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diversified as a C4 lineage in the New World tropics with
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Source: Willdenowia, 50(3) : 345-381

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: <https://doi.org/10.3372/wi.50.50301>

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Gomphrena (Amaranthaceae, Gomphrenoideae) diversified as a C₄ lineage in the New World tropics with specializations in floral and inflorescence morphology, and an escape to Australia

Version of record first published online on 31 August 2020 ahead of inclusion in December 2020 issue.

Abstract: The genus *Gomphrena* comprises about 120 species in the Americas and 35 in Australia. Previous research revealed that *Gossypianthus*, *Lithophila* and *Philoxerus* are closely related but the monophyly of *Gomphrena* remained unresolved. Our aim was to clarify phylogenetic relationships in *Gomphrena* and allies based on a thorough sampling of species and to reconstruct the evolution of morphological characters including C₄ photosynthesis, and to explore the disjunction of the Australian taxa. We generated datasets of plastid (*matK-trnK*, *trnL-F*, *rpl16*) and nrITS representing 45 taxa of *Gomphrena* plus relatives and analysed them with parsimony, likelihood and Bayesian methods. Ancestral states of phenotypic characters were reconstructed with BayesTraits. BEAST was employed for divergence time estimates using an extended *Amaranthaceae–Chenopodiaceae* dataset to place fossil calibration points. *Gossypianthus* is closely related to a *Gomphrena radiata–G. umbellata–G. tomentosa* clade and *G. meyeniana*, whereas *Lithophila* and *Philoxerus* appear as successive sisters of the Australian species of *Gomphrena*. The majority of Andean species appears in a large clade including annual and perennial species. The Cerrado species *Gomphrena mollis* and *G. rupestris*, which are C₃, constitute an early-branching lineage, whereas the core *Gomphrena* clade is C₄ and has the inner two sepals strongly compressed as synapomorphy. A major subclade evolved inflorescences with subglobose paracladia in a whorl, supported by pseudanthial leaves. Whereas the core *Gomphrena* clade started to diversify around 11.4 Ma (8.45–14.5 95% highest posterior density [HPD]) the Australian lineage split at only 4.8 Ma (2.61–7.18 HPD). Our detailed phylogenetic analysis of *Gomphrena* depicts 10 major lineages including segregate genera. We hypothesize that an adaptation to coastal habitats was followed by long-distance dispersal to Australia. We also propose a revised genus concept of *Gomphrena* including *Gossypianthus*, *Lithophila* and *Philoxerus*, considering that these small segregate genera were based on states of vegetative characters exhibiting adaptations to specific habitats rather than phylogeny and overall morphology.

Key words: *Amaranthaceae*, androecium, C₄ photosynthesis, *Caryophyllales*, classification, *Gomphrena*, *Gomphrenoideae*, *Gossypianthus*, *Lithophila*, molecular phylogenetics, *Philoxerus*, pseudanthium

Article history: Received 17 April 2020; peer-review completed 2 June 2020; received in revised form 10 August 2020; accepted for publication 11 August 2020.

Citation: Ortuño Limarino T. & Borsch Th. 2020: *Gomphrena* (Amaranthaceae, Gomphrenoideae) diversified as a C₄ lineage in the New World tropics with specializations in floral and inflorescence morphology, and an escape to Australia. – Willdenowia 50: 345–381. doi: <https://doi.org/10.3372/wi.50.50301>

Introduction

Gomphrena L. is one of the largest genera of the *Amaranthaceae* with c. 120 species (Townsend 1993; Müller & Borsch 2005) and includes subshrubs, perennial and annual herbs, which are native in the New World tropics

and subtropics (Holzhammer 1955, 1956; Eliasson 1988) and Australia (Palmer 1998). Considerable species diversity (c. 40 spp.; Zuloaga & al. 2008; Borsch & al. 2015b) can be found in the Xeric Puna, the Bolivian-Tucuman forest region and the Chaco Boreal of southwestern Bolivia and northern Argentina. New species from these

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regions continue to be discovered and described, many of them endemic (Ortuño & Borsch 2005, 2006). The Cerrado and Caatinga habitats in mid-western and north-eastern Brazil also are diverse in *Gomphrena* (c. 50 spp.; Siqueira 1992), whereas Central America and the desert regions of Mexico and North America harbour only c. 20 species (Robertson & Clemants 2003). A second and disjunct centre of diversity is in Australia, where c. 33 species predominantly occur in the arid and semi-arid regions of western, central and northeastern Australia (Palmer 1998).

Linnaeus (1753) formally described the genus *Gomphrena* and added further species in later publications (1756, 1762). From the eleven species he described only three remained in the genus, as it is currently widely accepted (Eliasson 1988; Townsend 1993), whereas others were transferred to *Alternanthera*, *Froelichia* and *Philoxerus* (= *Blutaparon*) by subsequent authors (e.g. Holzhammer 1956). *Alternanthera* and *Froelichia* are morphologically well-defined genera. *Alternanthera* is distinguished from *Gomphrena* and allies by the globose stigma on a more or less elongated style and the presence of entire or fringed androecium tube appendages (Vrijdaghs & al. 2014; previously called “pseudostaminodia”, e.g. Eliasson 1988; Townsend 1993) alternating with the stamens, using the genus concept of Schinz (1893, 1934), adopted by Eliasson (1988) and Townsend (1993). The situation is different in *Philoxerus*, which cannot be easily separated from *Gomphrena* as it just differs by the general lack of stamen tube appendages or filament appendages, an androecium morphology that also occurs in some Australian species of *Gomphrena*. *Froelichia* differs from all other *Gomphrenoideae* by sepals fused for more than half, with this tube developing two lateral wings at maturity (Eliasson 1988). The morphology of the inner two sepals can differ and has been regarded as one of the diagnostic characters of *Lithophila* and *Philoxerus* (Townsend 1993). In these studies the term “tepals” was used for the perianth organs. More recent work converges on the opinion that these organs are in fact sepals (e.g. Ronse de Craene & Brockington 2013).

The currently widely used genus concept of *Gomphrena* (Townsend 1993; Hernández-Ledesma & al. 2015) is still pre-phylogenetic and goes back to Schinz (1893). Based on this circumscription, Holzhammer (1955, 1956) provided the last full synopsis of *Gomphrena* at species level for the New World and Palmer (1998) treated the Australian taxa. Pedersen (1990) more recently resurrected the genus *Xerosiphon* Turcz. with two species and removed them from *Gomphrena* based on the difference that their sepals are united until the middle.

According to the resulting slightly narrower genus circumscription, *Gomphrena* is characterized by flowers with five free and symmetric sepals, a gynoeceum with an inconspicuous to elongated style and two filiform stigma branches and the five filaments forming a tube to varying degrees, in some species almost completely

(Townsend 1993; Eliasson 1988). Sánchez-del Pino & al. (2019) showed that this tube does not result from post-genital fusion but develops from a ring-like meristem. Most species of *Gomphrena* possess stamen appendages on each side of the filament in a terminal position, leaving the impression of anthers “sunken” between them (Borsch & Ortuño 2005, 2006; Pedersen 1997, 2000). *Lithophila* also shares these androecium characteristics but the number of filaments and anthers is reduced to two or three (Eliasson 1988), whereas *Gossypianthus* has a shortly fused androecial cup, lacks appendages but the androecium is fused to the sepals for the most part (Schinz 1934; Eliasson 1988). The gynoeceia of the genera *Gossypianthus* and *Lithophila* are morphologically similar to *Gomphrena*.

Within the *Amaranthaceae*, *Gomphrena* belongs to subfamily *Gomphrenoideae*. This subfamily is characterized by the presence of unilocular anthers and has been shown as monophyletic with high statistical support (Müller & Borsch 2005; Sánchez-del Pino & al. 2009; Borsch & al. 2018). Following the *matK-trnK* study by Müller & Borsch (2005), who presented an overall phylogenetic analysis of the *Amaranthaceae*, Sánchez-del Pino & al. (2009) focused on the *Gomphrenoideae* with an increased taxon sampling of this clade. Based on the combined *trnL-F* and *rpl16* sequence data Sánchez-del Pino & al. (2009), three highly supported subclades of the *Gomphrenoideae* were found, and informally called alternantheroids, gomphrenoids and iresinoids. The iresinoid clade contains the genus *Iresine* and is sister to the remaining *Gomphrenoideae* (Borsch & al. 2018). Alternantheroids and gomphrenoids, referred to as the core *Gomphrenoideae* by Müller & Borsch (2005), share the presence of metareticulate pollen (Borsch 1998; Borsch & Barthlott 1998) as a synapomorphy. The alternantheroid clade consists of the monophyletic genera *Alternanthera*, *Pedersenia* and *Tidestromia* (Sánchez-del Pino & al. 2009, 2012; Borsch & al. 2011), whereas all remaining genera of the core *Gomphrenoideae* are in the gomphrenoid clade.

Molecular trees of Sánchez-del Pino & al. (2009), Sage & al. (2007) and Bena & al. (2017) show that the gomphrenoid clade contains species of *Gomphrena* in two different lineages: The first lineage comprises *Lithophila*, *Gossypianthus* and *Philoxerus* (= *Blutaparon*) along with most species of *Gomphrena* (= *Gomphrena* s.str.), and including *G. globosa* as the type species of the genus in a terminal clade, with *Xerosiphon*, *Froelichia* and *Guilleminea* appearing as successive sisters. Phylogenetic results thus confirmed the view of Pedersen (1990) to treat *Xerosiphon* as different from *Gomphrena*. The second lineage is composed of *Hebanthe*, *Pfaffia* and some species of *Gomphrena* such as *G. vaga* and *G. elegans*. Interestingly, the two different lineages containing species of *Gomphrena* are also characterized by pollen morphology. The first lineage (“clade a” in Sánchez-del Pino & al. [2009]) is characterized by metareticulate pollen

with strongly reduced tectum (Borsch 1998), whereas the second lineage has metareticulate pollen with the tectum completely covering the mesoporia and possessing just small perforations or foveolae (Borsch 1998; Borsch & Pedersen 1997). However, in all these studies relationships within each of these two lineages remained unresolved.

This investigation focuses on the first lineage. Sánchez-del Pino & al. (2009) published the hitherto most resolved trees with plastid *trnL-F+rpl16* sequences but included just 11 species. They found three lineages in a polytomy, among which one depicted *Gossypianthus* sister to *Gomphrena boliviana*, another *Gomphrena flaccida* sister to *Blutaparon+Lithophila*, and the third the remaining species of *Gomphrena*. Recently, Bena & al. (2017) added *trnL-F* sequences of a dozen further species from Argentina, but their trees remained statistically unsupported. Here we improve the sampling of *Gomphrena* from the different ecoregions (such as Andean dry valleys, Caatinga, Prepuna and Puna ecosystems in south America, and tropical and subtropical ecosystems in Australia) and of the different morphologically allied species groups present in the genus (Holzhammer 1955, 1956) using a set of genomic regions that have been shown to harbour high levels of phylogenetic signal in the plastid (e.g. Borsch & Quandt 2009; Korotkova & al. 2011) as well as nuclear ITS to test for congruence between genomic partitions.

Regarding morphology, Eliasson (1988) provided a comparative assessment of floral morphology for all genera of *Gomphrenoideae* then accepted, but he did not carry out any analysis of character evolution in a phylogenetic context. Nevertheless, hypotheses on androecium evolution within *Gomphrena* were put forward by Fries (1920) who proposed that *Gomphrena* comprises groups of species in which the complexity of the androecium was reduced, so in *G. tomentosa* and allies which lack stamen appendages. Eliasson (1988) hypothesized a stepwise character state transformation in the androecium from species with “pseudostaminodes” alternating with the stamens to species with apical filament lobes such as *Gomphrena* spp. through varying degrees of fusion. Vrijdaghs & al. (2014) examined the ontogeny of the androecium in *Gomphrenoideae* and concluded that the androecial tube develops from a circular intercalary meristem, from which also the alternating appendages arise as androecial tube appendages which are thus not homologous to residual stamens, and which therefore cannot be called “pseudostaminodia”. However, Vrijdaghs & al. (2014) only examined *Alternanthera*, *Iresine* and *Tidestromia*. More recently, Sánchez-del Pino & al. (2019) studied the ontogeny of *Blutaparon*, *Guilleminea* and several species of *Gomphrena* and *Pfaffia* which have lateral appendages on both sides of the filament but no alternating stamen tube appendages, and concluded that these lateral appendages are *de novo organs* not homologous to the stamen tube appendages. Acosta & al. (2009) compared the

structure of synflorescences across *Amaranthaceae*, and found that *Gomphrenoideae* possess thyrsoid structures with paracladia reduced to solitary flowers but they did not examine *Gomphrena* in more detail. We therefore selected a set of 21 vegetative and floral characters to assess the morphological variation of *Gomphrena* and allies, the matrix of which was then used to reconstruct character evolution in a phylogenetic context.

As a further character we investigated the distribution of C₄ photosynthesis in *Gomphrena* and allies, which was previously analysed in the whole *Amaranthaceae* s.str. by Sage & al. (2007). The authors determined carbon isotope data for three quarters of the species of *Amaranthaceae* among which were also most species of *Gomphrena* from the Americas and Australia. However, Sage & al. (2007) only included five *Gomphrena* species to map the evolution of C₄ photosynthesis on the tree of *Amaranthaceae* and revealed a common origin of C₄ in species of *Gomphrena* belonging to “clade a” alongside with *Philoxerus*, *Guilleminea* and *Froelichia*. This result was confirmed by Bena & al. (2017) who tested if the evolution of the C₄ pathway correlated with changes in macroclimatic niches and found that C₄ *Gomphrenoideae* specialized to dryer regions compared to their C₃ relatives and then expanded into colder environments. That is consistent with the current distribution of C₄ species of *Gomphrena* growing at high elevations of the Andes in Argentina and Bolivia (Sage & al. 2007; Borsch & al. 2015b). Here we use a representative sampling of C₃ and C₄ species of *Gomphrena* and allies, to more accurately reconstruct the evolution of photosynthetic pathways.

The disjunct distribution of *Gomphrena* between the Americas (majority of species) and Australia and the hypothesis that Australian species (e.g. *G. flaccida*) could be closely related to segregate genera with a Caribbean (*Lithophila*) and neotropical to Pacific distribution (*Philoxerus*) underscores the need to consider intercontinental plant migration between South America and Australia to understand the diversification of *Gomphrena* and allies. South American-Australian disjunct distribution patterns can be explained by two main hypotheses. The first is vicariance resulting from Gondwanan land connections up to terrestrial “Austral-Antarctic” migration routes during the Palaeocene-Eocene thermal maximum (Barker & al. 2007a; Pennington & Dick 2004; Upchurch 2008). The second is long-distance dispersal (LDD) between remote continental land masses, for which suitable means of dispersal such winds or sea currents must be present (Cook & Crisp 2005; Barker & al. 2007b). Using data from published phylogenetic and biogeographic analyses, Sanmartín & al. (2007) tested if directional dispersal can explain diversity among Southern Hemisphere plant groups. The authors could not detect any significant pattern, which, however, has to be viewed in light of the then available dated phylogenies. The clade of *Gomphrena* and allies therefore also offers an interesting case to illuminate South American-Australian biogeographic relationships.

