination not validly published.

*Cyathula meruensis* (Suess.) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, **comb. nov.** ≡ *Sericocomopsis meruensis* Suess. in Mitt. Bot. Staatssamml. München 1(1): 7. 1950 – Holotype: TANZANIA. Meru Crater, T.T., alt. 4700 m, Jan 1941, *G. Babault B 1808* (K barcode K000243589!; isotype: M barcode M-0107375 [image!]).

- “*Cyathula lindaviana* Volkens ex Lopr.” in Bot. Jahrb. Syst. 27: 62. 1900, nom. nud.
- “*Achyranthes lindaviana* Schinz ex Peter” in Repert. Spec. Nov. Regni Veg. Beih. 40(2.3): 230. 1938, nom. nud.
- “*Sericocomopsis lindaviana* Peter” in Repert. Spec. Nov. Regni Veg. Beih. 40(2.3): 229. 1938, not validly published (no Latin description or reference to description; Art. 39.1).

*Notes.* – This taxon is resurrected here from its former treatment as a synonym of *Sericocomopsis hildebrandtii* (Townsend, 1985) and is represented by the clade comprising samples AC0961, AC1130, AC1311, AC1312, AC1313, AC1314, AC1315, AC1319 and AC1320. The earlier designation “*Sericocomopsis lindaviana* Peter” would fit to this entity but is a name not validly published according to Art. 39.1. Volkens annotated the specimen *G. Volkens 2180* (in HBG barcode HBG-502344) in 1894 with “*Cyathula lindaviana* Volkens”, but apparently never published this name. In 1911, Schinz considered it as part of *Achyranthes* also just annotating this name on the same specimen. Peter (1938) also recognized this entity in addition to *Sericocomopsis hildebrandtii* and *S. pallida* and listed a number of specimens from Kenya and Tanzania under the name “*Sericocomopsis Lindaviana* A. Peter” but without providing any description. The taxon was then finally described by Suessenguth (1950).

*Cyathula porphyrgyrea* (Suess. & Overkott) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, **comb. nov.** ≡ *Pandiaka porphyrgyrea* Suess. & Overkott in Bot. Arch. 41: 77. 1940 – **Lectotype (designated here):** ANGOLA. Between R. Ndamba (Mundamba) and R. Nkoki, on shallow soil overlying “laterite”, 8 Jan 1938, *Milne-Redhead 3985* (M barcode M-0107299 [image!]; isolectotypes: BM barcode BM000910333 [image!], BR barcode 0000008819925 [image!], K barcode K000243754 [image!], PRE barcode PRE0388726-0 [image!]).

*Note.* – Suessenguth & Overkott (1940) cite three different gatherings by Milne Redhead from Angola for their newly described species, which are technically syntypes. Therefore, a lectotype had to be selected using one gathering, which is the M specimen of *Milne-Redhead 3985* because it has Suessenguth’s original pencil drawings on floral morphology, and has duplicates in several herbaria.

*Cyathula quadrangula* (Engl.) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, **comb. nov.** ≡ *Sericocoma quadrangula* Engl. in Bot. Jahrb. Syst. 10: 7. 1889 ≡ *Sericocomopsis quadrangula* (Engl.) Lopr. in Bot. Jahrb. Syst. 27(1–2): 42. 1899 ≡ *Cyphocarpa quadrangula* (Engl.) C.B.Clarke in Thiselton-Dyer, Fl. Trop. Afr. [Oliver] 6 (1): 54. 1909 ≡ *Nelsia quadrangula* (Engl.) Schinz in Vierteljahrsschr. Naturf. Ges. Zürich 56: 247. 1911 – Type: NAMIBIA. Hereroland: Usakos, alt. 900 m, May 1886, *H. Marloth 1255* (PRE barcode PRE0381229-0 [image!]).

- = *Sericocoma welwitschii* Baker in Bull. Misc. Inform. Kew 1897: 278. 1897, nom. illeg. – Syntypes: ANGOLA. Province of Mossamedes, *Welwitsch 6501* (K barcode K000243601[image!], BM barcode BM000910354 [image!]).
- “*Sericocoma nelsii* Schinz” in Engler & Prantl, Nat. Pflanzenfam. 3(1a): 107. 1893, not validly published.
- “*Sericocomopsis welwitschii* (Baker) Lopr.” in Bot. Jahrb. Syst. 27(1–2): 42. 1899, combination not validly published.
- “*Cyphocarpa welwitschii* (Baker) C.B.Clarke” in Thiselton-Dyer, Fl. Trop. Afr. [Oliver] 6(1): 53. 1909, combination not validly published.
- “*Kyphocarpa quadrangula* (Engl.) C.B.Clarke” [fide African Plant Database (2007–)] is orthographic variant for *Cyphocarpa quadrangula* (Engl.) C.B.Clarke].

*Note.* – The name *Sericocoma nelsii* Schinz was first mentioned in the discussion of a subdivision of the genus *Sericocoma* (Schinz, 1893) as it differs by a glabrous ovary and also a ringlike structure distally (“[...] oben vertieften Fruchtknoten [...]”) but apparently Schinz never published the species name. Independently, Engler must have found the same entity as different from all other species of *Sericocoma* by the quadrangular inflorescence, when working through the plants collected by Marloth, and validly described it as new species (Engler, 1889) using *Marloth 1255*. Schinz became aware of this because he used Engler’s name when listing plants from “Deutsch-Südwest-Afrika” (Schinz, 1897), also citing *Nels 56* that he apparently had examined originally, along with *Marloth 1255*. However, Schinz then honoured Nels with a new genus name (Schinz, 1911).

*Sericocoma welwitschii* Baker is a later homonym (nom. illeg. according to Art. 53.1) of *Sericocoma welwitschii* Hook.f. [in Bentham & Hooker, Gen. Pl. 3(1): 30. 1880] – Lectotype (designated by Turner in Ann. Bot. Fenn. 53: 288. 2016): ANGOLA. Distr. Mossamedes, in sandy thickets by the river Bero, 1859, *Welwitsch Iter Angolense*

no. 6508 (K barcode K000243580 [image!]; isolectotypes: BM barcode BM000910343 [image!], BR barcode 0000008819871 [image!], P barcode P00482811 [image!]), which actually belongs to the genus *Marcellipsis* and therefore is a member of the achyranthoid subclade I.

*Cyathula ramulosa* (Hiern) Di Vincenzo, Berendsohn, M. Wondafrash & Borsch, **comb. nov.** ≡ *Pandiaka ramulosa* Hiern, Cat. Afr. Pl. 1: 894. 1900 – Lectotype (designated by Cavaco in Mém. Mus. Natl. Hist. Nat., B, Bot. 13: 132. 1962): ANGOLA. Mumpulla, Oct 1859, *Welwitsch 6498* (LISU barcode LISU221234 [image!]; isolectotype: BM barcode BM000910332 [image!]).

= *Pandiaka polystachya* Suess. in Bull. Jard. Bot. État Bruxelles 15: 67. 1938 – Lectotype (first-step, designated by Cavaco in Mém. Mus. Natl. Hist. Nat., B, Bot. 13: 146. 1962): CONGO (D.R.C.). District des Oberen Katanga: Plateau de la Manika, Bianco (environ Katentania), Nov 1911, *Homblé 755*; **Lectotype (second step, designated here)**: (BR barcode 0000008819901 [image!]; isolectotypes: BR000008820228 [image!], M barcode M-0107308 [image!]).

= *Pandiaka incana* Suess. & Overkott in Bot. Arch. 41: 75. 1940 ≡ *Pandiaka polystachya* var. *incana* (Suess. & Overkott) Cavaco in Notul. Syst. (Paris) 16: 98. 1960 – Lectotype (first-step, designated by Cavaco in Notul. Syst. (Paris) 16: 98. 1960): ZAMBIA. Regio Mwinilunga: S.W. Dobeka Bridge, auf Termitenhügeln, 13 Oct 1937, *Milne-Redhead 2738*; **Lectotype (second step, designated here)**: (M barcode M-0107312 [image!]; isolectotypes: BM barcode BM000910334 [image!], BR barcode 0000008819918 [image!], K barcode K000243749 [image!], PRE barcode PRE0388727-0 [image!]).

*Note.* – At species level, *Pandiaka ramulosa* was accepted by Baker & Clarke (1909) as different from other species of the genus *Pandiaka*. In the absence of detailed investigations of species limits, we follow the African Plant Database (2007–). For *P. incana*, the M specimen has the original pencil drawings by Suessenguth of the floral morphology, and thus is the appropriate specimen as lectotype, whereas the K, BR and PRE specimens only have labels in Suessenguth's handwriting. For *P. polystachya*, two syntypes are cited by Suessenguth (1938), of which only the *Homblé* specimen is present, whereas *Overlaet 704* could not be discovered. Suessenguth cited “*Homblé 799*” in his protologue, but this is obviously an error caused by a misinterpretation of handwriting on the label as this collecting number 799 is a completely different species (*Satyrium buchananii*) with a different locality. The specimen examined by Suessenguth in M has a label “Biano, Manika”, corresponding to the place of gathering of *Homblé 755*. Cavaco (1962) noticed this by citing explicitly this specimen as type, and he also accepted *P. polystachya* as species.

*Cyathula richardsiae* (Suess.) Di Vincenzo, Berendsohn, M. Wondafrash & Borsch, **comb. nov.** ≡ *Pandiaka*

*richardsiae* Suess. in Mitt. Bot. Staatssamml. München 1(6): 192. 1953 – Holotype: ZAMBIA. Abercorn District: By old Katwe Road above Inono Valley. Escarpment above Chilongowelo. In sandy soil in open, alt. 5000 ft., *H.M. Richards 65* (K barcode K000243750 [image!]; isotype: M barcode M-0110450 [fragment; image!]).

*Note.* – The species was accepted as different from the other species of *Pandiaka* by Townsend (1988). The isotype in M with an illustration has a label in Suessenguth's handwriting that it is an illustration from the type at K, which he explicitly cited as “*H.M. Richards 65*, Herb. Kew”.

*Cyathula rubrolutea* (Lopr.) Di Vincenzo, Berendsohn, M. Wondafrash & Borsch, **comb. nov.** ≡ *Achyranthes rubrolutea* Lopr. in Bot. Jahrb. Syst. 27(1–2): 57. 1899 ≡ *Pandiaka rubrolutea* (Lopr.) C.C. Towns. in Kew Bull. 34(3): 428. 1980 – Lectotype (designated by Townsend in Kew Bull. 34: 428. 1980): ZAÏRE. M'Puetto, Mar 1896, *Descamps s.n.* (Z+ZT n.v.; isolectotypes: BR barcode 0000008820150 [image!]).

= *Pandiaka andongensis* Hiern, Cat. Afr. Pl. 1: 895. 1900 – Lectotype (designated by Cavaco in Mém. Mus. Natl. Hist. Nat., B, Bot. 13: 144. 1962): ANGOLA. *Welwitsch 6567* (BM barcode BM000910331 [image!]; isolectotypes: K barcode K000243758 [image!], LISU barcode LISU221235 [image!]).

= *Pandiaka aristata* Suess. in Bull. Jard. Bot. État Bruxelles 15: 64. 1938 – Holotype: TANZANIA. Iringa, auf Granit, 1932, *Lynes 1h.215e* (K barcodes K000243745 [image!] & K000243746 [image!]) [mounted on two sheets labelled Sheet I and II]).

= *Pandiaka lindiensis* Suess. & Beyerle in Repert. Spec. Nov. Regni Veg. 44: 46. 1938 – Holotype: TANZANIA. *H. Schlieben 6083* (B barcode B 10 0154189 !; isotypes: BR barcodes 0000008820211 [image!], 0000008820204 [image!], K barcode K000243747 [image!]).

= *Pandiaka andongensis* var. *gracilis* Suess. in Mitt. Bot. Staatssamml. München 1(8): 341. 1953 – Holotype: TANZANIA, *Tanner 767* (K barcodes K000243743 [image!] & K000243744 [image!]) [mounted on two sheets labelled Sheet I and II]).

*Cyathula trichinioides* (Suess.) Di Vincenzo, Berendsohn, M. Wondafrash & Borsch, **comb. nov.** ≡ *Pandiaka trichinioides* Suess. in Bull. Jard. Bot. État Bruxelles 15: 68. 1938 – Holotype: CONGO (D.R.C.), Distrikt des Uele circa Bambesa, 1936, *Pittery 136* (BR barcode 0000008820167 [image!]; isotypes: BR barcode 0000008820174 [image!], M barcode M-0107304 [image!]).

*Cyathula welwitschii* (Schinz) Di Vincenzo, Berendsohn, M. Wondafrash & Borsch, **comb. nov.** ≡ *Achyranthes welwitschii* Schinz in Bot. Jahrb. Syst. 21: 187. 1895 ≡ *Pandiaka welwitschii* (Schinz) Hiern., Cat. Afr. Pl. 1: 894. 1900 ≡ *Centrostachys welwitschii* (Schinz) Standl. in J. Wash. Acad. Sci. 5(3): 76. 1915 – Lectotype (designated



- by Cavaco in Mem. Mus. Natl. Hist. Nat., B, Bot. 13: 141. 1962): ANGOLA. *Welwitsch 6488* (LISU barcode LISU221232 [image!]; isolectotypes: BM barcode BM000910330 [image!], C barcode C10000111!, K barcode K000243756 [image!], Z+ZT barcode Z-000056078 [image!]).
- = *Achyranthes schweinfurthii* Schinz in Bull. Herb. Boissier 4: 421. 1896 ≡ *Pandiaka schweinfurthii* (Schinz) C.B. Clarke in Thiselton-Dyer, Fl. Trop. Afr. [Oliver] 6(1): 69. 1909 ≡ *Centrostachys schweinfurthii* (Schinz) Standl. in J. Wash. Acad. Sci. 5(3): 76. 1915 – Type: SUDAN. Dem Gudju, Dar Fertit, 26 Jun 1871, *G. Schweinfurth ser. 3, 66* (Z+ZT barcode Z-000056075 [image!]), **syn. nov.**
- = *Psilotrichum debile* Baker in Bull. Misc. Inform. Kew 128–129: 279. 1897 ≡ *Pandiaka debilis* (Baker) Hiern, Cat. Afr. Pl. 1: 894. 1900 ≡ *Pandiaka welwitschii* var. *debilis* (Baker) Suess. in Repert. Spec. Nov. Regni Veg. 44: 47. 1938 – Lectotype (designated by Cavaco in Mém. Mus. Natl. Hist. Nat., B, Bot. 13: 141. 1962): ANGOLA. *Welwitsch 6570* (LISU [fide Cavaco in Mém. Mus. Natl. Hist. Nat., B, Bot. 13: 141. 1962]; isolectotypes: BM barcode BM000910335 [image!], BR barcode 0000008820105 [image!], K barcode K000243757 [image!], MEL barcode MEL 2460640 [image!]).
- = *Pandiaka kassneri* Suess. in Bull. Jard. Bot. État Bruxelles 15: 66. 1938 – **Lectotype (designated here)**: CONGO (D.R.C.), Shaba, Kasanga, 23 Mar 1908, *Kässner 2665* (B barcode B 10 0154188 [image!]; isolectotypes: BR barcode 0000008820082 [image!], K barcode K000243740 [image!], M barcode M-0107315 [just fragments of inflorescence; image!], P barcode P00466162 [image!], Z+ZT barcode Z-000056076 n.v.).
- “*Achyranthes welwitschii* Schinz” in Engler, Pflanzenw. Ost-Afrikas 2C: 174. 1895, isonym.
- “*Achyranthes kassneri* Schinz ex Peter” in Repert. Spec. Nov. Regni Veg. Beih. 40(2): 240. 1938, nom. nud.
- “*Pandiaka welwitschii* var. *debilis* (Baker) Cavaco” in Mém. Mus. Natl. Hist. Nat., B, Bot. 13(1): 141. 1962, isonym.
- Note.* – Townsend (1988) did not accept *Pandiaka kassneri* Suess. in contrast to Cavaco (1962) and Hauman (1951). We provisionally follow this but further research is needed. Peter (1938) listed “*Pandiaka kassneri* Schinz” referring to a specimen in B (barcode B 10 0154188 [image!]) that was identified by Schinz in 1911, who apparently never published this name. Suessenguth (1938) then described the species under *Pandiaka* using Schinz’s epitheton as evident by a handwritten label of Suessenguth on the B specimen “= *Achyranthes kassneri* Schinz in sched.”