Our goal is to better understand the evolutionary history of *Gomphrena* and allies and to develop a modern phylogeny-based taxonomic treatment for this group of plants. Therefore, this investigation has the specific objectives to (i) analyse the phylogenetic relationships of *Gomphrena* and closely allied genera *Gossypianthus*, *Guilleminea*, *Lithophila* and *Philoxerus*; to (ii) assess the variation of morphological characters and reconstruct their evolution, in particular of those characters that have been used or potentially are diagnostic to delimit these genera; to (iii) clarify overall phylogenetic relationships within *Gomphrena* s.str. using extended *matK-trnK* and ITS datasets; to (iv) determine the phylogenetic position and divergence time of the disjunct Australian taxa of *Gomphrena*. Moreover, our aim was to (v) illuminate the evolution of C₄ photosynthesis on the basis of our new phylogenetic results and to test in how far a realigned genus *Gomphrena* is characterized by C₄ photosynthesis.

Material and methods

Taxon sampling and composition of datasets

We used four datasets to complete the objectives of this investigation. The first dataset comprises major entities of *Gomphrena* (12 species) and allied genera (*Lithophila*, *Gossypianthus*, *Guilleminea*, *Philoxerus*) and also covers the other lineages of the gomphrenoid clade sensu Sánchez-del Pino & al. (2009) such as *Xerosiphon*, *Froelichia*, *Hebanthe* and *Pfaffia*. *Pedersenia* as a representative of the Alternantheroid clade served as outgroup. We selected 27 taxa to generate a dataset of plastid regions (*rpl16* intron, *matK* gene and *trnK* intron as well as the *trnL* intron and the *trnL-F* spacer; dataset A) and a corresponding matrix of morphological characters. In most cases, molecular and morphological character data were obtained from the same individuals. For *Froelichia*, *Hebanthe*, *Lithophila*, *Philoxerus*, and *Xerosiphon* and some species of *Gomphrena* s.str. (*G. boliviana*, *G. haenkeana*, *G. pulchella*) the *trnL-F* and *rpl16* data came from Sánchez-del Pino & al. (2009). In two exceptions, data from two closely related taxa were concatenated to represent the respective lineages: *Pfaffia fruticulosa* (*matK-trnK*, morphology, this study), and *P. tuberosa* (*rpl16* and *trnL-F* from Sánchez-del Pino & al. 2009), as well as *Gomphrena mandonii* (*matK-trnK*, morphology, this study), and *G. elegans* (*rpl16* and *trnL-F* from Sánchez-del Pino & al. 2009).

The second dataset includes a much higher number of samples (80 for plastid *matK-trnK* = dataset B-1 and 82 for nrITS = dataset B-2) with the aim to illuminate the overall tree space of the “*Gomphrena* clade” (= 45 taxa of *Gomphrena* s.str. including *Gossypianthus*, *Lithophila*, and *Philoxerus*, plus *Guilleminea*). Sampling was guided by morphological diversity, the sectional classification recognized so far (Holzhammer 1956) and the distribu-

tion of species in different biogeographical regions of the Americas and Australia. Since species limits in many cases are not yet well understood, plastid and nuclear sequences were obtained from the same individuals. In addition, some previously published *matK-trnK* sequences (e.g. Müller & Borsch 2005) were used for some species (*Gomphrena ferruginea*, *G. fuscipellita*, *G. pulchella*, *Guilleminea densa*, *Philoxerus vermicularis*). Voucher information and EMBL/GenBank accession numbers are provided in Appendix 1.

A third, extended *matK-trnK* dataset (dataset C) of the *Amaranthaceae*–*Chenopodiaceae* alliance was used for molecular clock dating in order to accommodate fossil calibration points. The sequence matrix employed the same representatives as in Di Vincenzo & al. (2018) for *Chenopodiaceae*, other *Caryophyllales* and eudicot lineages. For the *Amaranthaceae*, the representation of the achyranthoids was reduced here whereas *Gomphrenoideae* were sampled as in dataset B-1 of this investigation with some terminals belonging to the same species not included.

A fourth dataset (D-1 for *matK-trnK* and D-2 for ITS) was created by extending datasets B to include the further C₄ genera of *Gomphrenoideae* (species of *Alternanthera* and *Tidestromia*) into the ancestral character reconstruction of photosynthesis types. The sampling followed Borsch & al. (2018), from which most of the sequences were taken, with additions in *Alternanthera* from Sage & al. (2007) and Sánchez-del Pino & al. (2012). The ITS sequence of *Pseudoplantago* was newly generated. *Chamissoa* was used to root the trees as it is an early branching lineage (Müller & Borsch 2005) with *Ptilotus* and *Pandiaka* representing the aervoid and achyranthoid clades of the *Amaranthoideae*, respectively. However, the greater distance in particular of the sequences from *Alternanthera* and *Tidestromia* led to unalignability in two hotspots (which therefore needed to be excluded); thus this dataset is inferior for calculating precise relationships within *Gomphrena* as it has fewer characters.

DNA isolation and sequencing

Genomic DNA was isolated from silica-gel-dried leaf tissue or herbarium specimens using a triple CTAB extraction method (Borsch & al. 2003). The *matK-trnK*, *trnL-F* and *rpl16* regions were selected because of their high phylogenetic structure (Borsch & Quandt 2009; Korotkova & al. 2011) and to achieve consistency with other *Amaranthaceae* datasets (Müller & Borsch 2005; Di Vincenzo & al. 2018; Borsch & al. 2018). Primers were used as in Borsch & al. (2018) to amplify two overlapping halves of the *matK-trnK* region, whereas DNAs isolated from herbarium specimens often required to amplify even shorter fragments. Also the additional *Gomphrena*-specific primers ACmatK442F (5'-AGTCAAAAGAGCGATTGGG-3'), ACmatK602F (5'CTTGTTTTGACTGTATCGC-3'), AC-

matK465R (5'-TCTTATAACAAAATAAGATGG-3') and ACmatK631R (5'-ACAAAAGTAAAAATAGAGG-3') designed here were used. Primer ACmatK442F served as forward sequencing primer to complement the pherograms made with ACmatK1400R that could not read over a large microsatellite located in the *trnK* intron in several species of *Gomphrena* about 90 nt upstream of the *matK* start codon. The *rpl16* intron was amplified with flanking primers rpl16-1216F and rpl16-18R that were also used for sequencing along with the additional internal forward primer GOMrpl16-495F (Borsch & al. 2018). The *trnL-F* region was either amplified as a whole using primers trnTc and trnTf (Taberlet & al. 1991) or in two parts when DNA was isolated from herbarium material with primers trnTc and trnTd as well as trnL460F (Worberg & al. 2007) and trnTf. Primers trnTd and trnL460F were used for sequencing.

The ITS region was amplified and sequenced with the universal primers ITS4 and ITS5 (White & al. 1990). For some difficult samples from herbarium specimens, the new internal primers ACITS3F (5'-TTGGTGTGAATTGCAGAATCCC-3') and AC-ITS2R (5'-GATGGTTCCACGGGATTCTGC-3') were used to amplify and sequence the ITS region in two halves.

The PCR conditions were as described in Di Vincenzo & al. (2018). Sanger sequencing was performed by Macrogen Inc. (Seoul, South Korea) on an ABI 3730 XL capillary sequencer. Both strands were sequenced for ITS.

The sequences were submitted to ENA in bulk as annotated multiple sequence alignments by means of the program *annex2embl* (Gruenstaedl 2020).

Alignment and coding of length mutational events

Sequences were edited and aligned manually using PhyDE (Phylogenetic Data Editor) v. 0.9971 (Müller & al. 2012), using a motif alignment approach (Morrison 2009; Ochoterena 2009) following the rules by Löhne & Borsch (2005). Positions of uncertain homology (mutational hotspots) were excluded from the analysis (for exact delimitation see Appendices S1–S6). Indels were coded using the Simple Indel Coding method (Simmons & Ochoterena, 2000) as implemented in SeqState 1.40 (Müller 2005a).

Phylogenetic analyses

Maximum Parsimony (MP) analyses were performed using the Parsimony Ratchet (Nixon 1999) implemented in the software PRAP (Müller 2004) in combination with PAUP v.4.0b10 (Swofford 1998). Settings were 200 ratchet iterations with 25% of the positions randomly up-weighted (weight = 2) during each replicate and 10 random addition cycles. The command files generated with PRAP were then run in PAUP, using the heuristic search with the following parameters: all characters have equal weight, gaps are treated as “missing”, TBR branch swapping, initial swapping on 1 tree

already in memory, Maxtrees set to 100 (auto increased by 100) and branches collapsed actively if branch length is zero. Jackknife (JK) support for nodes was also performed in PAUP with 10,000 replicates, using a TBR branch swapping algorithm with 36.788% of characters deleted and one tree held during each replicate, following Müller (2005b).

The substitution models for the individual data partitions were determined with jModelTest 2 (Darriba & al. 2012) and using the Akaike information criterion (Akaike 1974). The best-fitting model was TVM+ Γ for *trnL-F* and *rpl16* and GTR+ Γ for *matK-trnK* (datasets A and B-1). The best-fitting substitution model found for ITS was SYM+ Γ .

Bayesian inference (BI) was carried out using MrBayes v. 3.2 (Ronquist & al. 2012) using the specifications from the best fitting models. A sampling frequency of 1000 was applied with the first 25% discarded as burn-in, four independent runs were performed with 4 chains each and 10 million MCMC generations. The convergence and effective sample size (ESS) of each replicate were checked using Tracer v. 1.5.0 (Rambaut & al. 2013). The remaining population of trees was summarized as majority rule consensus tree also using MrBayes 3.2.

Maximum Likelihood (ML) analysis was performed using RAxML GUI 1.3 v. 7.2.8 with 1000 bootstrap replicates Stamatakis (2006). Searches were performed using the general time-reversible (GTR) model with among-site rate heterogeneity modelled by a GAMMA distribution with 25 rate categories based on the available model choice in RAxML.

Assessment of morphological characters and ancestral character state reconstruction

A set of 21 morphological characters was defined covering vegetative, inflorescence and floral morphology. Therefore, characters used in previous studies of *Amaranthaceae* (e.g. Holzhammer 1955; Pedersen 1976, 1990, 1999; Eliasson 1988; Borsch & Pedersen 1997) were re-analysed and also new features and compared with the observed variation in the plant specimens in order to arrive at clear definitions of characters and their states reflecting hypotheses of homology (see Appendix 2). Also new characters on vegetative and inflorescences morphology were assessed. The selection of characters also considered their previous use as diagnostic features for the various generic concepts that were applied to *Gomphrena* and allies. Since the purpose of this investigation was not species delimitation, we did not include the usually much more variable characters with often many states (e.g. shape or texture of sepals) or quantitative data (e.g. length of sepals). These will be dealt with in future studies.

The 21 morphological characters were scored for the same species as in the 27-taxon combined plastid dataset based on herbarium specimens corresponding to the sam-

ples used for molecular analyses. To depict the ancestral states we used the maximum clade credibility tree from the Bayesian analysis, which was identical in topology to the Bayesian Majority rule consensus and the best ML trees. Ancestral states were reconstructed using BayesTraits, v. 2.0 (Pagel & al. 2004) sampling 1000 randomly selected trees after the burn-in. Commands for BayesTraits were generated by TreeGraph2 (Stöver & Müller 2010). Ancestral state probabilities were imported into TreeGraph2 to simultaneously visualize them on the branches.

Molecular clock dating

Dating was carried out with BEAST v. 1.8.0 (Drummond & al. 2012) using the broad *Amaranthaceae*–*Chenopodiaceae* *matK-trnK* dataset C. Because no fossils for the *Gomphrenoideae* are known, the same three fossil calibration points used by Di Vincenzo & al. (2018) in *Chenopodiaceae* were also employed here. A maximum age of 125 Ma was assumed which corresponds to the most likely age of the crown group of core eudicots (Bell & al. 2010). Age distribution priors for fossil primary calibration points were set as “exponential” (Ho & Philips 2009), whereas the three secondary calibration points (using age estimates of Bell & al. 2010) were included with “normal” age distributions equal to the 95% highest posterior densities interval (HPD) of Bell & al. (2010). Thus, our priors and calibration points for the dating of the gomphrenoid clade in *Amaranthaceae* were equal to the dating of *Amaranthaceae* with a focus on the achyranthoid clade as recently carried out by Di Vincenzo & al. (2018). A birth-death model was employed to model lineage diversification, using a random starting tree. Trees were sampled every 1000th generation after a burn in of 50%, calculating a total of 50 million generations for two MCMC runs. Adequate parameter sampling was checked with Tracer v. 1.4.0 (Rambaut & Drummond 2007). The combined post-burn-in tree distribution of both runs was then summarized as a maximum clade credibility tree using TreeAnnotator v. 1.8.0 (Drummond & al. 2012).

Evolution of C₄ photosynthesis

To assess the type of the photosynthetic pathway, δC_{13} values were taken from Sage & al. (2007). Many of the specimens studied there are also included into our phylogenetic analysis. Some additional specimens (out of the mostly Andean clade of *Gomphrena*) were examined for Kranz anatomy, which all were close relatives of taxa previously studied for isotopes. Presence of C₄ versus C₃ was then coded as a binary character. Ancestral states were reconstructed as reported for the other morphological characters. An analysis of ancestral states was implemented both for the plastid and the ITS trees to account for the incongruence in the position of the *G. mollis*–*G. rupestris* clade using datasets D-1 and D-2.

Generation of the distribution map

The distribution map of the coastal species (*Philoxerus portulacoides* and *P. vermicularis*) was produced in ArcGIS 10.3, based on the data obtained from the label of herbarium specimens reviewed in the National Herbarium of Bolivia (LPB), the Instituto Darwinion (SI) in Buenos Aires, and Berlin (B). In addition, the data entries from the online registers of TropicOMBOT (MO), Jardim Botânico do Rio de Janeiro (JABOT) specimens from Brazil; and the African Plant Database (<https://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php>) were considered. The georeferenced data was used in “DECIMAL DEGREES” format and all coordinates were verified with Google Earth. To assess the distribution in Australia occurrence data were obtained by querying the GBIF Portal (GBIF 2016).

Results

Characteristics of the sequence datasets

Statistics of the multiple sequence alignments for the 27 samples of *trnL-F*, *rpl16*, *matK-trnK*, the individual and consensus information are in Table 1. The length of the alignment of 27 samples of the regions *trnL-F*, *rpl16*, *matK-trnK* (dataset A) had 1082, 1150, 2499 characters, respectively, with eight hotspots (HS) of unclear homology excluded (most being poly A/T stretches). The number of parsimony informative characters were 91 in *trnL-F*, 118 in *rpl16*, and 178 in *matK-trnK*. The alignment of *matK-trnK* in the larger dataset B-1 had 2510 characters including 45 indels, excluding three HS. The ITS alignment (dataset B-2) had 722 characters including 81 indels, of which 269 were parsimony informative (See Table 1).

Molecular phylogenetic trees

The combined plastid tree (*matK-trnK*, *trnL-F*, *rpl16*; Fig. 1) depicts a basal split into a clade of *Pfaffia* and allies on one hand and *Gomphrena* s.str. and relatives on the other. Almost all nodes receive maximum support under MP, BI and ML. Several lineages were identified within a major clade that is here called “*Gomphrena* clade”: the first two branches are a *Gomphrena prostrata*–*Guilleminea* clade and a *Gomphrena mollis*–*G. rupestris* clade whereas all other lineages form the “core C₄ *Gomphrena* clade” (Fig. 1–3). Within the latter, a clade comprising *G. meyeniana* sister to *G. radiata* plus *G. tomentosa*, *Gossypianthus* and *Gomphrena boliviana*; a clade of *Lithophila*, *Philoxerus* and *G. flaccida* from Australia; a clade of *G. haenkeana* and *G. celosoides*; and a clade with *G. agrestis*, *G. lanigera* and *G. pulchella* were found. *Xerosiophon* and *Froelichia* are successive sisters to the “*Gomphrena* clade”.