***Evelynastra*** Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, **gen. nov.** – Type: *Evelynastra pallida* (S.Moore) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch (≡ *Sericocoma pallida* S.Moore).

*Description.* – Perennial shrubs or subshrubs; leaves distinctly petiolate and within single individuals varying from

elliptic to obovate, spatulate or oblanceolate; indumentum of stem and leaves constituted of branched hairs: stellate hairs on leaf surfaces and condensed-dendroid hairs on inflorescence axes, upper branches and sometimes leaf veins stellate; paracladia globose or elongate to cylindrical with cymes densely aggregated; paracladia solitary on main axes as well as on lateral branches; cymes with more than one order of branches, and sometimes with very few sterile flowers on uppermost branches in relation to many fertile flowers per cyme; sterile flowers always unmodified (not modified to hooks or spines as common in other achyranthoid genera); androecial tube appendages quadrate to oblong, furnished with fimbriate dorsal scales and the apex denticulate or fringed; tepals: 2 outer lanceolate with an acuminate tip, up to 3 veins, and the midrib mucronate to shortly excurrent, 3 inner smaller but similar in shape; texture of tepals remaining herbaceous or scarious at maturity; bracteoles ovate with an acuminate tip, the midrib mucronate to shortly excurrent; bracts ovate with an acuminate tip, the midrib not excurrent; ovary glabrous.

*Etymology.* – The genus name *Evelynastra* is dedicated to my beloved daughter Evelyn Alicia Di Vincenzo. The ending *-astra* points to the main characteristic of the genus – the stellate hairs of the indumentum of stem and leaves – which is an almost unique character within Achyranthoids.

***Evelynastra pallida*** (S.Moore) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, **comb. nov.** ≡ *Sericocoma pallida* S.Moore in J. Bot. 15: 70. 1877 ≡ *Sericocomopsis pallida* (S.Moore) Schinz in Bot. Jahrb. Syst. 21: 185. 1895 ≡ *Cyphocarpa pallida* (S.Moore) C.B. Clarke in Thiselton-Dyer, Fl. Trop. Afr. [Oliver] 6(1): 54. 1909 – Holotype: SOMALIA. Meid, Ahl Mountains, alt. 1200 m, Apr 1875, *J. Hildebrandt 1521* (K barcodes K000243585!, K000243584!, both on one sheet).

= *Sericocomopsis pallida* var. *parvifolia* Suess. in Kew Bull. 4 (4): 480. 1949 – Holotype: SOMALIA. Wanad, Protection Plot, Burao, 6 Oct 1944, *P. Glover & H. Gilliland 70* (K barcode K000243586 [image!]; isotype: EA barcode EA000002257 [image!]).

= *Sericocomopsis pallida* var. *grandis* Suess. in Mitt. Bot. Staatssaml. München 1(8): 343. 1953 – Holotype: KENYA. Northern Province, Moyale, alt. 780–1200 m, 22 Jul 1952, *J. Gillett 13614* (M barcode M-0107374 [image!]; isotypes: BR barcode 0000008820921 [image!], EA barcode EA000002256 [image!], PRE barcode PRE0824140-0 [image!], S No. 07-12210 [image!]).

***Sebsebea*** Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, **gen. nov.** – Type: *Sebsebea orthacantha* (Hochst. ex Asch.) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch (≡ *Pupalia orthacantha* Hochst. ex Asch.).

*Description.* – Annual herbs; leaves distinctly to long petiolate and within single individuals varying from ovate to elliptic or lanceolate; indumentum of stem and leaves constituted of uniseriate hairs; paracladia globose or elongate

to cylindrical with cymes densely aggregated; paracladia solitary on main axes as well as on lateral branches; cymes with more than one order of branches, in which fertile and sterile flowers are arranged together; sterile flowers and their bracteoles modified to spines serving dispersal by animals; in fruit the axis and branches of the lateral cymes become indurate and inseparably connate, so that each cyme falls as a complete burr; androecial tube appendages broadly cuneate-obovate with a dentate to fimbriate apex and a furcate dorsal scale; tepals all similar, lanceolate with an acute tip, up to 3–5 veins, and the midrib mucronate to shortly excurrent; tepals becoming slightly indurate at their base at maturity; bracteoles broadly ovate with an acuminate tip, the midrib distinctly to long excurrent; bracts lanceolate with an acuminate tip, the midrib mucronate to shortly excurrent; ovary glabrous.

*Etymology.* – In honour of the Ethiopian botanist Sebsebe Demissew, for his outstanding knowledge on the Ethiopian flora and his life-long work towards its conservation.

*Sebsebea orthacantha* (Hochst. ex Asch.) Di Vincenzo, Berendsohn, M. Wondafrash & Borsch, **comb. nov.** ≡ *Pupalia orthacantha* Hochst. ex Asch. in Schweinfurth, Beitr. Fl. Aethiop.: 181. 1867 ≡ *Cyathula orthacantha* (Hochst. ex Asch.) Schinz in Engler & Prantl, Nat. Pflanzenfam. 3(1a): 108. 1893 ≡ *Cyphocarpa orthacantha* (Hochst. ex Asch.) C.B. Clarke in Thiselton-Dyer, Fl. Trop. Afr. [Oliver] 6(1): 55. 1909 ≡ *Sericocomopsis orthacantha* (Hochst. ex Asch.) Peter in Repert. Spec. Nov. Regni Veg. Beih. 40(2.3): 230. 1938 – **Lectotype (designated here):** ETHIOPIA. Goelleb and Dschadsche, alt. 4000 – 6000 m, Aug–Sep 1854, *G. Schimper 2153* (JE barcode JE00026022 [image!]; isolectotypes: GOET barcode GOET005657 [image!], K barcode K000243624 [image!], S No. 07-12231!; isolectotypes: BR barcode 0000008357076!, P barcode P00482810!, S No. 07-12231!).

= *Cyathula kilimandscharica* Suess. & Beyerle in Repert. Spec. Nov. Regni Veg. 44: 44. 1938 – **Lectotype (designated here):** TANZANIA. Deutsch-Ost-Afrika, Kilimandscharo, Kil. N. Soitokilok, Buschsteppe, alt. ca. 1700 m, 23 Apr 1934, *H. Schlieben 5122* (M barcode M-0107349 [image!]).

= *Pupalia erecta* Suess. in Repert. Spec. Nov. Regni Veg. 44: 47. 1938 – Holotype: TANZANIA. Bezirk Iringa, Ruahatal zw. Dodoma und Iringa, Akaziensteppe, alt. 700 m, 7 Mar 1934, *C. Troll 5212* (B barcode B 10 0154186!).

= *Cyathula orthacanthoides* Suess. in Mitt. Bot. Staatssamml. München 1(1): 4. 1950 – Type: TANZANIA. Mpwapwa, 28 Mar 1945, *I.H. von Rensburg 28* (K n.v. [fide Suesenguth in Mitt. Bot. Staatssamml. München 1(1): 4. 1950]).

– “*Pupalia orthacantha* Hochst. ex Hohen.” in Bot. Zeitung (Berlin) 14: 597. 1856, nom. nud.

– “*Kyphocarpa orthacantha* (Hochst. ex Asch.) Schinz” (orthographic variant for *Cyphocarpa orthacantha* (Hochst. ex Asch.) C.B. Clarke).

*Note.* – Ascherson (1867), who treated the Amaranthaceae in Schweinfurth’s *Beitrag zur Flora Aethiopiens* mentions that Hochstetter just published the name, whereas he provided a detailed description. However, he just cited *Schimper* as a collector. Apart from the rich material of *G. Schimper 2153* there is another gathering *G. Schimper 2154* also from Ethiopia, Goelleb and Dschadsche, alt. 3000–6000 m, 24 Aug 1854 (S Nos. 07-12491 [image!], 07-12491 [image!]), rendering lectotypification necessary. Interestingly, Ascherson already discussed the morphological distinctness of this entity.