The trees inferred from the extended *matK-trnK* dataset B-1 (Fig. 2) show the same principal lineages but several of them are revealed with more diverse crown

Table 1. Sequence statistics. Taxon datasets: A: 27 taxa combined *matK-trnK+rpl16+trnL-F*; B: 80 sequences of *matK-trnK* of *Gomphrena* and relatives; C: 82 sequences of ITS of *Gomphrena* and relatives; D: *matK-trnK* of *Amaranthaceae–Chenopodiaceae* with representation of *Gomphrena* for molecular-clock dating.

Dataset A	alignment	HS positions	sequence chars	indel chars	variable	informative
<i>matK-trnK</i>	2570 [CDS 806-2352]	456–477, 605–618, 780–805*	2495	38	435	178
<i>rpl16</i>	1284	477–517, 576–591, 1015–1024, 1065–1104**	1150	54	249	117
<i>trnL-F</i>	1235	73–82, 184–202, 305–310, 342–345, 406–423, 522–544, 858–868, 1117–1129***	1082	45	211	91
Dataset B-1						
<i>matK-trnK</i>	2570 [CDS 806-2352]	456–477, 605–618, 780–805*	2495	38	512	253
Dataset B-2						
ITS	647****	–	647	87	394	270
Dataset C						
<i>matK-trnK</i>	3658 [CDS 1454–3192]	576–590, 716–779, 893–1112, 1418–1453, 3262–3380, 3543–3592	3153	n.a.	1726	1266
Dataset D-1						
<i>matK-trnK</i>	2760 [CDS 920–2429]	505–520, 634–674, 681–696, 876–919	2643	89	855	431
Dataset D-2						
ITS	701 [5.8S 291–445]	65–67, 469–477	689	155	516	361

* The *matK-trnK* dataset lacks the first 14 nucleotides in the *trnK-5'* intron and the downstream 67 nucleotides of the *trnK-3'* intron were trimmed because the sequences were incomplete at this end in most samples; those samples that were amplified and sequenced with primer psbA-5R at a later stage of the study are longer and also include the *trnK-3'* exon and the *trnK-psbA* spacer (submitted to ENA but included into the matrix). Two inversions are found in the *matK* CDS (AC0105 alignment pos. 1054–1062 and AC0051, AC0465, AC0931 and AC1214 alignment pos. 1421–1423).

** The first 12 nucleotides of the *trnL* intron are not included into the matrix.

*** The first 27 nucleotides of the *rpl16* dataset are not included into the matrix; the sequences are trimmed at the end of the matrix shortly before the *rpl16-3'* exon but in some samples the sequences extend some 300 nucleotides further due to different primers used for PCR and sequencing (submitted to ENA but not included into the matrix).

**** In ITS, the flanking 18S and 26S are trimmed from the alignment and matrix but included in the sequences submitted to ENA.

groups. These are a central and southern Andean dry Puna and Prepuna *Gomphrena radiata–G. umbellata–G. tomentosa* clade, and a *G. boliviana–G. martiana* clade. All species sampled from Australia are resolved together with *G. flaccida* in a *Philoxerus*+Australian *Gomphrena* clade. The clade with *G. agrestis* and *G. lanigera* from the Cerrado of Bolivia and Brazil, *G. pulchella* ranging from the Cerrado to the Chaco is extended by *G. cardenasii*, an endemic from the Cerrado-Chiquitania of Bolivia and thus comprises species from the lowlands of southeastern South America. The most noteworthy result is that *G. haenkeana* represents a species-rich Andean clade with two well supported subclades (A and B), whereas the Mexican *G. nitida* appears unresolved to them (Fig. 2).

The ITS data (Fig. 3) recover the same principal clades and also largely the same topology. Nevertheless, the position of the *Gomphrena mollis–G. rupestris* clade is incongruent in the ITS trees, where it diverges before the *G. prostrata–Guilleminea* clade. The Australian species of *Gomphrena* clade are also retrieved with high support as close relatives to *Philoxerus* and *Lithophila* (Fig. 3).

Morphological characters

Six characters describe the habit and vegetative morphology in *Gomphrena* and allies as defined in Appendix 2. Character 1 (life cycle) is a complex trait, which is relevant because of many species being annuals. Characters 7 to 10 relate to inflorescences. The paracladia in *Gomphrena*

(Fig. 4) and allies are complex structures that resemble different levels of expansion of a complex synflorescence architecture, including the reduction of internodes, and a specific whorl-like arrangement of the paracladia (character 8, state 3; Fig. 4). In particular, character 9 (apical leaves subtending paracladia) is grouped into different states that resemble different forms of transition of cauline-like to very specialized pseudanthial leaves (state 2). Characters 12 and 13 refer to floral morphology, whereas characters 14 to 21 describe the variation of the androecium in detail (Appendix 2). The androecia of all 27 species included in dataset A are also illustrated schematically in Fig. 6. The matrix of morphological characters and their states is found in Appendix S7.

Evolution of morphological characters

Ancestral state probabilities for vegetative characters are depicted as pie charts (chars 1–6, 8, 9, 12, 13 are illustrated in Fig. 5; characters 7 and 10 see Appendix S8). Note that heteromorphic sepals with the inner two smaller than the outer and strongly compressed in fruit (character 12, state 1 in grey) is a synapomorphy for the core C₄ *Gomphrena* clade. *Pseudanthia* (in Fig. 5 character 8, state 3 in blue for the stellately arranged paracladia; character 9 state 2 in green for the specialized leaves) is derived three times, in *G. meyeniana*, *G. boliviana* and *G. haenkeana*. The evolution of the androecium (characters 14, 16, 17, 19; for chars 15, 18, 20, 21 see Appendix S9) is shown in Fig. 6. The size of the androecial tube varies considerably. Long androecial tubes appear in two lineages and are associated with showy, often colourful inflorescences. Staminal tube appendages alternating with the filaments only appear in *Pederseniana* (alternantheroids) and *Froelichia* but otherwise are completely lacking in the gomphrenoid clade (Fig. 6).

Diversification of *Gomphrena* and allies in time

The age of the crown group corresponding to the monophyletic subfamily *Gomphrenoideae* was inferred to be 30.9 Ma (Fig. 7; 21.16–43.22 95% HPD, node number 14 in Appendix S10), whereas the *Gomphrena* clade (see Fig. 1, 2) (15.1 Ma, 8.92–23.6 95% HPD, node 21) and the less inclusive core C₄ *Gomphrena* clade (node 23; 11.4 Ma, 6.69–18.78 95% HPD) are much younger. The Australian subclade has a stem age of 10 Ma (5.7–16.9 95% HPD) and thus started to diversify at a similar time to the speciose Andean subclades A and B (Fig. 1, 3, 7).

Evolution of C₄ photosynthesis

The reconstruction of ancestral states using the Bayesian trees inferred from the extended datasets D-1 (for *matK-trnK*) and D-2 (for ITS) is depicted for all nodes in Appendices S11 and S12, respectively. The plastid trees show C₄ photosynthesis to have originated in the com-

mon ancestor of the *Gomphrena* clade plus *Froelichia*, and two more times independently in a sublineage of *Alternanthera* and in *Tidestromia* (Fig. 7). The plastid topology also suggests a reversal from C₄ to C₃ (Fig. 7). To the contrary, the nuclear ITS tree, that resolves the *G. mollis*–*G. rupestris* clade in a different position not as second but as first branch of the *Gomphrena* clade (Fig. 3), suggests a single gain of C₄ photosynthesis in *Gomphrena* and *allies* (Appendix S12).

Discussion

Phylogeny of the *Gomphrena* clade and relationships of *Lithophila*, *Gossypianthus*, *Guilleminea* and *Philoxerus*

All plastid trees converge on a deep split into a lineage comprising *Hebanthe*, *Pfaffia* and allies (the *Pfaffia* clade) and a lineage including *Gomphrena* and allies, with *Xerosiphon* and *Froelichia* branching as successive sisters to the remaining taxa (Fig. 1, 2). The deep nodes received maximum support under MP, BI, and ML in *matK-trnK* alone (Fig. 2) as well as plastid regions combined (Fig. 1). The same topology for the principle lineages of the gomphrenoids as one of the tree major clades of the monophyletic subfamily *Gomphrenoideae* (in addition to alternantheroids and iresinoids) was found by Sánchez-del Pino & al. (2009) based on *trnL-F* and *rpl16* sequences alone. The trees recovered from nrITS show the same branching order of *Froelichia* and *Xerosiphon* (Fig. 3) although support of the respective nodes is less. The clade that includes the majority of *Gomphrena* species in addition to *Xerosiphon* and *Froelichia* depicts *Guilleminea*, *Gossypianthus*, *Philoxerus* and *Lithophila* nested among other species of *Gomphrena* (Fig. 1–3). This major clade is characterized by metareticulate pollen with the tectum reduced to distal bands (see also Borsch & al. 2018 for a detailed analysis of pollen evolution where this clade is represented by *Froelichia* and *Gomphrena lanigera*). The clade of *Gomphrena* including *Guilleminea*, *Gossypianthus*, *Lithophila* and *Philoxerus* is here annotated as the “*Gomphrena* clade” (Fig. 1–3) and receives maximum support in all analyses both from plastid and nrITS.

The taxon sampling of the *Gomphrena* clade in this investigation is several times higher and now includes a representative sampling of *Gomphrena* compared to the only 13 species in Sánchez-del Pino & al. (2009). Our trees inferred from plastid and nrITS sequence data congruently reveal ten lineages within the *Gomphrena* clade (see Fig. 1–3). The earliest diverging lineages are a *Gomphrena prostrata*–*Guilleminea* clade and a *Gomphrena mollis*–*G. rupestris* clade. These are inferred as successive sisters from the plastid data, although the combined analysis of *trnK-matK+rpl16+trnL-F* sequence data shows only moderate support for the second-branching position of the *G. mollis*–*G. rupestris* clade under MP

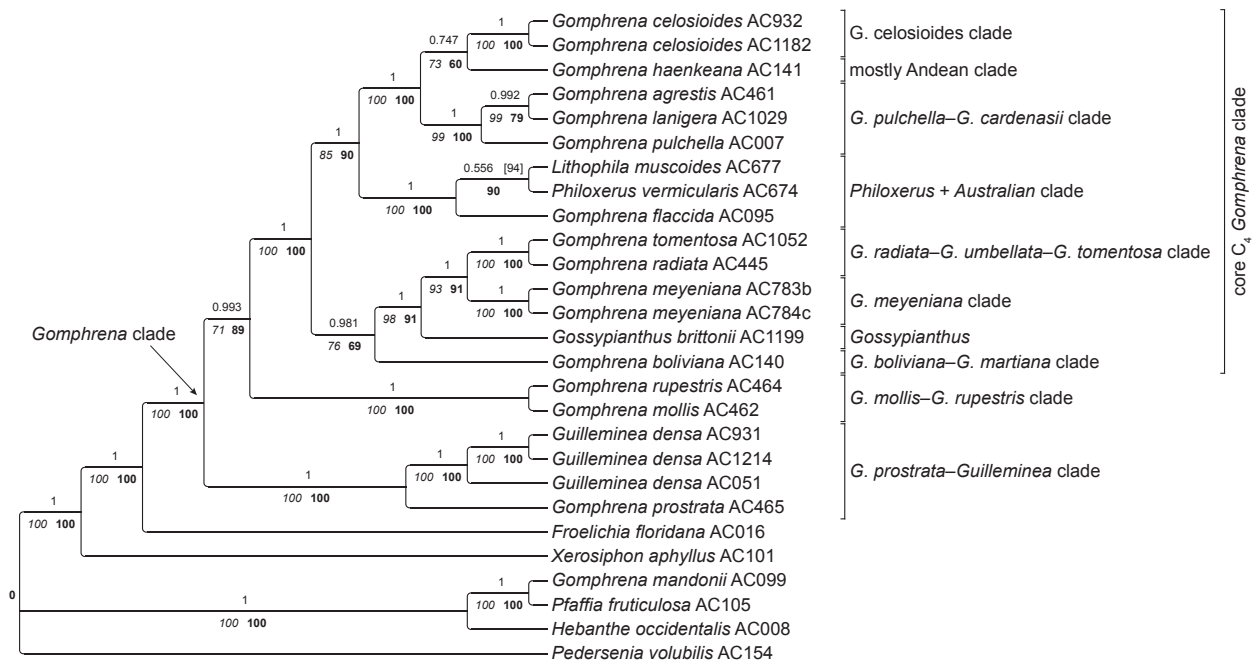


Fig. 1. Cladogram reconstructed from the combined matrix of *matK-trnK+rpl16+trnL-F* sequence data including indels (dataset A). The majority rule consensus tree obtained from MrBayes is depicted. Support values shown above branches are posterior probabilities; below are JK percentages from parsimony (left) and BS percentages from likelihood reconstruction (right).

(71% JK) and ML (89% BS; Fig. 1). The signal for this topology of the *trnK-matK* partition alone (Fig. 2) is much stronger. The nrITS partition depicts the *G. mollis*–*G. rupestris* clade in a switched position, branching before the *G. prostrata*–*Guilleminea* clade. Further analysis with a spectrum of loci from nuclear and organellar genomic partitions will be needed to test if this is hard incongruence, being the result of a reticulate evolutionary event.

The relationship of *Guilleminea* and *Gomphrena prostrata* receives maximum support in all plastid trees, whereas nrITS is less conclusive (0.89 PP, 80% JK, 69% BS). *Guilleminea densa* has a procumbent habit and is characterized perigynous flowers in terminal paracladia, with the androecium united in the sepals, and the five sepals of similar size, like the other species in the genus (Eliasson 1988, Pedersen 1990). Whereas most of the six species occur in the Chaco, Puna, and Andean dry valleys of Bolivia, Peru, Argentina and Paraguay (365 to 5000 m), *G. densa* ranges throughout the neotropics to the southern United States, and can be found as an introduced plant in Africa. *Gomphrena prostrata* has procumbent to ascending stems, flowers in terminal paracladia, a largely fused androecial tube, the anthers attached between two small filament appendages, and five sepals of similar size, being densely pubescent in the dorsal part. The plant occurs in Caatinga and Cerrado habitats of Brazil, where it is adapted to sandy soils. *Gomphrena mollis* and *G. rupestris* have detrital trichomes in the leaves and stems, while the rest of species in the *Gomphrena* clade have uniseriate and linear trichomes. The genera *Philoxerus* and *Lithophila* are

deeply nested within the *Gomphrena* clade and appear closely related to the Australian species of *Gomphrena* in a well-supported clade in all analyses (Fig. 1–3).

Evolution of vegetative morphology in *Gomphrena* and allied genera

Vegetative characters tend to be homoplastic rather than exhibiting synapomorphies for major clades (Fig. 5). The annual life cycle (character 1, state 0) thereby was derived multiple times from perennial ancestors and is depicted as an independent transition in four lineages of the core C₄ *Gomphrena* clade, so in *G. haenkeana*, *G. flaccida*, *G. radiata*, *G. boliviana*, but also in *Froelichia floridana*. The annual life form therefore is mostly associated with plants occurring in dry (*G. flaccida*, *G. radiata*) or seasonally dry environments (*G. haenkeana*) indicating the adaptive nature with plants only appearing in the wet season. Multiple origins of annuals have also been observed in other lineages of angiosperms radiating in areas with specific geographical patterns of dry environments such as *Nemesia* Vent. (*Scrophulariaceae*; Datson & al. 2008). The evolution of root types shows a similar homoplastic adaptive pattern, linked to different survival strategies in the different environments where species grow. For example, *G. meyeniana* is distributed along the Andes (1890–4800 m) and presents taproots that represent 82% of its total biomass (Patty & al. 2010), whereas aerial parts can be largely lost during the dry season. These features occur in many unrelated plant lineages and are an adaptation to high mountain ecosystems (Körner 2003). In a similar way,



Fig. 3. Extended phylogeny of *Gomphrena* based on nrITS including indels (dataset B-2). The Bayesian topology is shown as phylogram. Support values shown above branches are posterior probabilities; below are JK percentages from parsimony (left) and BS percentages from likelihood reconstruction (right). Major lineages are annotated as well as the geographic origin (country, department) of the respective samples.

G. meyeniana which all belong to the same clade (Fig. 2, 3, 5).

Complex branched main stems are the rule in woody species (character 5, state 1) such as *Hebanthe*, *Pedersea* or *Pfaffia fruticosa* and are ancestral in *Gomphrenoideae* (Fig. 5). Nevertheless, stems with secondary and tertiary branches also occur in perennial or annual herbaceous plants. In the latter this is a strategy to produce numerous axes that can quickly develop flowers and thus foster reproduction. Those species that only have unbranched stems generally possess a paracladium or at or near the terminal or node of the stem. This feature (state 0) has evolved independently several times (in *Xerosiphon aphyllus*, *Froelichia floridana*, *Gomphrena flaccida*, *G. mollis*, *G. agrestis* and *G. meyeniana*). Among the species of *Gomphrena*, *G. tomentosa* presents indeterminate growth, and as well *Gossypianthus* and *Guilleminea*. According to our ancestral character state reconstruction, this feature (character 6, state 0) in only a few cases, where it seems to be associated with plants possessing a tap root and procumbent stems.

Evolution of inflorescence and floral morphology, especially the androecium in *Gomphrena* and allied genera

The ancestral inflorescence in *Gomphrenoideae* was a globose to subglobose paracladium with densely adjacent solitary flowers (character 7, state 0) appearing terminal on a more or less elongated axis, without any specialized subtending leaf organs (character 9, state 1; Fig. 5). The head-like shape was maintained in the *Gomphrena* clade whereas elongate to cylindrical paracladia with remote flowers were independently derived in *Hebanthe* and *Froelichia* (not illustrated). The arrangement of paracladia into more complex synflorescences (character 8; partial florescences) is variable in *Gomphrenoideae* (Acosta & al. 2009) and also considerably differs in *Gomphrena* and allies depending on the branching system of more or less complex synflorescences. Because no detailed insights on the development or anatomy of inflorescences in *Amaranthaceae* are available that would support further hypotheses on homology, we coded the different arrangements of paracladia as unordered multiple



Fig. 4. Morphological diversity in flowers and inflorescences of *Gomphrena* and allies. – A: inflorescence of *Gomphrena* spec. 7 with less prominently visible paracladia but bright yellow pseudanthial leaves (Ortuño & al. 1677); B: *Gomphrena meyeniana* with pseudanthial leaves from lower surface (Borsch & Ortuño 3561); C: inflorescence of *G. fuscipellita* with six paracladia supported by broadly rounded, green pseudanthial leaves (Borsch & Ortuño 3594); D: *Gomphrena haenkeana* showing long, pink sepals and androecial tubes with reflexed pale yellow filament appendages, whereas stamens are dark yellow (Borsch & Ortuño 3627); E: *Philoxerus vermicularis* without pseudanthial leaves in the terminal inflorescence and two opposite leaf-like ones in the lateral inflorescence, and a pair of succulent cauline leaves (Borsch & al. 3444); F: *Lithophila muscoides*, part of a cushion-like plant in a limestone crevice (Greuter & al. 26915); G: Terminal part of flowering stem of *Guilleminea densa* (Borsch & al. 3437). – Photo credits: A: T. Ortuño; B–G: Th. Borsch.

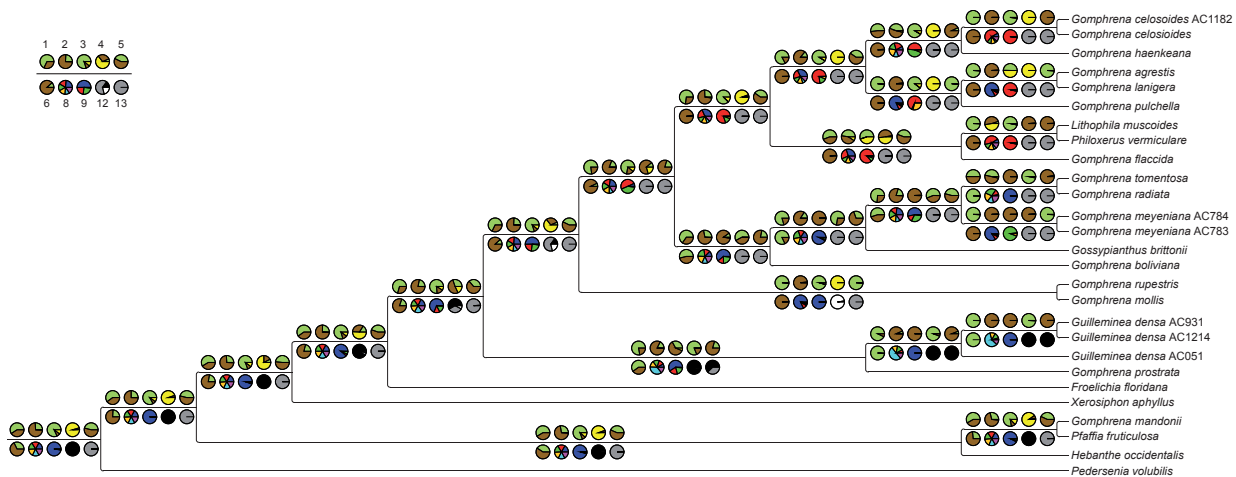


Fig. 5. Evolution of vegetative (characters 1 to 6), inflorescence (characters 8 and 9) and floral morphology (characters 12 and 13) in *Gomphrena* and relatives (see Appendix 2 for the definition of characters and their states as well as the full matrix in Appendix S7). The pie charts represent probabilities for ancestral states as reconstructed with BayesTraits and depicted on the maximum clade credibility tree obtained by Bayesian Inference of the combined plastid dataset. Pie charts were omitted for some deep nodes with minor changes and for characters 7 and 10 where changes appeared not to be relevant for *Froelichia*, *Hebanthe*, *Pedersenia* and *Xerosiphon*, all of which are well-defined distant genera (see Appendix S8).

states (character 8 with 6 states). Whereas all states reach nearly equal probabilities to be ancestral at deeper nodes (Fig. 5), it can be shown that the very specific architecture of a terminal florescence surrounded by usually 5 paracladia in a whorl-like structure (character 8, state 3) evolved two times independently in *G. boliviana* and *G. haenkeana* (Fig. 5). In fact, all relatives of *G. boliviana* (the *G. boliviana*–*G. martiana* clade) and of *G. haenkeana* in the two Andean subclades A and B (see Fig. 2, 3) possess the same states, so that the two species depicted in Fig. 5 are good representatives for their respective clades with a whorl-like arrangement of paracladia. It will be interesting to study the ontogeny of this structure to determine in how far it is the result of a strong condensation of a thyrsoid branching system or also involves collateral duplication of buds developing into paracladia.

This feature is correlated with the presence of pseudanthial leaves that are arranged in a whorl (character 9, state 2), earlier noted by Holzhammer (1956) and Siqueira (1992) as “involucral leaves”. Whereas two opposite, small subtending cauline leaves (state 1) is reconstructed as the ancestral state in the core C_4 *Gomphrena* clade, whorl-like pseudanthial leaves are derived even three times. Once in the speciose clade of *G. haenkeana* and relatives to which also *G. fuscipellita* and *G. pallida* belong, in the *G. boliviana*–*G. martiana* clade, and a third time in *G. meyeniana* that grows with a short upright stem at high elevations in the Andes (Fig. 4, 5). In the case of *G. meyeniana* pseudanthial leaves surround a single main florescence with relatively large white flowers appearing in good contrast to the dark pseudanthial leaves. Some populations of *G. pallida* have even been found to possess yellow-coloured pseudanthial leaves (Fig. 4). Conspicuously coloured leaves also serve as optical attractants in inflorescences of other *Caryophyllales* lineages

such as *Bougainvillea* Comm. ex Juss. (*Nyctaginaceae*; Brockington & al. 2009). *Gomphrena pulchella* represents a further specialization (autapomorphy, character 9, state 3), where an increased number of up to 10 leaves subtend a terminal solitary paracladium. The flowers in this species are the largest in *Gomphrenoideae* (>45 mm in length), and also androecial tube is very long (Fig. 6), leading to very conspicuous flower heads. These specialized leaves could also serve as a protection against fire before anthesis and during fruit development in *G. pulchella* which is a typical Chaco species (Pedersen 1976). This pattern of inflorescence evolution indicates that there is a trend toward the formation of pseudanthia in the core C_4 *Gomphrena* clade. Compared to several other families of flowering plants such as *Apiaceae*, *Asteraceae*, *Euphorbiaceae* (their cyathium), or *Rubiaceae*, the formation of pseudanthia in *Amaranthaceae* so far did not receive much attention. Classen-Bockhoff (1990) just mentioned their existence in *Gomphrena* and *Ptilotus*.

Gomphrena and allies as all *Caryophyllales* possess five perianth parts with opposite stamens, located in individual primordia in quincuncial order independently of the stamens (Vrijdaghs & al. 2014). Their arrangement results in two external, one intermediate, and two inner sepals, the latter of which can vary strongly in size and texture (Character 12). The state with the inner two sepals smaller than the outer two, which are cymbiform, compressed and carinate in fruit is resolved as synapomorphy for the core C_4 *Gomphrena* clade (Fig. 5). The *G. mollis*–*G. rupestris* clade, which also exhibits smaller inner sepals differs in that these inner sepals do not become thickened at maturity (state 2), which could represent a transitional state if the *G. mollis*–*G. rupestris* clade is assumed to be the sister of the core C_4 *Gomphrena* clade. Further analyses using reductive coding of this complex

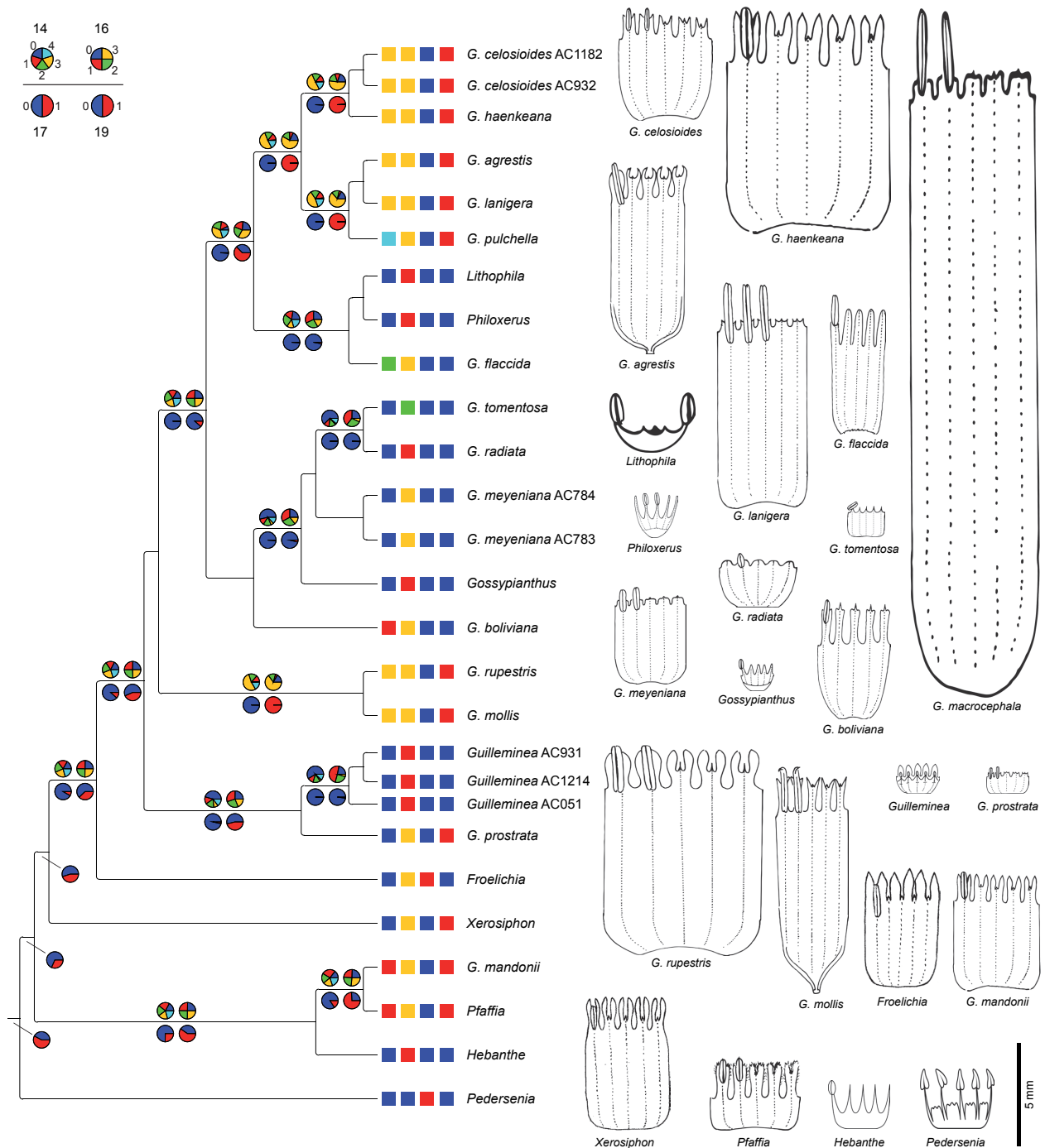


Fig. 6. Evolution of androecium characters 14 (length of androecial tube), 16 (shape of androecial tube), 17 (presence of androecial tube appendages), 19 (presence of filament appendages) in *Gomphrena* and related genera (see Appendix 2 for the definition of characters and their states as well as the full matrix in Appendix S7). The pie charts represent probabilities for ancestral states as reconstructed with BayesTraits and depicted on the maximum clade credibility tree obtained by Bayesian Inference of the combined plastid dataset. Ancestral states of characters 15, 18, 20 and 21 are shown in Appendix S9).

character (Torres-Montúfar & al. 2018) will be interesting but will require detailed anatomical analyses of the tissues. In *Guilleminea* perigynous flowers are derived as the only genus in *Gomphrenoideae* (character 13, state 0).