The protologue of *Cyathula kilimandscharica* cites the specimen *Schlieben 5122* for B, where it could not be located. The M specimen, which also has an annotation in Suessenguth’s handwriting is therefore designated as lectotype.

## ■ AUTHOR CONTRIBUTIONS

MW and VDV carried out field work and identified collections. TB and VDV generated the character list, analysed herbarium specimens with help from MW. VDV generated the molecular datasets and the character matrix and carried out analyses. VDV and WB compiled a first version of the checklist in the EDIT platform, which was then revised by all authors. VDV elaborated a draft for the revised circumscription of taxa, with further contributions by all authors. VDV wrote a first draft of the paper, which was finalized with contributions from all authors. The whole study was supervised by TB and was carried out in partial fulfilment of a doctoral thesis by VDV.

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## Appendix 1. List of analysed taxa.

Accepted taxon name and author, lab code (isolate), DNA bank number, locality, collector and collector number, herbarium and NCBI accession numbers for *trnK/matK*, *rpl16* intron, *rpl32-trnL* IGS, *rps4-trnT* IGS, *trnT-trnL* IGS, *trnL-F*, ITS, respectively. Taxa are listed in alphabetic order. Published sequences are from: <sup>1</sup>Di Vincenzo & al. (2018), <sup>2</sup>Sanchez-del Pino & al. (2009), <sup>3</sup>Müller & Borsch (2005a), <sup>4</sup>unpublished GenBank record, <sup>5</sup>Zúñiga & al. (2017). All others are newly sequenced in this study, “–” denotes missing sequences.

*Achyranthes aquatica* R.Br., AC1064, DB 36542, Nigeria, *K. Balkwill & M.-J. Balkwill 4356* (B), LT992591, LT992952, PQ042464, PQ053365, PQ053435, –, LT992991. *Achyranthes aspera* L., AC1069, DB 36547, Ethiopia, *M. Wondafrash 4076* (B, ETH), LT992592<sup>1</sup>, LT992953<sup>1</sup>, –, PQ053367, PQ053437, LT993043<sup>1</sup>, LT992992<sup>1</sup>; AC1099, DB 36577, Kenya, *V. Di Vincenzo, P. Kamau, M. Wondafrash, M. Mbale 281* (B: B101063648, EA, ETH), LT992595<sup>1</sup>, LT992529<sup>1</sup>, PQ042469, PQ053372, PQ053442, LT993046<sup>1</sup>, LT992995<sup>1</sup>; AC1100, DB 36578, Kenya, *V. Di Vincenzo, P. Kamau, M. Wondafrash, M. Mbale 287* (B: B101063649, EA, ETH), LT992596<sup>1</sup>, LT992526<sup>1</sup>, PQ042470, PQ053373, PQ053443, LT993047<sup>1</sup>, LT992996<sup>1</sup>; AC1112, DB 36590, Kenya, *V. Di Vincenzo, P. Kamau, M. Wondafrash, M. Mbale 308* (B: B101063652, EA, ETH), LT992597<sup>1</sup>, LT992521<sup>1</sup>, PQ042471, PQ053374, PQ053444, LT993048<sup>1</sup>, LT992997<sup>1</sup>; AC1119, DB 36597, Kenya, *V. Di Vincenzo, P. Kamau, M. Wondafrash, M. Mbale 325* (B: B101063656, EA, ETH), LT992598<sup>1</sup>, LT992955<sup>1</sup>, PQ042473, PQ053376, PQ053446, LT993049<sup>1</sup>, LT992998<sup>1</sup>; AC1165, DB 36643, Ethiopia, *V. Di Vincenzo, N. Korotkova 360* (B: B101063660, ETH), LT992602<sup>1</sup>, –, PQ042478, PQ053381, PQ053451, LT993053<sup>1</sup>, LT993002<sup>1</sup>; AC1206, DB 36684, Ethiopia, *V. Di Vincenzo, A. Hailu 85* (B: B101063611, ETH), LT992607<sup>1</sup>, LT992525, PQ042482, PQ053385, PQ053455, LT993057<sup>1</sup>, LT993006<sup>1</sup>. *Achyranthes avicularis* E.Mey. ex Moq., South Africa, *Venter 9671* (NY), –, EF688660<sup>2</sup>, –, –, EF688731<sup>2</sup>, –, *Achyranthes bidentata* Blume, AC0003, DB 35483, China: Yunnan, 1996, *unknown collector s.n.* (B), LT992574, LT992944, PQ042444, PQ053344, PQ053414, LT993014, LT992958. *Achyranthes leptostachya* E.Mey. ex Meisn., AC0247, DB 35727, South Africa, *K. Müller 876* (B, PRE), AY998117<sup>3</sup>, LT992523<sup>1</sup>, PQ042454, PQ053354, PQ053424, LT993028<sup>1</sup>, LT992975<sup>1</sup>. *Achyranthes schinzii* (Standl.) Cufod., AC1381, DB 36859, Kenya, *W.R.Q. Luke 15344* (EA), PQ042991, –, PQ042502, PQ053408, PQ053478, PQ044557, PQ036731. *Achyranthes splendens* Mart. ex Moq., AC1256, DB 36734, Hawaii, *S. Perlman 5803* (MO: MO3665264), LT999872<sup>1</sup>, –, PQ042485, PQ053388, PQ053458, –, LT995187<sup>1</sup>. *Centema subfusca* (Moq.) T.Cooke, AC0906, DB 36384, South Africa, *P. Bamps s.n.* (BR), LT999833<sup>1</sup>, LT995193<sup>1</sup>, PQ042456, PQ053357, PQ053427, LT995131<sup>1</sup>, LT995161<sup>1</sup>. *Centemopsis* sp., AC1117, DB 36595, Kenya, *V. Di Vincenzo, P. Kamau, M. Wondafrash, M. Mbale 318* (B: B101063765, EA, ETH), LT999856<sup>1</sup>, LT999821<sup>1</sup>, PQ042472, PQ053375, PQ053445, LT996933<sup>1</sup>, LT999806<sup>1</sup>. *Cyathula achyranthoides* (Kunth) Moq., AC1387, DB 36865, Ethiopia: Bale, I. Friis, M.G. Gilbert & K. Vollesen 3598 (B: B100012020), PQ042992, PQ042028, PQ042503, PQ053409, PQ053479, PQ044558, PQ036733; AC1388, DB 36866, Venezuela, *W. Meier 13874* (B: B100527007), PQ042993, PQ042029, PQ042504, PQ053410, PQ053480, PQ044559, PQ036734. *Cyathula capitata* Moq., AC1257, DB 36735, China, *unknown collector* (KUN), LT999873<sup>1</sup>, LT995219<sup>1</sup>, PQ042486, PQ053389, PQ053459, LT995155<sup>1</sup>, LT995188<sup>1</sup>. *Cyathula cylindrica* Moq., AC0241, DB 35721, South Africa, *K. Müller 877* (B, PRE), LT992575<sup>1</sup>, LT995233<sup>1</sup>, PQ042453, PQ053353, PQ053423, LT993027<sup>1</sup>, LT992974<sup>1</sup>; AC0964, DB 36442, Ethiopia, *M. Wondafrash 3605A* (ETH, B), LT992587<sup>1</sup>, LT992949<sup>1</sup>, PQ042462, PQ053363, PQ053433, LT993039<sup>1</sup>, LT992987<sup>1</sup>; AC1652, DB 37130, Burundi: prov. Bubanza, *M. Reekmans 10647* (BR: BR0000013742072), PQ042996, PQ042031, PQ042507, PQ053413, PQ053483, PQ044561, PQ036738. *Cyathula divulsa* Suess., AC1394, DB 36872, Zambia: Mweru-Wa-Ntipa, *J.B. Phipps & L.D.E.F. Vesey-Fitzgerald 3237* (B), –, –, –, PQ036736. *Cyathula heudelotii* (Moq.) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, AC0056, DB 35536, Burkina Faso, *J. Müller 324* (FR), AY514818<sup>1</sup>, LT995224<sup>1</sup>, PQ042447, PQ053347, PQ053417, LT993016<sup>1</sup>, LT992961<sup>1</sup>. *Cyathula hildebrandtii* (Schinz) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, AC0955, DB 36433, Ethiopia, *M. Wondafrash 3462* (B, ETH), LT999841<sup>1</sup>, LT995197<sup>1</sup>, PQ042460, PQ053361, PQ053431, LT995135<sup>1</sup>, LT995165<sup>1</sup>; AC0961, DB 36439, Ethiopia, *M. Wondafrash 3500* (B, ETH), LT999842<sup>1</sup>, LT995198<sup>1</sup>, PQ042461, PQ053362, PQ053432, LT995136<sup>1</sup>, LT995166<sup>1</sup>; AC1084, DB 36562, Ethiopia, *M. Wondafrash 2065* (B, ETH), LT999850, LT995205, PQ042467, PQ053370, PQ053440, LT995143<sup>1</sup>, LT995173<sup>1</sup>; AC1094, DB 36572, Ethiopia, *M. Wondafrash 2213* (B, ETH), LT999851<sup>1</sup>, LT995206<sup>1</sup>, PQ042468, PQ053371, PQ053441, LT995144<sup>1</sup>, LT995174<sup>1</sup>; AC1130, DB 36608, Kenya, *V. Di Vincenzo, P. Kamau, M. Wondafrash, M. Mbale 339* (B: B101063922, EA, ETH), LT999859<sup>1</sup>, LT995210<sup>1</sup>, PQ042477, PQ053380, PQ053450, LT995147<sup>1</sup>, LT995178<sup>1</sup>; AC1230, DB 36708, Ethiopia, *V. Di Vincenzo, A. Hailu 261* (B: B101063921, ETH), PQ042974, –, PQ042484, PQ053387, PQ053457, –, PQ036723; AC1310, DB 36788, Kenya, *A.F.H. Linsen & W.B.I.T. Giesen 24* (B), –, PQ042010, PQ042487, PQ053391, PQ053466, –, –, AC1311, DB 36789, Kenya, *A. Peter 2206* (B), PQ042975, PQ042011, PQ042488, PQ053392, PQ053462, PQ044544, –, AC1312, DB 36790, Tanzania, *A.A. Pesambili 6222* (B), PQ042976, PQ042012, –, PQ053393, PQ053463, –, –, AC1313, DB 36791, Tanzania, *E. Milne-Redhead & P. Taylor 11306* (B), PQ042977, PQ042013, PQ042489, PQ053394, PQ053464, –, –, AC1314, DB 36792, Kenya, *A. & P. Hiepo 2611* (B), PQ042978, PQ042014, PQ042490, PQ053395, PQ053465, –, –, AC1315, DB 36793, Tanzania, *A. Hemp 4007* (B), PQ042979, PQ042015, –, PQ053396, PQ053466, –, –, AC1319, DB 36797, Ethiopia, *V. Di Vincenzo, A. Hailu 175* (B: B101063909, ETH), PQ042980, PQ042018, PQ042491, PQ053397, PQ053467, PQ044546, PQ036724; AC1320, DB 36798, Ethiopia, *V. Di Vincenzo, A. Hailu 179* (B: B101063910, ETH), PQ042981, PQ042019, PQ042492, PQ053398, PQ053468, PQ044547, PQ036725; AC1321, DB 36799, Ethiopia, *V. Di Vincenzo, A. Hailu 185* (B: B101063911, ETH), PQ042982, PQ042020, PQ042493, PQ053399, PQ053469, PQ044548, PQ036726; AC1322, DB 36800, Ethiopia, *V. Di Vincenzo, A. Hailu 190* (B: B101063912, ETH), PQ042983, PQ042021, PQ042494, PQ053400, PQ053470, PQ044549, PQ036727; AC1323, DB 36801, Ethiopia, *V. Di Vincenzo, A. Hailu 192A* (B: B101063913, ETH), PQ042984, PQ042022, PQ042495, PQ053401, PQ053471, PQ044550, PQ036728; AC1324, DB 36802, Ethiopia, *V. Di Vincenzo, A. Hailu 198* (B: B101063915, ETH), PQ042985, PQ042023, PQ042496, PQ053402, PQ053472, PQ044551, –, AC1325, DB 36803, Ethiopia, *V. Di Vincenzo, A. Hailu 204* (B: B101063916, ETH), PQ042986, PQ042024, PQ042497, PQ053403, PQ053473, PQ044552, –, AC1326, DB 36804, Ethiopia, *V. Di Vincenzo, A. Hailu 211* (B: B101063917, ETH), PQ042987, PQ042025, PQ042498, PQ053404, PQ053474, PQ044553, PQ036729; AC1327, DB 36805, Ethiopia, *V. Di Vincenzo, A. Hailu 213* (B: B101063918, ETH), PQ042988, PQ042026, PQ042499, PQ053405, PQ053475, PQ044554, PQ036730; AC1328, DB 36806, Ethiopia, *V. Di Vincenzo, A. Hailu 257* (B: B101063919, ETH), PQ042989, PQ042027, PQ042500, PQ053406, PQ053476, PQ044555, –, AC1329, DB 36807, Ethiopia, *V. Di Vincenzo, A. Hailu 258* (B: B101063920, ETH), PQ042990, –, PQ042501, PQ053407, PQ053477, PQ044556, –, *Cyathula involucrata* (Moq.) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, AC1391, DB 36869, Togo, *U. Scholz, P. Koumassi, H. Kühn & H. Peuker 451* (B), PQ042994, PQ042030, PQ042505, PQ053411, PQ053481, –, PQ036735. *Cyathula natalensis* Sond., AC0237, DB 35717, South Africa, *K. Müller 879* (B, PRE), LT999825<sup>1</sup>, LT995189<sup>1</sup>, PQ042452, PQ053352, PQ053422, LT995127<sup>1</sup>, LT995156<sup>1</sup>. *Cyathula polycephala* Baker, AC1065, DB 36543, Ethiopia, *M. Wondafrash 3394* (B, ETH), LT999845<sup>1</sup>, LT995201<sup>1</sup>, PQ042465, PQ053366, PQ053436, LT995139<sup>1</sup>, LT995169<sup>1</sup>. *Cyathula prostrata* (L.) Blume, AC0022, DB 35502, Peru, *E. Russo 114* (B), AY514862<sup>3</sup>, LT995221, PQ042445, PQ053345, PQ053415, –, LT992959; AC0951, DB 36429, Ethiopia, *M. Wondafrash 3434* (B, ETH), LT992586<sup>1</sup>, LT995244<sup>1</sup>, PQ042458, PQ053359, PQ053429, –, LT992986<sup>1</sup>. *Cyathula quadrangula* (Engl.) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, AC0903, DB 36381, –, *E. Coppejam s.n.* (BR), LT992582<sup>1</sup>, LT995239<sup>1</sup>, –, PQ053356, PQ053426, LT993034<sup>1</sup>, LT992981<sup>1</sup>. *Cyathula rubrolutea* (Lopr.) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, AC0209, DB 35689, –, *Greenway & Kanuri 14399* (PRE), –, –, PQ042450, PQ053350, PQ053420, –, PQ036721. *Cyathula tomentosa* (Roth) Moq., AC1258, DB 36736, China: Shaanxi Province, *C. Zhengquan 1917* (KUN), LT999875<sup>1</sup>, –, –, PQ053390, PQ053460, –, –, *Cyathula uncinulata* (Schrad.) Schinz, AC1166, DB 36644, Ethiopia, *V. Di Vincenzo, N. Korotkova 361* (B: B101063803, ETH), LT999865<sup>1</sup>, LT995214<sup>1</sup>, PQ042479, PQ053382, PQ053452, LT995150<sup>1</sup>, LT995182<sup>1</sup>; AC1207, DB 36685, Ethiopia, *V. Di Vincenzo, A. Hailu 86* (B: B101063799, ETH), LT999869<sup>1</sup>, LT995218<sup>1</sup>, PQ042483, PQ053386, PQ053456, LT995154<sup>1</sup>, LT995186<sup>1</sup>. *Cyathula welwitschii* (Schinz) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, AC1384, DB 36862, Burundi, *M. Reekmans 90325* (EA), –, –, –, –, PQ036732. *Cyphocarpa angustifolia* (Moq.) Lopr., AC0189, DB 35669, South Africa, *K. Müller 860* (B, PRE), AY998111<sup>3</sup>, LT995225<sup>1</sup>, PQ042449, PQ053349, PQ053419, LT993017<sup>1</sup>, LT992963<sup>1</sup>. *Evelynastra pallida* (S.Moore) Di Vincenzo, Berendsohn, M.Wondafrash & Borsch, AC1080, DB 36558, Ethiopia, *M. Wondafrash 3928* (B: B101063935, ETH), LT999849<sup>1</sup>, LT995204<sup>1</sup>, –, PQ053369, PQ053439, LT995142<sup>1</sup>, LT995172<sup>1</sup>; AC1125, DB 36603, Kenya, *V. Di Vincenzo, P. Kamau, M. Wondafrash, M. Mbale 334A* (B, EA, ETH), LT999858<sup>1</sup>, LT995209<sup>1</sup>, PQ042475, PQ053378, PQ053448, LT995146<sup>1</sup>, LT995177<sup>1</sup>; AC1126, DB 36604, Kenya, *V. Di Vincenzo, P. Kamau, M. Wondafrash, M. Mbale 334B* (B: B101063936, EA, ETH), PQ042973, PQ042009, PQ042476, PQ053379,