Differences in the morphology of the androecium were used in the circumscription of *Gomphrena* and other genera of the *Amaranthaceae* (Schinz 1893; Eliasson 1988; Townsend 1993). Nevertheless, the homology of

interstaminal and staminal appendages has been a subject of debate. Eliasson (1988) suggested a stepwise character state transition from so-called “pseudostaminodes” alternating with stamens as present in *Alternanthera* and *Pedersenia* (Fig. 6) to “apical filament lobes” present in many species of *Gomphrena* (e.g. *G. haenkeana*), *Pfaffia* and *Xerosiphon* (Fig. 6). Vrijdaghs & al. (2014) investigated the ontogeny of the androecium in *Gomphrenoi-*

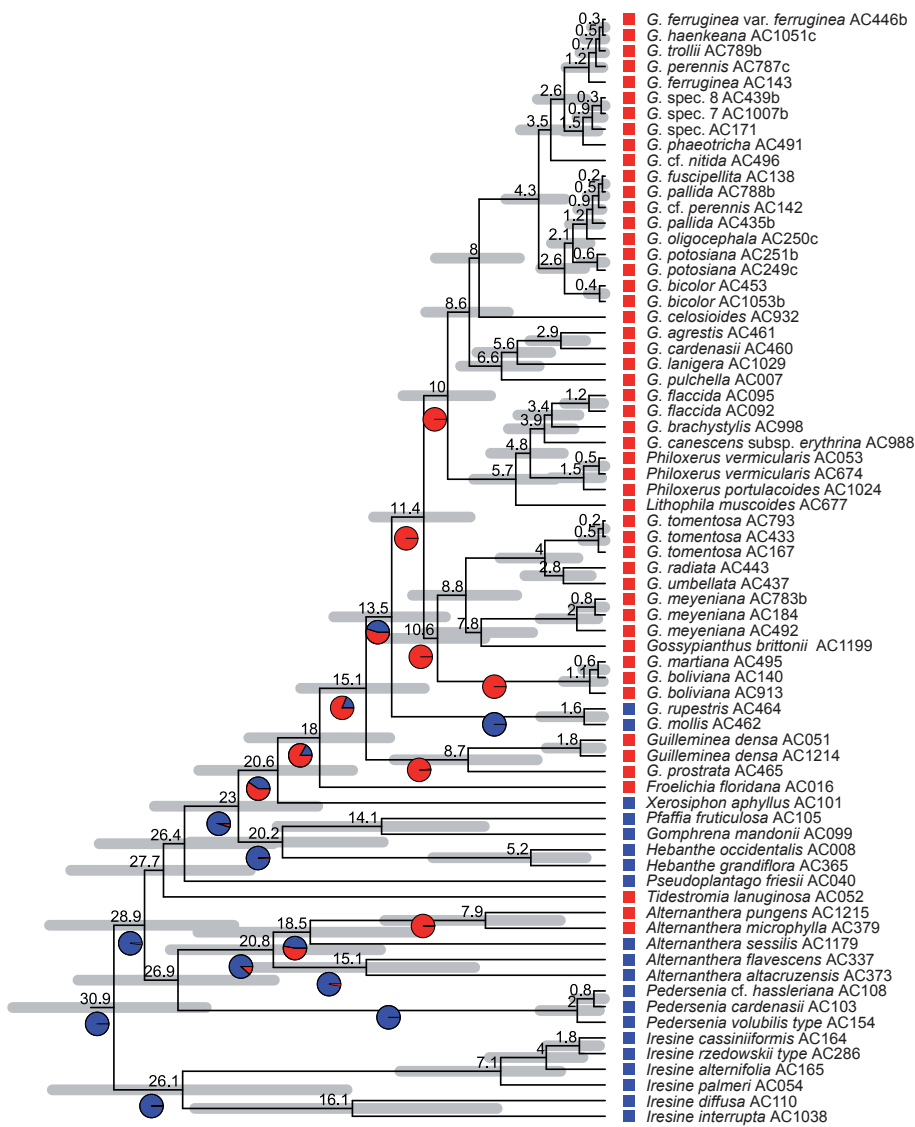


Fig. 7. Overview on the evolution of *Gomphrena* in time. The tree represents the clade of the *Gomphrenoideae* from the overall divergence time estimation of *Amaranthaceae* and *Chenopodiaceae* calculated with BEAST and 95% HPD intervals as grey bars (see Appendix S10 for the full tree with precise divergence times). Pie charts depict the evolution of C₄ photosynthesis in *Gomphrena* in the wider context of the *Gomphrenoideae* (C₃ in blue and C₄ in red). The core *Gomphrena* clade including *Lithophila*, *Gossypianthus* and *Philoxerus* constitutes the most diverse C₄ lineage in *Amaranthaceae*. Note the young crown group ages of the *Philoxerus*+Australian *Gomphrena* clade in a similar range than the mostly Andean clade.

deae and found that the androecium tube develops from a circular intercalary meristem, without any indication of postgenital fusion. Also the appendages develop from this meristem without any traces of veins, suggesting their interpretation as stamen-tube appendages without any organ identity. Moreover, Sánchez-del Pino & al. (2019) concluded that the lateral filament appendages in *Gomphrena* and *Pfaffia* are de novo organs, thus not being homologous to the stamen tube appendages. This is consistent with the observation that the *Amaranthaceae*–*Chenopodiaceae* clade generally has a single whorl of antesealous stamens without any trace of staminodes (Ronse de Craene 2013). Our reconstruction of ancestral states shows that the presence of androecial tube appendages (character 17,

state 0; Fig. 6) is ancestral in *Gomphrenoideae*. They were lost in the gomphrenoid clade but apparently re-gained in *Froelichia*. In line with our results (Fig. 6), Eliasson (1988) illustrated organs like stamen tube appendages in *Froelichia*. However, in the absence of any ontogenetic information for *Froelichia*, their homology may be further investigated as we cannot exclude any lateral fusion of de novo lateral stamen appendages that may have occurred together with the evolution of a completely closed androecial tube in that genus. Sánchez-del Pino & al. (2019) annotated the presence of stamen tube appendages on a tree of *Gomphrenoideae* and consistently show their absence in the gomphrenoid clade, indicating their loss after the divergence of *Pseudoplantago*. However, their character coding of *Froelichia* differs from ours. Other major lineages of the *Amaranthaceae* also exhibit similar variation patterns in the androecium such as the aervoid clade (Hammer & al. 2019).

The evolution of lateral filament appendages (character 19) shows strong homoplasy. They have arisen twice within the core C₄ *Gomphrena* clade but were lost again in the common ancestor of the *Philoxerus*+Australian *Gomphrena* clade (Fig. 1, 6). And they arose independently in *G. prostrata* in the *Pfaffia* clade (Fig. 6). Sánchez-del Pino & al. (2019) also showed the presence and absence of lateral filament appendages in *Gomphrena* and relatives, but their tree did not sample the genus *Gomphrena* in a representative way and also did not provide the necessary resolution of nodes to make more specific conclusions. Vrijdaghs & al. (2014) suggested the androecial tube appendages to be part of an insect-pollination syndrome, functioning as floral nectaries. This may be true for androecial tube appendages in *Iresine* or *Pedersen* but not for the lateral stamen appendages. These were attributed to attract pollinators by taking over this function from the corolla (Sánchez-del Pino & al. 2019). To the

contrary, our results show that the gain of filament appendages (character 19, Fig. 6) in species of *Gomphrena* coincides with either the evolution of large and showy flowers or pseudanthia (e.g. *G. haenkeana*, *G. mollis*; see Fig. 5).

Androecial tubes have extended in length two times during the evolution of *Gomphrena* (character 16, Fig. 6), to the extreme of the up to 30 mm long tubes in *G. pulchella*. Floral evolution in the *G. mollis*–*G. rupestris* lineage is therefore convergent to *G. haenkeana*, *G. pulchella* and allies (mostly Andean clade; see Fig. 1). Long androecial tubes also correlate to showy flowers, which appears to indicate a specialized pollination syndrome. However, the pollination biology of *Gomphrena* is not well known. Based on scattered observations, *Gomphrena* and allies seem to be pollinated by insects. During field work for this study, moths were observed visiting flowers of *G. pallida* that introduced their proboscis through the androecium tube, and butterflies were reported to pollinate the Australian *G. splendida* (Barrett & Palmer 2015). The position, length and shape of filament appendages (characters 20 and 21) is highly homoplastic (Appendix S9). On the other hand, *Lithophila muscoides* has true staminodes, which result from the reduction of the androecium to two or three functional stamens (Fig. 6; Eliasson 1988). This species was classified as an own genus based on this feature and its specific Caribbean habitat (Swartz 1788) but it is deeply nested within *Gomphrena*.

Overall phylogenetic relationships and diversification of the core C₄ *Gomphrena* clade

The extended taxon sampling based on plastid *matK-trnK* (Fig. 2) and nrITS (Fig. 3) sequence data revealed the same principal lineages of *Gomphrena* and allies as in the analysis of combined plastid markers (Fig. 1) but indicates that the majority of species of the more extensive taxon set belong to a large “mostly Andean clade” (Fig. 2, 3) that receives maximum statistical support in all analyses. In the 27-taxon set this clade is just represented by *G. haenkeana* (Fig. 1). The increased taxon sampling also reveals the *G. boliviana*–*G. martiana* clade, the high-Andean *G. meyeniana* clade and a more extensive central to south Andean *G. radiata*–*G. tomentosa* clade also comprising *G. umbellata* based on evidence from *matK-trnK* (Fig. 2) and nrITS (Fig. 3). Sequence data from *matK-trnK* alone show the *G. boliviana*–*G. martiana* clade in a tritomy with the other two before mentioned clades but like nrITS provide strong support for the monophyly of each of the three clades. *Gossypianthus* is part of this major lineage and may be the sister group to both the *Gomphrena radiata*–*G. tomentosa* clade and the *G. meyeniana* clade as depicted in the combined analyses of plastid data (1.0 PP, 98% MP-JK, 91% ML-BS).

Three further clades diverge after the lineage with *Gomphrena boliviana*, *G. meyeniana*, *G. radiata* and

relatives: one is the *G. pulchella*–*G. cardenasii* clade that consists of lowland species occurring in the Chaco (*G. pulchella*; Pedersen 1976), Cerrado (*G. agrestis*, *G. demissa*; Siqueira 1992). *Gomphrena lanigera* occurs in the Campo Rupestres in Brazil and reaches the eastern parts of Bolivia (Siqueira 1992; Borsch & al. 2015b), although ITS inconsistently depicts the latter species as sister to *G. celosioides* (the respective nodes are not well supported, Fig. 3). Furthermore, the Bolivian *G. cardenasii*, which is a small subshrub endemic to the Serrania de Chiquitos (eastern lowlands of Departamento La Paz) belongs here. *Gomphrena cardenasii* is a well-defined entity in terms of morphological characters and its samples appear on a long branch in the *matK-trnK* tree (Fig. 2). The other two major lineages within the core *Gomphrena* C₄ clade are the clade comprising all Australian species of *Gomphrena* plus *Philoxerus* and *Lithophila* (the *Philoxerus*+Australian *Gomphrena* clade) and *G. celosioides*, the specimens of which appear as a rather isolated clade (Fig. 2, 3). A sister group relationship of *G. celosioides* to *G. haenkeana* representing the mostly Andean clade is resolved in the analyses from the combined plastid dataset (Fig. 1), albeit with only weak support.

Trees inferred from plastid and nuclear partitions converge in depicting two sublineages (A and B) of a clade of mostly Andean species (Fig. 2, 3), both of which predominantly comprise perennial and annual species from dry valleys and Prepuna habitats (from 2500 to 4000 m a.s.l.) of the central Andes, with the exception of *Gomphrena perennis*, which is a morphologically variable species extending from the Chaco and Bosque Tucumano-Boliviano to the Andean dry valleys (Borsch & al. 2015b). *Gomphrena* cf. *nitida* from Oaxaca in Mexico appears in a relatively isolated position unresolved in a polytomy. However, further individuals representing the central American populations (Borsch 2001) need to be sampled to clarify if the morphologically allied plants from the region are closely related.

Our trees include samples of the annual *Gomphrena phaeotricha* from the South of Bolivia and the North of Argentina, depicted in sublineage A. The species was described by Pedersen (1976) based on differences in floral morphology in comparison to *G. pallida*. Our results agree with Pedersen (1976) by providing molecular evidence that *G. phaeotricha* and *G. pallida* are only distantly related, essentially belonging to two different sublineages A and B. However, the circumscription of both species in the sense of Pedersen (1976) and as currently accepted may not reflect natural entities. Pedersen recognized several infraspecific taxa in *G. pallida* to accommodate some of the morphological variation but at his time did not apply any evolutionary method. Further work is therefore underway on species limits in the mostly Andean clade (Ortuño & Borsch, unpubl. data). One other annual species was already described based on its deviant floral morphology (Ortuño & Borsch 2005), *G. mizqueensis* from dry valleys in the province of Mizque

(department of Cochabamba). The *matK-trnK* tree depicts it as closely related to samples of *G. pallida* within subclade B but also the perennial *G. fuscipellita*, a morphologically easily recognizable species described from rocky outcrops with herbaceous vegetation in the same area (Ortuño & Borsch 2005) but apparently extending to the Toro Toro National Park in northern Potosí (T. Ortuño, pers. obs.). Other perennials also belong to subclade B such as *G. oligocephala*, *G. bicolor* and *G. potosiana* according to both ITS and *matK-trnK* (Fig. 2, 3). On the other hand, subclade B comprises the perennials *G. perennis*, *G. trollii* and the annuals *G. haenkeana* and *G. ferruginea* alongside with *G. phaeotricha*. Our earlier hypothesis that the Andean annuals could represent a lineage that has adapted to survive the dry season with seeds as diaspores and then radiated in the inner Andean dry valleys (Ortuño & Borsch 2005) can thus not be fully accepted. The annual species of *Gomphrena* grow and flower in March and April after the rains (López 2003). Both Andean sublineages A and B comprise annuals and perennials, indicating multiple shifts in life forms, which in the case of *Gomphrena* could have occurred in conjunction with the origin of dry valleys, resulting in a strongly geographically governed pattern of diversity. The two Andean subclades of *Gomphrena* started to diversify about 2.6 Ma (0.7–7.1 and 0.2–5.0 95% HPD, respectively; Fig. 7, Appendix S10) and the annual lineages appear to be not much older than 1 Ma.

The *Gomphrena meyeniana* clades comprises plants growing at high altitudes that all possess a characteristic and unique morphology with leaves arranged in a rosette that arises from a reduced main axis, flower heads few to solitary on inflorescence axes arising from a stout, almost invisibly short stem, bracteoles without crest and stamens almost completely fused into a staminal tube lacking filament appendages Holzhammer (1955, 1956; see Fig. 4, 6). Our molecular phylogenetic data that depict the *G. meyeniana* clade as a highly supported lineage with a crown group diverging on a long stem (Fig. 2, 3) are in line with this. The latest treatment at species level is by Pedersen (1990), who only recognized *G. meyeniana* with several infraspecific taxa that reflect the morphological and ecological variation within the clade. Our results indicate significant phylogenetic diversity within the *G. meyeniana* clade but strongly diverging ITS ribotypes visible as polymorphic sites in our ITS pherograms within most individuals (Ortuño & Borsch pers. obs.) show that hybridization occurs within this clade that is likely to contribute to the phenotypic variation observed. Nevertheless, all ITS copies found within *G. meyeniana* and allies are clearly different from all other lineages of *Gomphrena*, underscoring that the role of reticulate patterns and incomplete lineage sorting needs to be analysed to delimit species within the clade but will not influence our view on the composition of the *G. meyeniana* clade.