## Appendix 1. Continued.

PQ053449, -, PQ036722; AC1203, DB 36681, Ethiopia, *V. Di Vincenzo, M. Wondafrash 42* (B: B101063923, ETH), LT999867<sup>1</sup>, LT995216<sup>1</sup>, PQ042481, PQ053384, PQ053454, LT995152<sup>1</sup>, LT995184<sup>1</sup>; AC1317, DB 36795, Tanzania, *R.B. Drummond & J.H. Hemsley 2305* (B), PQ042998, PQ042016, -, -, -, PQ044545, -, AC1318, DB 36796, Somalia, *N. Kilian 1767 & W. Lobin 6621* (B), PQ042999, PQ042017, -, -, -, -, *Leucosphaera hainesii* (Hook.f.) Gilg, AC0882, DB 36360, South Africa: Northern Province, *K. Müller 866* (B, PRE), LT992581<sup>1</sup>, LT995238<sup>1</sup>, PQ042455, PQ053355, PQ053425, LT993033<sup>1</sup>, LT992980<sup>1</sup>. *Nototrichium divaricatum* Lorence, no voucher data, -, -, -, -, -, AY174422<sup>4</sup>. *Nototrichium humile* Hillebr., U.S.A.: Hawaii, *B.A. Prigge 15249* (LA), AY514816<sup>3</sup>, -, -, -, -, -, *Nototrichium sandwicense* Hillebr., U.S.A., *van Neste 216* (US), -, -, -, -, -, MF348854<sup>5</sup>; U.S.A., *B.A. Prigge 15250* (LA), AY514817<sup>3</sup>, -, -, -, -, -, *Psilotrichum gnaphalobryum* (Hochst.) Schinz, AC1077, DB 36555, Ethiopia, *M. Wondafrash 2200* (B, ETH), LT992593<sup>1</sup>, LT992954<sup>1</sup>, PQ042466, PQ053368, PQ053438, LT993044<sup>1</sup>, LT992993<sup>1</sup>. *Psilotrichum scleranthum* Thwaites, AC0125, DB 35605, South Africa, *K. Müller 878* (B, PRE), AY514822<sup>3</sup>, LT999811<sup>1</sup>, PQ042448, PQ053348, PQ053418, LT996924<sup>1</sup>, LT999809<sup>1</sup>. *Pupalia lappacea* (L.) Juss., AC0983, DB 36461, Ethiopia, *M. Wondafrash 3922* (B, ETH), LT992590<sup>1</sup>, LT995262<sup>1</sup>, PQ042463, PQ053364, PQ053434, LT993042<sup>1</sup>, LT992990<sup>1</sup>. *Sebsebea orthacantha* (Hochst. ex Asch.) Di Vincenzo, Berendsohn, M. Wondafrash & Borsch, AC0930, DB 36408, South Africa: Northern Province, *K. Müller 872* (B, PRE), LT999836<sup>1</sup>, LT995195<sup>1</sup>, PQ042457, PQ053358, PQ053428, LT995133<sup>1</sup>, LT995163<sup>1</sup>; AC0954, DB 36432, Ethiopia, *M. Wondafrash 3461* (B, ETH), LT999840<sup>1</sup>, LT995196<sup>1</sup>, PQ042459, PQ053360, PQ053430, LT995134<sup>1</sup>, LT995164<sup>1</sup>; AC1122, DB 36600, Kenya, *V. Di Vincenzo, P. Kamau, M. Wondafrash, M. Mbale 330* (B: B101063797, EA, ETH), LT999857<sup>1</sup>, LT995208<sup>1</sup>, PQ042474, PQ053377, PQ053447, LT995145<sup>1</sup>, LT995176<sup>1</sup>. *Sericocoma avolans* Fenzl, AC0234, DB 35714, South Africa, *K. Müller 859* (B, PRE), AY998103<sup>3</sup>, LT995232<sup>1</sup>, PQ042451, PQ053351, PQ053421, LT993026<sup>1</sup>, LT992973<sup>1</sup>. *Sericostachys scandens* Gilg & Lopr., AC0042, DB 35522, Rwanda, *E. Fischer s.n.* (B), AY514819<sup>3</sup>, PQ042008, PQ042446, PQ053346, PQ053416, PQ044542, PQ036720. *Sericostachys scandens* Gilg & Lopr., AC1651, DB 37129, Democratic Republic of the Congo: Tshivanga PNKB, *Ntaowira Niranoa 563* (BR: BR0000013741808), PQ042995, -, PQ042506, PQ053412, PQ053482, PQ044560, PQ036737. *Volkensinia prostrata* (Volkens ex Gilg) Schinz, AC1201, DB 36679, Ethiopia, *M. Wondafrash 4200* (B, ETH), LT999866<sup>1</sup>, LT995215<sup>1</sup>, PQ042480, PQ053383, PQ053453, LT995151<sup>1</sup>, LT995183<sup>1</sup>.

## Appendix 2A. Character definiton.

## Habit and vegetative morphology

## 1 Life cycle

Comprises annual herbs or perennials which live for several years (including herbs, subshrubs, shrubs, lianas, or trees). In some cases (e.g., in *Achyranthes aspera*) the distinction between annual and perennial is difficult as young plants may not yet have developed the final vegetative branching although they exhibit axillary buds or short lateral branches (in these cases coded as “perennial”).

States: **annual (0), perennial (1)**

## 2 Life form

Lianas are rare in Amaranthaceae and are here only understood to occur in *Sericostachys*, which has long-twining stems growing to the top of canopy trees (stems not self-sustaining); the sometimes scandent and slender stems in species of *Cyathula* are included in the state “subshrub”.

States: **herb (0), subshrub (1), shrub (2), treelet (3), liana (4)**

## 3 Indumentum of stem and leaves

The stem and leaf surfaces of Amaranthaceae often exhibit an indumentum composed of different types of trichomes. In Achyranthoids most of the species possess uniseriate hairs (so called “simple hairs”; Townsend, 1985) whereas very few species exhibit branched hairs. In this dataset this is the case in *Sericocomopsis pallida* with stellate hairs on leaf surfaces and condensed-dendroid ones on inflorescence axes, upper branches and sometimes leaf veins (compare Fig. 4).

States: **simple (0), stellate and condensed-dendroid (1)**

## 4 Shape of cauline leaves

States: **ovate (0), elliptic (1), lanceolate (2), linear-narrowly lanceolate (3), obovate-spathulate-oblancheolate (4)**

## 5 Petiole length of cauline leaves [in cm]

States: **0 = sessile (0), ≤0.5 (1), 0.6–1.5 (2), 1.6–2 (3), ≥2.1 (4)**

## Inflorescence morphology

## 6 Shape of paracladia

Amaranthaceae possess a cymous inflorescence architecture (Acosta & al., 2009). In Achyranthoids the cymes are present in most taxa but can be reduced to solitary flowers (in *Achyranthes*, *Achyropsis* and *Nototrichium*; see character 8), like also in Gomphrenoideae (Ortuño Limarino & Borsch, 2020). The shape of paracladia ranges from globose to long spiciform with cymes or flowers clearly separated from each other (state at anthesis since inflorescences elongate during development). In some species (*Cyathula uncinulata*) the synflorescences appear as a single paracladium but the irregular subglobose shape is caused by the agglomeration of short paracladia on short lateral branches. This character corresponds to character 7 in Ortuño Limarino & Borsch (2020).

States: **spiciform with cymes or solitary flowers clearly separated during anthesis (0), globose or elongate to cylindrical with cymes densely aggregated (1), strongly condensed with cymes closely aggregated and paracladia agglomerated, thus synflorescences appear as a single subglobose to irregularly and thickly cylindrical paracladium (2)**

## 7 Arrangement of paracladia / Synflorescence structure

The complex synflorescence structures in the Amaranthaceae consist of paracladia (= partial florescences) arranged in different ways (Acosta & al., 2009). This character defines the respective structures of the branching system that is constituted by the axes bearing paracladia (corresponds to character 8 in Ortuño Limarino & Borsch, 2020). The species of *Achyropsis* exhibit richly branched synflorescences with branches still supported by smaller cauline leaves but not scales, so that they are coded with state 0. This is in contrast to the branched inflorescences in *Sericostachys* where branches are supported by brownish scales. The globose paracladia in *Pandiaka involucreta* appear on the main axis and very short terminal branches supported by smaller cauline leaves but contrary to the cyathia in several species of *Gomphrena* (Ortuño Limarino & Borsch 2020) these branches are still visible (here coded as state 0).

States: **paracladia solitary on main axes as well as on lateral branches (0), paracladia arranged in a complex thyrsoid structure (a terminal paracladium as main florescence and lateral paracladia are co-florescences, with up to two orders of branching (1)**

## Floral morphology

## 8 Structure of cymes

Amaranthaceae bear cymous inflorescence structures which are varying in the degree of branching in different genera and species. Cymes with only first-order branches (simple cymes) are rare and found in two species: in *Sericostachys* where the lateral flowers are sterile and subtending the fertile main flower, and in *Centemopsis*, where only one of the lateral branches is developed and thus cymes are not fully symmetric. More richly branched cymous structures (with second-order branches and higher) are often not fully symmetric as well and can contain sterile flowers in various proportions (e.g., all flowers of

## Appendix 2A. Continued.

second-order branches sterile and very reduced as in *Cyathula prostrata* or only very few sterile flowers on uppermost branches in relation to many fertile flowers present as in *Sericocomopsis pallida*.

States: **cymes reduced to single flowers (0), cymes with first-order branches (1), cymes with more than one order of branches (2)**

## 9 Position (angle) of cymes in relation to the inflorescence axis during maturity

In *Achyranthes* and *Centrostachys* the reduced cymes are deflexed and closely appressed to the inflorescence axis in fruit ripening.

States: **cymes not deflexed and closely appressed to the inflorescence axis (0), cymes deflexed and appressed to the inflorescence axis (1)**

## 10 Presence or absence of sterile flowers

States: **absent (0), present (1)**

## 11 Shape of sterile flowers

In Achyranthoids several species exhibit unique inflorescence structures in which fertile flowers are arranged together with sterile flowers in the cymes of partial inflorescences. In several species tepals and partially also the bracteoles of sterile flowers are modified to hooks, scales or bristles serving dispersal by animals or rarely to hairs serving dispersal by wind (Di Vincenzo & al., 2018). Since modifications of sterile flowers are diverse, the different states account for different kinds of modified sterile flowers. In *Nelsia*, the at maturity conspicuous stiff and spine-like hairy structures appear opposite on the first-order branch of cymes and are thus interpreted as bracteoles, whereas tepals are very rudimentary (state 3).

States: **unmodified (0), hooks (1), straight spines (2), with dominating plumose-pilose spine-like bracteoles (3), filiform hairs rapidly elongating and feathery during fruit from modified linear tepals (4)**

## 12 Androecial tube appendages

Androecial tube appendages, formerly known as “interstaminodial appendages” or “pseudostaminodes” (e.g., Eliasson, 1988; Townsend, 1993), are found in a wide range of shape and size in several Amaranthaceae species. In accordance with Ortuño Limarino & Borsch (2020), we follow the approach of Vrijdaghs & al. (2014) and Sánchez-del Pino & al. (2019) and consider androecial tube appendages (originating from primordia on the androecial tube rim) to be non-homologous with the appendages on the filaments (originating from the bases of the filaments).

States: **absent (0), present (1)**

## 13 Homogeneity of tepals

We focus only on size and shape of the tepals. State 1 is limited to the monotypic genus *Centrostachys*.

States: **all equal (0), outermost tepal different in size and shape, remaining tepals equal (1), 2 outer and 3 inner distinctly different in size and shape (2), 2 outer, 3 inner smaller but similar in shape (3)**

## 14 Shape of outer tepals of fertile flowers

As tepals in Achyranthoids can be different within single flowers (compare character 9). We focus on the outer tepals here since they offer a higher variability compared to inner tepals. For *Centrostachys aquatica* the outermost tepal is coded here which is different from all remaining tepals (compare character 9). We distinguish between the following states regarding to the flat part of the tepal (differences of the excurrent midrib are coded in the subsequent character):

States: **lanceolate with acute tip (0), lanceolate with acuminate tip (1), narrowly lanceolate with acute tip (2), narrowly lanceolate with acuminate tip (3), elliptic-oblong or lanceolate-oblong with a blunt tip (4)**

## 15 Midrib of outer tepals

The midribs of the outer tepals within achyranthoid species can be excurrent to various degrees. Also, they can differ in their quality, by forming hooks. The latter state has evolved supporting dispersal by animals (Di Vincenzo & al., 2018). Therefore, we defined the following states:

States: **not excurrent (0), mucronate to shortly excurrent (1), distinctly/long excurrent (2), uncinately hooked (3)**

## 16 Veination of outer tepals

In some species with indurate tepals the number of veins is difficult to assess and may also differ among different flowers. We coded therefore the presence of up to 3 or up to 5 veins if in any flower of a given individual this vein number could be observed.

States: **1-veined (0), up to 3 veins (1), up to 5 veins (2), >5 veins (3)**

## 17 Veination of inner tepals

Inner tepals with only one vein where not observed in any taxon. Thus, we coded the following states:

States: **up to 3 veins (0), up to 5 veins (1), >5 veins (2)**

## 18 Texture of tepals at maturity

Several achyranthoid taxa exhibit indurate tepals. In *Sericocomopsis meruensis* the tepals are becoming indurate at base between the abaxially prominent veins. There are also some species of *Centemopsis* where tepals become conspicuously indurate in the lower half at maturity or even at anthesis (in *Lopriorea*, not included in this dataset).

States: **remaining herbaceous or scarious (0), becoming slightly indurate at base (1), becoming conspicuously indurate in lower part (2)**

## 19 Shape of bracteoles

As bracteoles of fertile and sterile flowers can be different and not all achyranthoid species bear sterile flowers, here we focus on the bracteoles of the fertile flowers. We distinguish between the following states:

States: **lanceolate with acuminate tip (0), ovate with acuminate tip (1), broadly ovate with acuminate tip (2), ovate-broadly ovate with obtuse tip (3), orbicular with an emarginate/retuse tip (4)**

## 20 Midrib of bracteoles of fertile flowers

The midribs of the bracteoles within achyranthoid species can be excurrent to various degrees. Also, they can differ in their quality, by forming hooks. The latter state has evolved supporting dispersal by animals (Di Vincenzo & al., 2018). Therefore, we defined the following states:

States: **not excurrent (0), mucronate to shortly excurrent (1), distinctly/long excurrent (2) uncinately hooked (3)**

## 21 Bracteoles at anthesis

In some taxa bracteoles become strongly recurved during anthesis. Since bracteoles fall with the fruits and therefore are part of the dispersal units during fruit fall, this might be correlated with a function in dispersal in taxa where bracteoles become spiny (e.g., in *Achyranthes aspera*, *Centemopsis kirkii*, *Nelsia quadrangula* and *Sericocomopsis hildebrandtii*).