The *Gomphrena radiata*–*G. umbellata*–*G. tomentosa* clade appears with maximum support in plastid and

nuclear trees (see Fig. 2, 3) and encompasses species adapted to dry habitats. Trees show two subclades, one of which includes all the *G. tomentosa* specimens, whereas the other subclade includes *G. umbellata* and *G. radiata*. The main morphological difference between these subclades is the life form present. *Gomphrena tomentosa* and close relatives are perennials (Fries 1920; Hunziker & Subils 1977), whereas *G. radiata* and *G. umbellata* are annuals (Pedersen 1976). *Gomphrena umbellata* is extremely adapted to sandy places at high elevations (2800 to 4400 m a.s.l.; Borsch & al. 2015b). Its leaves are reduced to the uppermost cauline leaves and the apical leaves subtending paracladia whereas the stems are under the sand. In all species of the *G. radiata*–*G. umbellata*–*G. tomentosa* clade the filaments are fused into a tube for their most part lacking lateral filament appendages (Fig. 6). Based on the absence of these appendages Fries (1920) proposed the “*Chnoanthus* group”, later formally described as a section by Holzhammer (1956). Fries (1920) hypothesized that *Gomphrena* comprises a series of species, where the filament appendages were reduced in steps during the evolution of the genus, and *G. tomentosa* appears at the end of this series. Although the evolution of lateral filament appendages is homoplastic (Fig. 6, Appendix S9), the section *Chnoanthus* appears as a natural group. Recently, Bena & al. (2017) generated *trnL-F* sequences of an individual of each *G. umbellata*, *G. radiata*, *G. cladotrichoides* and *G. mendocina*, the latter two of which are close relatives of *G. tomentosa*. They also recovered these four taxa in a clade, albeit without statistical support of any of the nodes.

All three before mentioned clades within *Gomphrena* diversified at higher elevations in the Andes (Fig. 7). The mostly Andean clade diverged around 8 Ma (4.0–13.6 95% HPD) from lowland ancestors whereas the crown group has an age of just 4.3 Ma (1.8–10.3 HPD). The *G. meyeniana* clade (stem group age 7.8 Ma; 2.9–13.5 HPD) and the *G. radiata*–*G. tomentosa* clade (stem group age 8.8 Ma; 3.5–15.8 HPD) must have colonized the rising Andes independently. Considering that the central Andes had only about half of its modern elevation by the late Miocene (Gregory-Wodzicki 2000; Garzzone & al. 2008; Jiménez & al. 2009) followed by a continuous uplift in the last 10 Ma to reach the modern elevation of the central Andean plateau of ~4 km further exceeded by the Eastern and Western Cordilleras, the dates estimated for the origin of the Andean clades of *Gomphrena* fit well to the geological history. Compared to the radiation of the Andean clade of *Lupinus* L. (*Fabaceae*) with a crown group age of about 1.5 Ma (Hughes & Eastwood 2006) the Andean diversification within *Gomphrena* started somewhat earlier (crown group ages of 2.6 Ma [0.7–7.1 and 0.2–5.0 95% HPD, respectively] for the Andean subclades A and B, and 2 Ma for the *G. meyeniana* clade). The youngest crown group within *Gomphrena* (*G. meyeniana* and allies) exclusively grows above 3000 m (up to 4700 m; Borsch & al. 2015b) whereas members of

Andean subclades A and B are often range-restricted in dry inner Andean valleys or at elevations >3000 m. This underscores the importance of valley systems with dry climates that originated as a consequence of the Andean uplift (Strecker & al. 2007) in particular in the Eastern Cordillera (Bolivia and northwestern Argentina) and probably fuelled reproductive isolation as well as adaptation to dry habitats. However, better resolved species trees and a more thorough understanding of species limits and their exact geographical distribution will be needed to further illuminate the diversification of *Gomphrena* in the Andes (e.g. testing if the morphologically variable and widespread *G. perennis* is in fact a single species). Nevertheless, *Gomphrena* is an interesting model to study plant diversification with the uplift of the Andes as it contains at least three independent ascents onto the Andes.

The *Philoxerus*+Australian *Gomphrena* clade comprises all sampled Australian species as well as *Lithophila* and *Philoxerus*, the latter two of which are plants adapted to coastal environments with fleshy leaves (Fig. 4). The species of *Lithophila* and *Philoxerus* appear morphologically similar but *Lithophila* differs in the reduced number of two stamens (Eliasson 1988, Fig. 6). The filaments of *Lithophila* and *Philoxerus* are united only basally, forming a cup, and lateral filament appendages are absent. To the contrary, the Australian species have morphologically variable filaments, some with lateral filament appendages (Townsend 1993). Some Australian species differ from the neotropical species by longer stigmas (Palmer 1998), but this variation will be analysed in more detail in a future study. Nevertheless, all the species of the *Philoxerus*+Australian *Gomphrena* clade share the main morphological characteristics of the core C₄ *Gomphrena* clade (Fig. 5, 6) so that it is proposed here to include the two genera into *Gomphrena*.

An Australian lineage derived recently from South American ancestors

The crown group of the Australian clade is of very recent origin (3.9 Ma, 1.3–8.6 95% HPD) as is the more inclusive clade comprising *Philoxerus* and *Lithophila* (crown group age of 5.7 Ma [2.0–12.4 95%], Fig. 7 and Appendix S10). Therefore, a Gondwanan vicariance hypothesis (Upchurch 2008; Barker & al. 2007a) for the origin of the Australian *Gomphrena* clade can be clearly rejected. Our results further show that this Australian clade is very deeply nested among South American and Caribbean ancestors, underscoring that long distance dispersal is the only plausible explanation for the origin of the Australian *Gomphrena* clade.

In Fig. 8 we present an overview on the global distribution of the core C₄ *Gomphrena* clade (pale yellow signature) as well as *Philoxerus* (dot map for each of the three currently accepted species). *Gomphrena* is not native in Africa (Townsend 1985) and therefore is not recorded for this continent although our two samples of *G.*

celosioides are of African origin (Fig. 2, 3). The possible first branch of the *Philoxerus*+Australian *Gomphrena* clade is *Lithophila* (Fig. 2, 3), which is endemic to all Caribbean islands (Acevedo-Rodríguez & Strong 2012; not illustrated), where it grows in limestone crevices at the coast. *Gomphrena* and *Philoxerus* do not occur in the southernmost part of South America, nor on Tasmania or New Zealand, indicating that a trans-Tasmanian dispersal route is very unlikely for *Gomphrena* and relatives. Sanmartín & al. (2007) inferred this as a frequent pattern, apparently facilitated by westward directed circumpolar currents, but more in temperate plant groups.

A striking result of this investigation is to find the Australian *Gomphrena* clade nested among species that inhabit coastal habitats. Their adaptations such as fleshy leaves, resistance to high concentrations of salt and adventitious roots allowing vegetative reproduction from broken off stems (Cordazzo 2007; Cordazzo & Seeliger 2003, T. Borsch pers. obs.) have apparently led to marine dispersal. *Philoxerus* (= *Blutaparon*) has reached the west coast of tropical Africa (see Fig. 8) but also the islands of Galapagos. *Blutaparon rigidum* is reported as a Galapagos endemic, which has some similarities to *Lithophila* in floral morphology (Eliasson 1990) but is a morphologically distinct plant with upright habit. However, it is only known from two historical collections and now extinct because it was covered by the eruption of the volcano on the island of Santiago (Eliasson 1971). But Galapagos harbours at least two other species of *Lithophila* (*L. radicata* Standl., *L. subscaposa* Hook. f.). And interestingly, other lineages of *Amaranthaceae* also reached Galapagos, so species of *Alternanthera*, which have a derived position among neotropical ancestors within this monophyletic genus (Sánchez-del Pino & al. 2012).

Based on the above, we hypothesize that *Philoxerus* (= *Blutaparon*) or *Lithophila*-like plants adapted to coastal environments were the ancestors of the Australian *Gomphrena*. They were dispersed to Australia across the Pacific Ocean through marine currents (Fig. 8, based on Kasang 2018) such as the North and South Equatorial current, which then leads over into the East Australian current and which were present since about 6 Ma. Interestingly, the dispersal of the ancestor of *Philoxerus wrightii* could be explained with the Kuroshio current (Fig. 8). Grehan (2001) reported Galapagos-Central-America-Caribbean tracks were also reported in other organisms such as isopods (*Nesophilosia*, *Troglophiloscia*), snakes (*Antillophis*) or beetles (*Ablechrus*) and even Galapagos-Australia tracks in angiosperms (*Nicotiana*), termites (*Insitermes*) and beetles (*Pitinus*). The latter dispersals may have occurred in the late Miocene, which roughly corresponds to the stem age of the *Philoxerus*+Australian *Gomphrena* clade dated 10 Ma (5.7–16.9 95% HPD). A detailed phylogeographic analysis as well as the inclusion of all available specimens of this clade into a well-resolved dated phylogeny will certainly further illuminate this scenario in the future.

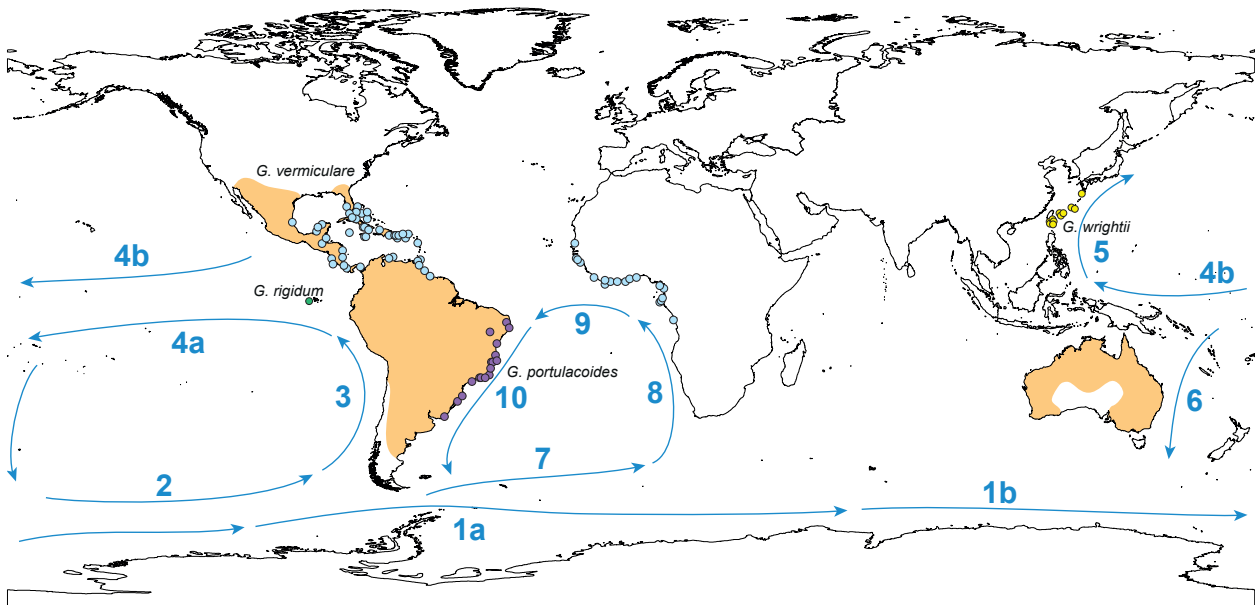


Fig. 8. Distribution of *Gomphrena* sensu stricto (the core C_4 *Gomphrena* clade including *Gossypianthus*, *Lithophila* and *Philoxerus* as well as *Gomphrena mollis* and *G. rupestris*) in the Americas and Australia. Only the native range is shown. Specimen records corresponding to the geographic occurrence of species so far classified as *Philoxerus* and now found to be part of *Gomphrena* are shown as dots. *Gomphrena vermiculare* is widespread along the coasts of the Caribbean islands and adjacent mainlands, as well as along the coast of tropical East Africa. *Gomphrena portulacoides* extends further south along the eastern coast of South America. Other species have reached the Galapagos Islands (*G. rigida*) as well as the islands extending from southern Japan to Taiwan (*G. wrightii*). This pattern can best be explained by long-distance dispersal through sea currents (Kasang 2018), which are therefore hypothesized to have transported a coast-adapted ancestor of the Australian *Gomphrena* lineage to Australia. The blue line shows the extension of major surface currents of the oceans that appear to be relevant in this context, such as the Antarctic circumpolar (1a/b), the South Pacific (2), the Humboldt (3), the South (4a) and North Equatorial (4b), the Kuroshio (5), the East Australian (6), the South Atlantic (7), the Benguela (8), part of the South Equatorial in the Atlantic (9) and the Brazil current (10).

C_4 evolution in *Gomphrena* and allies

Within the subfamily *Gomphrenoideae* the C_4 photosynthetic pathway was reported from a large number of species of *Gomphrena*, as well as from several members of *Alternanthera* and the genera *Blutaparion*, *Froelichia*, *Guilleminea*, *Lithophila* and *Tidestromia* (Sage & al. 2007). Our results show that the C_4 species of *Gomphrena* (Fig. 2, 3, 7) all belong to a single clade. The members of this core *Gomphrena* clade are characterized by metareticulate pollen where the tectum is reduced to a distal band (Borsch 1998; Fig. 7). On the other hand, most C_3 species of *Gomphrena* (e.g. *G. elegans*, *G. mandonii*) have pollen with closed tecta similar to *Pfaffia*. They are resolved in a distant lineage together with the C_3 genera *Hebanthe* and *Pfaffia* in both chloroplast and nrITS trees (Fig. 2, 3, 7 and Appendix S10). The only exception are the two C_3 species *G. mollis* and *G. rupestris* that belong to the core *Gomphrena* clade in which they share the morphology of pollen with reduced tecta (Ortuño & Borsch, unpubl. data).

Ancestral character state reconstruction using the chloroplast trees (Fig. 7 for *matK-trnK*; MCMC model; the same results are found with the 27-taxon set, not shown) indicates that C_4 photosynthesis arose in the common ancestor of the core *Gomphrena* clade plus *Froelichia* but reversed back to C_3 in the clade of *G. mollis* and

G. rupestris. Analyses under a ML model in BayesTraits slightly favour a reversal in the common ancestor of the core C_4 *Gomphrena* clade plus the *G. mollis*–*G. rupestris* clade and a regain of the C_4 syndrome by the ancestor of a core C_4 *Gomphrena* clade (Appendix S11). However, this would be a much more complicated scenario that therefore seems less probable. To the contrary, the ITS trees favour a single origin of C_4 photosynthesis in a common ancestor of the core C_4 *Gomphrena* clade plus the *Gomphrena prostrata*–*Guilleminea* clade (Appendix S12). The about ten species of the core C_4 *Gomphrena* clade, for which leaf anatomy has been investigated so far (Carolin 1978; Estelita-Teixeira & Handro 1984; Fank-de-Carvalho & al. 2015), show thick-walled parenchymatous bundle-sheath, and in most cases dimorphic chloroplasts corresponding to an NADP-ME subtype. Similar anatomy was also found in *Froelichia* (Carolin 1978) and *Guilleminea* (Filippa & Espinar 1993). This was called “*Gomphrena* type” (Carolin 1978; Kadereit & al. 2003), and considered to be present in all C_4 *Gomphrenoideae*. *Gomphrena prostrata* has thickened and lignified bundle sheath cell walls (Estelita-Teixeira & Handro 1984), but this may be rather seen as an adaptation to xeric environments like white sand habitats. Leaf anatomical characters seem therefore not informative indicating a sole in the whole subfamily, contrary to the strong differentiation of leaf anatomy in *Chenopodiaceae*

(Kadereit & al. 2003). It is nevertheless remarkable that a potential C₃ reversal coincides with a possibly reticulate origin of the respective reversed C₃ lineage (*G. mollis*–*G. rupestris* clade). An alternative explanation would there be a hybridization of a C₃ ancestor with an early branch of the *Gomphrena* C₄ lineage as a maternal parent, so we actually see a captured C₄-type chloroplast. Experimental hybrids of C₃ and C₄ species in *Atriplex* and *Flaveria* (see Kadereit & al. 2017 for review) rather showed differential segregation of different characters of photosynthesis types, leading to C₂-like offspring. Further biochemical and physiological analysis of *G. mollis* and *G. rupestris* would be needed to see if they differ from other C₃ *Gomphrenoideae*. Nevertheless, the $\delta^{13}\text{C}$ values of *G. mollis* and *G. rupestris* (Sage & al. 2007) are not different from those C₃ species.