States: **bracteoles not or only slightly recurved in most fertile flowers at anthesis (0), bracteoles strongly recurved in all fertile flowers at anthesis (1)**

## 22 Shape of bracts

States: **lanceolate with acuminate tip (0), ovate with blunt tip (1), ovate with acuminate tip (2), broadly ovate with obtuse tip (3), broadly ovate with acuminate tip (4)**

## 23 Midrib of bracts

States: **not excurrent (0), mucronate to shortly excurrent (1), distinctly/long excurrent (2)**

## 24 Hairiness of ovary

States: **glabrous (0), pilose (1), lanate (2)**

**Appendix 2B.** Morphological character matrix applied for ancestral character reconstructions. Taxa for which the same individual was used for morphological and molecular analyses are marked with an asterisk and voucher information is given in Appendix 1. For the remaining taxa, barcodes are given and voucher data can be assessed from the Virtual herbarium of the Herbarium Berolinense (<http://ww2.bgbm.org/herbarium/default.cfm>).

Taxon with sample number or barcode	Character																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
<i>Achyranthes aspera</i> AC1069*	1	0	0	1,2	3	0	0	0	1	0	n.a.	1	0	3	1	1	0	1	4	2	1	0	2	0
<i>Achyranthes aspera</i> AC1099*	1	1	0	1,4	2	0	0	0	1	0	n.a.	1	0	2	0	1	0	1	4	2	0	0	1	0
<i>Achyranthes aspera</i> AC1100*	1	1	0	0,2	2	0	0	0	1	0	n.a.	1	0	3	0	1	0	1	4	2	1	0	2	0
<i>Achyranthes aspera</i> AC1112*	1	0	0	0	3	0	0	0	1	0	n.a.	1	0	3	0	1	0	1	4	2	1	0	2	0
<i>Achyranthes bidentata</i> B101074034	1	0	0	0,2	3	0	0	0	1	0	n.a.	1	0	3	0	1	0	1	4	2	1	4	1	0
<i>Achyranthes splendens</i> B101077184	1	2	0	0,4	2	0	0	0	1	0	n.a.	1	0	0	0	1	0	1	1	2	1	2	0	0
<i>Achyropsis avicularis</i> B101074120	1	0	0	0,2	1	0	0	0	0	0	n.a.	1	0	0	0	1	0	1	3	0	0	2	1	0
<i>Achyropsis leptostachya</i> AC0247*	1	0	0	0,2	1	0	0	0	0	0	n.a.	1	0	0	0	1	0	1	3	0	0	2	1	0
<i>Centema subfusca</i> B101076970	1	1	0	3	0,1	1	0	2	0	1	2	0	2	4	0	3	1	2	2	1	0	4	1	0
<i>Centemopsis</i> sp. AC1117*	0	0	0	3	0	1	0	1	0	0	n.a.	1	3	4	1	1	0	2	3	2	1	0	1	1
<i>Centrostachys aquatica</i> AC1064*	1	0	0	2	2	0	0	0	1	0	n.a.	1	1	2	2	1	2	1	4	1	0	2	2	0
<i>Cyathula achyranthoides</i> AC1387*	1	0	0	1,2,4	1	0	0	2	0	1	1	1	0	1	2,3	2	0	1	1	3	0	0	1	0
<i>Cyathula cylindrica</i> AC0964*	1	0	0	0,1	4	1	0	2	0	1	1	1	3	3	1	1	1	0	2	3	0	1,2	1	0
<i>Cyathula natalensis</i> AC0237*	1	1	0	1,4	1	2	0	2	0	1	1	1	3	4	1	1	0	1	0	2	0	4	2	0
<i>Cyathula orthacantha</i> AC0954*	0	0	0	0,1,2	3	1	0	2	0	1	2	1	0	0	1	1	1	1	2	2	0	0	1	0
<i>Cyathula polycephala</i> AC1065*	1	0	0	0,2	2	0	0	2	0	1	1	1	2	1	3	0	0	0	1	3	0	2	1	0
<i>Cyathula prostrata</i> MW 4087	1	0	0	4	1	0	0	2	0	1	1	1	0	1	1	1	0	1	0,1	2	0	0	1	0
<i>Cyathula tomentosa</i> B101077186	1	0	0	0,1	2	0	0	2	0	1	1	1	2	1	3	1	0	0	1	3	0	2	1	0
<i>Cyathula uncinulata</i> AC1166*	1	0	0	1	4	2	0	2	0	1	1	1	2	3	3	0	0	0	0	3	0	2	1	0
<i>Kyphocarpa angustifolia</i> AC0189*	0	0	0	3	0	1	0	2	0	1	2	1	2	2	1	1	0	2	3	1	0	2	2	1
<i>Leucosphaera bainesii</i> AC0882*	1	2	0	4	1	2	0	2	0	1	3	0	0	1	2	1	0	1	0,1	2	1	2	2	2
<i>Nelsia quadrangula</i> B101073864	1	0	0	0,2	2	0	0	2	0	1	3	1	3	0	2	1	0	1	2	2	1	4	2	0
<i>Nototrichium humile</i> B101073894	1	3	0	0	1	0	0	0	0	0	n.a.	0	0	0	0	1	0	1	1	1	0	1	1	0
<i>Nototrichium sandwicense</i> B101073908	1	3	0	0	2	1	0	0	0	0	n.a.	0	0	0	0	1	0	1	1	0,1	0	2	0	0
<i>Pandiaka angustifolia</i>	0	0	0	3	0	1	0	0	0	0	n.a.	1	3	0	0	3	0	2	1	2	0,1	4	1	0
<i>Pandiaka involucreta</i> AC1391*	1	1	0	1,2	1	1	0	0	0	0	n.a.	1	3	2	0	2	0	0	0	1	0	2	0	0
<i>Pandiaka lanuginosa</i> B101074059	1	0	0	0,2	2	0	0	0	1	0	n.a.	1	0	3	0	2	1	1	0,1	2	1	2	1	0
<i>Pandiaka rubrolutea</i> B101073949	0	0	0	4	0,1	1	0	0	0	0	n.a.	1	3	3	2	2	0	1	0	2	0	0	1	0
<i>Psilotrichum gnaphalobryum</i> AC1077*	1	1	0	0	2	0	1	0	0	0	n.a.	0	2	4	0	1	0	0	3	1	0	1	1	0
<i>Psilotrichum scleranthum</i> AC0125*	1	2	0	0	1	0	0	0	0	0	n.a.	0	3	0	0	3	2	2	3	1	0	2	1	0
<i>Pupalia lappacea</i> AC0983*	1	1	0	0	2	0	0	2	0	1	1	0	0	4	0	1	0	0	2	1	0	0	1	0
<i>Sericocoma avolans</i> AC0234*	1	2	0	3	0	1	0	0	0	0	n.a.	0	0	0	0	1	0	0	3	1	0	2	2	2
<i>Sericocomopsis meruensis</i> AC0961*	1	2	0	4	1	0	0	2	0	0	n.a.	1	3	0	1	1	0	1	1	2	0	1	1	0
<i>Sericocomopsis hildebrandtii</i> AC1094*	1	2	0	0,1	1	1	0	2	0	0	n.a.	1	3	0	1	1	0	0	1	2	1	1,2	1	0
<i>Sericocomopsis pallida</i> AC1125*	1	2	1	1,4	2	1	0	2	0	1	0	1	3	1	1	1	0	0	1	1	0	2	0	0
<i>Sericostachys scandens</i> AC1651*	1	4	0	0	2	0	1	1	0	1	4	1	3	0	0	3	2	0	3	0	0	1	0	0
<i>Volkensinia prostrata</i> B101077233	1	0	0	0	2	0	0	2	0	1	3	1	0	2	0	1	0	0	3	1	0	3	1	0