Sage & al. (2007) mapped the taxonomic distribution of C₄ photosynthesis using a *matK-trnK* tree of the *Amaranthaceae* under parsimony and depicted three C₄ clades in subfamily *Gomphrenoideae*: (1) a clade of *Froelichia*–*Guilleminea*–*Blutaparon*–*Gomphrena* (species with distal tectal bands in their pollen grains), (2) a sublineage of *Alternanthera*, and (3) *Tidestromia*. The plesiomorphic condition in the monophyletic genus *Alternanthera* was later confirmed to be C₃ in a much more detailed study by Sánchez-del Pino & al. (2012) whereas C₄ was considered to be derived within their clade B3. This clade is represented in our dataset D by *A. microphylla* and *A. pungens*, which is congruently inferred as nested within *Alternanthera* in our analyses (Fig. 7, Appendices S11, S12). However, the position of C₄ *Tidestromia* is inconsistently shown as sister to *Pedersenian* (with ITS, Appendix S12), in a grade with *Alternanthera* and *Pedersenian* as successive sisters (with *matK-trnK*; Fig. 7) or as sister to *Alternanthera* (Sánchez-del Pino & al. 2009). This makes a precise dating of the age of *Tidestromia* as a C₄ lineage difficult, but otherwise does not change the picture of three independent C₄ origins in the *Gomphrenoideae* (Sage & al. 2007). Nevertheless, the early C₄ evolution of the *Gomphrena* clade is more complex as evidenced by the improved sampling in this investigation. *Amaranthaceae* s.str. like the chenopod lineages (Kadereit & al. 2012) therefore exhibits multiple gains and losses of C₄.

Recently, Bena & al. (2017) studied macroclimatic niche limits and C₄ evolution in *Gomphrenoideae*. The authors compiled available plastid sequences from GenBank (mostly from Müller & Borsch 2005; Borsch & al. 2012; Sage & al. 2007; Sánchez-del Pino & al. 2009, 2012) and added new *trnL-F* sequences from ten species. However, they did not obtain any significant statistical support on nodes within in the gomphrenoids (sensu Sánchez-del Pino & al. 2009) which may be explained by the patchy matrices, and also they did not sample relevant taxa like *Gomphrena mollis* or *G. rupestris*, thus limiting conclusions on the origin of C₄ in *Gomphrenoideae*. Nevertheless, the general conclusion of Bena & al. (2017) that C₄ *Gomphrenoideae*, unlike C₄ grasses, shift-

ed their niches into regions with colder winter climates is in line with the results presented here.

The age of the crown group of the speciose core *Gomphrena* C₄ clade plus *Froelichia* is inferred as 18 Ma (10.2–28.4 95% HPD; the stem diverged from C₃ *Xerosiphon* at 20.6 Ma [11.8–32.9 95% HPD]), and thus is slightly younger than the earliest inferred gain of C₄ in the crown group of *Salsoloideae/Camphorosmoideae* (Kadereit & al. 2012). The stem of the C₄ clade within *Alternanthera* originated at 18.5 Ma (7.8–33.7 95% HPD) and the C₄ genus *Tidestromia* diverged at 27.7 Ma (19.3–38.9 95% HPD). *Tidestromia* is very different morphologically to the other extant genera and C₄ photosynthesis might have evolved at some along the stem later (we have only included one of the 14 species here; and morphologically intermediate ancestors might now be extinct). Thus, we can therefore assume that C₄ originated in *Gomphrena* and other *Gomphrenoideae* in roughly the same time interval than in *Chenopodiaceae* s.str. subsequently to the drop of CO₂ concentrations at Eocene-Oligocene boundary (Christin & al. 2011; Kadereit & al. 2012). Nevertheless, the core *Gomphrena* clade stands out by being a C₄ clade that diversified at least twice into high elevation Andean environments. Species such as *G. umbellata* (3800–4400 m a.s.l.) and *G. meyeniana* (2600–4000 m a.s.l.) and allies probably constitute the highest populations of any C₄ plant, thereby being competitive in sub-arid as well as humid Puna vegetation.

Toward a phylogeny-based circumscription of *Gomphrena*

The genus *Gomphrena* has a complex taxonomic history. It was established by Linnaeus (1753) with *G. globosa* L. and *G. flava* L. [= *Alternanthera flava* (L.) Mears]. In later publications, Linnaeus added nine more species which now belong to four genera: *Gomphrena*, *Philoxerus*, *Froelichia* and *Alternanthera*. The type of the genus *Gomphrena* was chosen later as *G. globosa* with the typification effectively published by Hitchcock (Hitchcock & Green 1929). *Gomphrena globosa* is included in the molecular trees of Sánchez-del Pino & al. (2009) in a position that corresponds to the mostly Andean clade (Fig. 2, 3) and thus belongs to the core C₄ *Gomphrena* clade.

Martius (1826) then treated 57 species of *Gomphrena* with detailed descriptions and also described the genera *Pfaffia*, *Hebanthe* and *Serturnera*. Endlicher (1837) reduced these genera to sections of *Gomphrena*. This extended generic concept was largely followed by Moquin-Tandon (1849), who in addition recognized the section *Xerosiphon*, and also reduced the genera *Ninanga* and *Wadapus* described by Rafinesque (1837) to sectional level within *Gomphrena*. The currently used generic circumscription goes back to Seubert (1875) who excluded the sections *Hebanthe*, *Pfaffia* and *Serturnera* from *Gomphrena*. This was followed by Schinz (1893), Holzhammer (1955; 1956) and Townsend (1993), and confirmed

by more recent investigations using molecular and morphological characters (Borsch & Pedersen 1997; Müller & Borsch 2005; Sánchez-del Pino & al. 2009). The resurrection of *Xerosiphon* as an own genus contrary to its treatment as a section of *Gomphrena* since Seubert (1875) was proposed by Pedersen (1990), and is in line with results of this study as well as Müller & Borsch (2005) and Sánchez-del Pino & al. (2009). Siquera (1992) included *Pseudogomphrena* R. E. Fr. which has pollen and floral morphology similar to *Pfaffia* and therefore is probably distantly related to the *Gomphrena* clade (Eliasson 1988; Borsch 1998). The same applies to some other species currently included in *Gomphrena* with *Pfaffia*-type pollen (here represented by *G. mandonii*; see Fig. 1–3).

Generic concepts should be based on phylogenetic insights, rendering genera monophyletic, but there should also be morphological characters that allow to recognize genera. This investigation provides robust evidence from nuclear and plastid genomic compartments that *Lithophila*, *Philoxerus* and also *Gossypianthus* are derived within the core C₄ *Gomphrena* clade. As currently classified (Eliasson 1988; Townsend 1993; Hernández-Ledesma & al. 2015) they represent cases of segregate genera that show morphological adaptations to specific habitats. Morphological synapomorphies of the core C₄ *Gomphrena* clade including *Lithophila*, *Gossypianthus* and *Philoxerus* (see previous paragraphs) further underscore that the species of these three genera should in fact be classified within *Gomphrena*.

The situation in *Guilleminea* is different. The species of *Guilleminea* could represent a convergent origin of a procumbent habit in relation to *Gossypianthus* and the *Gomphrena radiata*–*G. tomentosa* clade. Whereas *Guilleminea* stands out by a perigynous flowers (Fig. 6, character 13; Eliasson 1988), its phylogenetic position and origin is not yet clear. This unique floral morphology historically always led authors to maintain *Guilleminea* at generic rank. *Guilleminea* could therefore (together with *G. prostrata*) be viewed as the earliest diverging branch in an even more widely circumscribed genus *Gomphrena* or maintained as an own genus. The latter would imply to find morphological characters that would support an inclusion of *G. prostrata* into *Guilleminea* or a generic status of *G. prostrata*. Our case of *Gomphrena* also exemplifies the stepwise progress in recognizing natural entities that can only be followed by a stepwise adjustment of classification systems to better reflect the natural history of the group (Borsch & al. 2015a). Based on the results of this investigation which consistently reveal the core *Gomphrena* clade as a distinct entity we propose to include *Blutaparon*, *Gossypianthus* and *Lithophila* into *Gomphrena* whereas any change of classification appears to be premature for *Guilleminea*.

The relationships of the Australian species of *Gomphrena* were debated since the early days of botanical systematics, even affecting the use of *Philoxerus* R. Br. and *Blutaparon* Raf. as generic names. Robert Brown (1810) created an own genus *Philoxerus* to accommodate *P. conicus*

and *P. diffusus*. Standley (1917) lectotypified the genus name with *P. conicus*, which is a species of sandy soils close to coasts in Australia. This was in line with Hooker (1880) who had defined *Philoxerus* as a genus of coastal plants from the Americas, Africa and Australia rather than using discrete morphological characters to support his genus concept. When Mears (1982 a, b) proposed to use the name *Blutaparon* for the American (and African) taxa, he neither had solid morphological nor phylogenetic evidence for the distinctness of these taxa that could have supported his view. Consequently, Hernández-Ledesma & al. (2015) pointed out that *Blutaparon* should be treated as a synonym of *Philoxerus*. The phylogenetic results now presented in this paper solve this long-standing debate. Our phylogenetic data also show that the only partially fused androecium used by Robert Brown to discriminate species of *Philoxerus* from the then known New World species of *Gomphrena* with a complete staminal tube and lateral stamen appendages, represents a character state that is homoplastic within the *Gomphrena* clade (Fig. 6).

Taxonomic treatment

In this section we provide a taxonomic backbone for the species formerly classified under the segregate genera *Gossypianthus*, *Lithophila* and *Philoxerus*, including a full synonymy and type information. We also extend the synonymy of the genus *Gomphrena* to reflect the inclusion of the segregate genera as proposed here. Where relevant, provisions of the *International Code of Nomenclature for algae, fungi, and plants* (Turland & al. 2018) are cited (e.g. “Art. 52.1”).

- Gomphrena* L.**, Sp. Pl. 1: 224. 1753 ≡ *Coluppa* Adans., Fam. Pl. 2: 268. 1763, nom. illeg. (Art. 52.1) ≡ *Xeraea* Kuntze, Revis. Gen. Pl. 2: 545. 1891, nom. illeg. (Art. 52.1). – Type (designated by Standley, N. Amer. Fl. 21: 147. 1917; affirmed by Hitchcock, Prop. Brit. Bot.: 137. 1929): *Gomphrena globosa* L.
 = *Lithophila* Sw., Prodr.: 1, 14. 1788, **syn. nov.** – Type: *Lithophila muscoides* Sw.
 = *Philoxerus* R. Br., Prodr. Fl. Nov. Holland.: 416. 1810 ≡ *Caraxeron* Vaill. ex Raf., Fl. Tellur. 3: 38. 1837, nom. illeg. (Art. 52.1), **syn. nov.** – Type (designated by Standley, N. Amer. Fl. 21: 168. 1917): *Philoxerus conicus* R. Br.
 = *Ninanga* Raf., Fl. Tellur. 3: 76. 1837. – Type: *Ninanga bicolor* Raf., nom. illeg. (Art. 52.1, ≡ *Gomphrena perennis* L.).
 = *Blutaparon* Raf., New Fl. 4: 45. 1838, **syn. nov.** – Type (designated by Mears in Taxon 31: 113. 1982): *Blutaparon repens* Raf., nom. illeg. (Art. 52.1, ≡ *Gomphrena vermicularis* L.).
 = *Gossypianthus* Hook. in Icon. Pl. 3: t. 251. 1840, **syn. nov.** – Type (designated by Swart, ING card 09817. 1959): *Gossypianthus rigidiflorus* Hook.

- = *Chnoanthus* Phil. in *Anales Univ. Chile* 21: 405. 1862. – Type: *Chnoanthus mendocinus* Phil.
 – *Wadapus* Raf., *Fl. Tellur.* 3: 77. 1837, nom. inval., nom. nud. (Art. 38.1(a)).

Gomphrena brittonii (Standl.) T. Ortuño & Borsch, **comb. nov.** ≡ *Gossypianthus brittonii* Standl. in *Contr. U.S. Natl. Herb.* 18: 92. 1916 ≡ *Guilleminea brittonii* (Standl.) Mears in *Sida* 3: 150. 1967. – Holotype: Cuba, Santa Clara, rocky hill in a palm plantation, Apr 1912, *Britton & Cowell 13318* (NY [NY00073684!]; isotypes: CAS [CAS0002838!], GH [GH00037093!], K [K000582943!], S [S-R-2461], TEX [TEX000370686!], US [00102746!], US [00102747!]).

= *Gossypianthus jackianus* Ekman & Suess. in *Repert. Spec. Nov. Regni Veg.* 35: 317. 1934. – Holotype: Cuba, Matanzas, Canasi, locis siccissimis, May 1923, *Ekman 16507* (S; isotypes: M [M-0009653!], NY).

= *Gossypianthus heterophyllus* Ekman & Suess. in *Repert. Spec. Nov. Regni Veg.* 35: 317. 1934 ≡ *Guilleminea brittonii* var. *heterophylla* (Ekman & Suess.) Mears in *Sida* 3: 150. 1967. – Holotype: Cuba, Matanza, Ponce, sterile Örtlichkeiten, *Ekman 17079* (S [S-R-2462!]; isotype: M [M0009654!]).

Gomphrena lanuparonychioides T. Ortuño & Borsch, **nom. nov.** ≡ *Paronychia lanuginosa* Poir. in *Lamarck & al., Encycl. Suppl.* 4: 303. 1816 [non *Gomphrena lanuginosa* Span. in *Linnaea* 15: 346. 1841] ≡ *Gossypianthus lanuginosus* (Poir.) Moq. in *Candolle, Prodr.* 13(2): 337. 1849 ≡ *Guilleminea lanuginosa* (Poir.) Hook. in *Bentham & Hooker, Gen. Pl.* 3: 37. 1880. – **Lectotype** (first step designated by Henrickson 1987: 319; **second step designated here**): Dominican Republic, *Poiteau s.n.* (P-JU [P00610545!]; isolectotypes: K [K000582944!], P [P00610546!], P [P00610547!]).

= *Gossypianthus rigidiflorus* Hook. in *Icon. Pl.* 3: t. 251. 1840 ≡ *Guilleminea lanuginosa* var. *rigidiflora* (Hook.) Mears in *Sida* 3: 149. 1967. – Lectotype: (designated by Henrickson in *Sida* 12: 319. 1987): United States, Texas, *Drummond 262* (K [K000848062!]; isolectotypes: G [00236996!], GH [00037091!], K [K000848063!], NY [00324513!], P [00610544!]).

= *Gossypianthus tenuiflorus* Hook. in *Icon. Pl.* 3: t. 251. 1840 ≡ *Guilleminea lanuginosa* var. *tenuiflora* (Hook.) Mears in *Sida* 3: 147. 1967 ≡ *Gossypianthus lanuginosus* var. *tenuiflorus* (Hook.) Henrickson in *Sida* 12: 321. 1987. – Lectotype (designated by Henrickson l.c.) or possibly holotype: United States, Texas, *Drummond 262* (K [possibly K000848061!]).

= *Gossypianthus lanuginosus* var. *sheldonii* Uline & W. L. Bray in *Bot. Gaz.* 20: 342. 1895 ≡ *Gossypianthus sheldonii* (Uline & W. L. Bray) Small, *Fl. S.E. U.S.*: 395, 1330. 1903 ≡ *Guilleminea lanuginosa* var. *sheldonii* (Uline & W. L. Bray) Mears in *Sida* 3: 149. 1967. – Holotype: United States, Oklahoma, (Indian Territory) near Cash (Cache) Creek, Jul 1891, *Sheldon*

170 (US [00102748]; isotype: US [00102749]).

– *Achyranthes piloselloides* Poit. ex Moq. in *Candolle, Prodr.* 13(2): 337. 1849, nom. inval., pro syn. (Art. 36.1(b)).

– *Celosia piloselloides* Poit. ex Moq. in *Candolle, Prodr.* 13(2): 337. 1849, nom. inval., pro syn. (Art. 36.1(b)).

Notes — The name *Gomphrena lanuginosa* Span. already exists and is a synonym of the accepted name *G. canescens* R. Br., an Australian species (Palmer 1998). Therefore, a new name had to be found. It is inspired by the habit and appearance of this species that indeed has some superficial similarity with species of *Paronychia* Mill. (*Caryophyllaceae*). Because the epithet “*paronychioides*” is also part of the accepted name of a widespread species of *Alternanthera*, which may appear in the same habitat, we maintained the word particle “*lanu*” (Greek, woolly) to make the new species name unique and at the same time connect to the meaning of the old epithet “*lanuginosa*”.

Although Henrickson (1987) cited a “holotype” at P, there may be no holotype because Poirer merely mentioned a specimen that he had seen in “herb. Desfont.” Because there are three specimens at P, all labelled as “isotype” by Mears, Henrickson’s citation of “holotype” is interpreted as a first-step lectotypification (Art. 9.17). Here we designate the second-step, in order to narrow down to a single specimen.

Gomphrena muscoides (Sw.) T. Ortuño & Borsch, **comb. nov.** ≡ *Lithophila muscoides* Sw., *Prodr.*: 14. 1788 ≡ *Iresine muscoides* (Sw.) Kuntze, *Revis. Gen. Pl.* 2: 542. 1891 ≡ *Alternanthera muscoides* (Sw.) Hitchc. in *Rep. (Annual) Missouri Bot. Gard.* 4: 122. 1893 [wrongly attributed to Benth. & Hook. f.]. – **Lectotype (designated here)**: United States, Navaza island, *Swartz s.n.* (S [S-R-3294!]; isolectotypes: BM [BM000993153!], LD [LD 1756579!]).

= *Achyranthes linearifolia* Sw. ex Wikstr. in *Kongl. Vetensk. Acad. Handl.* 1825: 428. 1826 ≡ *Lithophila muscoides* var. *linearifolia* (Sw. ex Wikstr.) Urb., *Symb. Antill.* 5: 338. 1907. – Holotype: Saint Barthelemy, *Forsström s.n.* (S [S-R-34!]).

= *Alternanthera caribaea* Moq. in *Candolle, Prodr.* 13(2): 354. 1849. – Holotype: Guadeloupe, 1839, *Beaupertuis s.n.* (P [P00622601!]; isotype: P [P00622602!]).

– *Illecebrum lineare* Thunb., *Diss. Mus. Acad. Uppsal.* 17(App.): 6. 1794, nom. inval., nom. nud. (Art. 38.1(a), confirmed to be a nomen nudum, no description or types mentioned).

– *Iresine linearis* Moq. in *Candolle, Prodr.* 13(2): 339. 1849, comb. inval. (Art. 41.5).

Gomphrena portulacoides (A. St.-Hil.) T. Ortuño & Borsch, **comb. nov.** ≡ *Philoxerus portulacoides* A. St.-Hil., *Voy. Distr. Diam.* 2: 436. 1833 ≡ *Iresine portulacoides* (A. St.-Hil.) Moq. in *Candolle, Prodr.* 13(2): 341. 1849 ≡ *Blutaparon portulacoides* (A. St.-Hil.) Mears in *Taxon* 31: 115. 1982. – Holotype: Brazil, Province

de Rio de Janeiro, bord de la mer près Rio de Janeiro, 1816–1821, *Saint-Hilaire* 304 [“Catal. A² N° 82”] (P [P00622606!]); isotype: P [P00622607!].

= *Philoxerus portulacoides* var. *commersonii* A. St.-Hil., Voy. Distr. Diam. 2: 436. 1833 ≡ *Iresine portulacoides* var. *commersonii* (A. St.-Hil.) Moq. in Candolle, Prodr. 13(2): 341. 1849 ≡ *Blutaparon portulacoides* var. *commersonii* (A. St.-Hil.) Mears in Taxon 31: 115. – Holotype: Uruguay, planta reptans in littorale [sic] arenosis freti & promontorii Montevideo, 1767, *Commerson s.n.* (P [P00622609!]; isotypes: P [P006226010!], P [P006226011!]).

= *Telanthera philoxeroides* var. *carnosa* Moq. in Candolle, Prodr. 13(2): 363. 1849 ≡ *Philoxerus carnosus* (Moq.) Benth. & Hook. f., Gen. Pl. 3: 40. 1880. – **Lectotype (designated here)**: Uruguay, “found on the sandy shores of the Island of Gorritá running to a great extent” [protologue: “in ins. Gorritá ad Plata”], *Tweedie* (K [K000583057!]).

Note — The sheet is annotated as the holotype by Mears (Nov 1980), although there are three Tweedie specimens in the Hooker herbarium with different barcodes mounted on the same sheet. They are from the Isla Gorritá (34°57'12.2"S, 54°58'19.2"W), probably originating from three different gatherings as the locality information given on the respective labels is different.

Gomphrena radicata (Hook. f.) T. Ortuño & Borsch, **comb. nov.** ≡ *Alternanthera radicata* Hook. f. in Trans. Linn. Soc. London 20: 262. 1847 ≡ *Lithophila radicata* (Hook. f.) Standl. in J. Wash. Acad. Sci. 5: 396. 1915. – Holotype: Ecuador, Galapagos, Chatham Island, *Darwin s.n.* (K [K000583052!]; isotype: CGE).

= *Alternanthera acaulis* Andersson, Galapagos Veg.: 164. 1854. – Holotype: Ecuador, Galapagos, Chatham Island, *Anderson s.n.* (S-R-219!; isotype: BR [0000005235810!]).

Note — There is further historical material of *A. acaulis* collected by N. J. Andersson from Galapagos under different numbers: no 64 in P [P00622604!] and no. 67 in C [C10005439!], LD [LD1567025!], M [M-0241868!] and MEL [MEL2458701!].

= *Alternanthera scirpoides* Hook. f. in Bentham & Hooker, Gen. Pl. 3: 39. 1880 ≡ *Lithophila scirpoides* (Hook. f.) Schinz in Engler & Harms, Nat. Pflanzenfam., ed. 2, 16c: 84. 1934. – Lectotype (designated by Turner in Ann. Bot. Fenn. 53: 288. 2016): Ecuador, Galapagos, Chatham Island, *Captain Wood s.n.* ([K000583050!]).

Gomphrena rigida (B. L. Rob. & Greenm.) T. Ortuño & Borsch, **comb. nov.** ≡ *Alternanthera rigida* B. L. Rob. & Greenm. in Amer. J. Sci. Arts 3: 143. 1895 ≡ *Achyranthes rigida* (B. L. Rob. & Greenm.) Standl. in J. Wash. Acad. Sci. 5: 74. 1915 ≡ *Lithophila rigida* (B. L. Rob. & Greenm.) Standl. in J. Wash. Acad. Sci. 5: 396. 1915 ≡

Philoxerus rigidus (B. L. Rob. & Greenm.) J. T. Howell in Proc. Calif. Acad. Sci., ser. 4, 21: 98. 1933 ≡ *Blutaparon rigidum* (B. L. Rob. & Greenm.) Mears in Taxon 31: 116. 1982. – Holotype: Ecuador, Galapagos Islands, James Bay Island, Orquilla Bay, 1891, *Baur* 387 (GH [GH00036970]).

Gomphrena subscaposa (Hook. f.) T. Ortuño & Borsch, **comb. nov.** ≡ *Alternanthera subscaposa* Hook. f. in Trans. Linn. Soc. London 20: 189. 1847 ≡ *Iresine subscaposa* (Hook. f.) Kuntze, Revis. Gen. Pl. 2: 542. 1891 ≡ *Lithophila subscaposa* (Hook. f.) Standl. in J. Wash. Acad. Sci. 5: 396. 1915. – Holotype: Ecuador, Galapagos Islands, Charles Island, *Darwin s.n.* (K [K00583053!]; isotype: M [M-0241869!]).

Gomphrena vermicularis L., Sp. Pl. 1: 224. 1753 ≡ *Illecebrum vermiculare* (L.) L., Sp. Pl., ed. 2, 2: 300. 1762 [‘vermiculatum’] ≡ *Philoxerus vermicularis* (L.) Sm. in Rees, Cycl. 27: *Philoxerus* no. 3. 1814 [‘vermiculatus’] ≡ *Achyranthes vermicularis* (L.) Elliott in Sketch Bot. S. Carolina 1: 310. 1817 ≡ *Caraxeron vermicularis* (L.) Raf., Fl. Tellur. 3: 38. 1837 ≡ *Blutaparon repens* Raf., New Fl. 4: 46. 1838, nom. illeg. (Art. 52.1) ≡ *Iresine vermicularis* (L.) Moq. in Candolle, Prodr. 13(2): 340. 1849 ≡ *Cruzeta vermicularis* (L.) M. Gómez in Anales Inst. Segunda Enseñ. 2: 312. 1896 ≡ *Lithophila vermicularis* (L.) Uline in Publ. Field Columbian Mus., Bot. Ser. 2: 39. 1900 [‘vermiculata’] ≡ *Blutaparon vermiculare* (L.) Mears in Taxon 31: 113. 1982. – Lectotype (designated by Iamónico & Sánchez-del Pino in Taxon 63: 404. 2014): [icon] “AMARANTHOIDES Corassavicum humile Cepeae folio. p. 15.” in Hermann, Parad. Bat.: unnumbered plate [7] after p. 18, 2 figures at bottom of plate. 1698.

= *Gomphrena aggregata* Willd., Enum. Pl.: 294. 1809 ≡ *Philoxerus aggregatus* (Willd.) Kunth in Humboldt & al., Nov. Gen. Sp. (quarto ed.) 2: 203. 1818 ≡ *Iresine aggregata* (Willd.) Moq. in Candolle, Prodr. 13(2): 340. 1849. – **Lectotype (designated here)**: Venezuela, in salsis maritimis prope Cumana, *Bonpland* 95 (P [P00136026!]).

= *Philoxerus crassifolius* Kunth in Humboldt & al., Nov. Gen. Sp. (quarto ed.) 2: 203. 1818 ≡ *Gomphrena crassifolia* (Kunth) Spreng., Syst. Veg. 1: 824. 1824 ≡ *Iresine crassifolia* (Kunth) Moq. in Candolle, Prodr. 13(2): 340. 1849 ≡ *Cruzeta crassifolia* (Kunth) M. Gómez in Anales Inst. Segunda Enseñ. 2: 312. 1896. – Type: Cuba, Habana, *Humboldt & Bonpland* (P [not located]).

= *Blutaparon breviflorum* Raf., New Fl. 4: 45. 1838. – Type: United States, Florida, *W. Baldwin* [not located, see Mears 1982].

= *Iresine surinamensis* Moq. in Candolle, Prodr. 13(2): 339. 1849. – Holotype: Surinam, Aquas ad urbem Paramaribo, *Kappeler* 1591 (P [P00622603!]; isotypes: S [S 07-12723!], U [U 0098697!]).

Note — *Iresine surinamensis* was synonymized with *Blutaparon vermiculare* var. *vermiculare* by Mears (1982). Moquin Tandon (1849) cited “A. Kappe-ler !” without any collecting number. The P material is wrongly annotated by Mears (1975 in sched.) as *Lithophila muscoides*. The P specimen is weak material and the protologue also mentions the 3-veined tepals but no description of the androecium.

= *Iresine vermicularis* var. *longispicata* Moq. in Candolle, Prodr. 13(2): 340. 1849 ≡ *Blutaparon vermiculare* var. *longispicatum* (Moq.) Mears in Taxon 31: 115. 1982. – Holotype: Brazil, Bahia, *Glocker 93* (P [P00622612!]).

= *Iresine vermicularis* var. *microcephala* Moq. in Candolle, Prodr. 13(2): 340. 1849. – Holotype: Brazil, Minas Gerais, *Saint-Hilaire 309* (P [P00622615!]; isotypes: P [P00622613!], P [P00622614!]).

= *Gomphrena albiflora* Moq. in Candolle, Prodr. 13(2): 392. 1849. – Holotype: Venezuela, Maracaybo, *Plee s.n.* (P [P00622647!]).

Note — Compared to other individuals of *Gomphrena vermiculare*, the plants called *G. albiflora* deviate by longer tepals and very narrow, linear cauline leaves. The species, in addition to *Blutaparon vermiculare*, was accepted by Medina & al. (2008), who illustrated plants from the Caribbean coast of Venezuela that are clearly halophytes with succulent leaves. It will therefore be important to include specimens corresponding to this entity into molecular phylogeographic analyses of *G. vermiculare* and relatives.

= *Philoxerus litoralis* Suess. in Repert. Spec. Nov. Regni Veg. 39: 13. 1935. – Holotype: Colombia, Goajira, *Daw 527* (K [K000583117!]; isotype: P [P00622646!]).

– *Philoxerus surinamensis* Miq. ex Moq. in Candolle, Prodr. 13(2): 339. 1849, nom. inval., pro syn. (Art. 36.1(b)).

– *Philoxerus maracaybensis* Klotzsch ex Benth. & Hook. f., Gen. Pl. 3: 40. 1880, nom. inval., nom. nud. (Art. 38.1(a)).

Note — Suessenguth annotated the specimen *Moritz 1016* in BM (BM000839401!) from Venezuela, Maracaybo, as “*Philoxerus maracaybensis* Suess.,” which was considered an isotype by Mears (in sched.). However, this name was never published by Suessenguth.

Gomphrena wrightii (Hook. f. ex Maxim.) T. Ortuño & Borsch, **comb. nov.** ≡ *Philoxerus wrightii* Hook. f. ex Maxim. in Bull. Acad. Imp. Sci. Saint-Petersbourg 31: 91. 1886. – **Lectotype (designated here)**: Japan, Loo Choo [Ryukyu] Islands, U.S. North Pacific Exploring Expedition under Commanders Ringgold and Rodgers, 1853–1856, *Wright 240* (K [K000848116!]; isolectotypes: GH [00037131!]; NY [00341966!]).

– *Philoxerus wrightii* Hook. f. in Bentham & Hooker, Gen. Pl. 3: 40. 1880, nom. inval., nom. nud. (Art. 38.1(a)).

– *Blutaparon wrightii* Mears in Taxon 31: 116. 1982, comb. inval. (Art. 41.5).

Notes — Turner (2016) pointed out that the name ascribed to Hooker (1880) in *Genera plantarum* was not validly published because the only and insufficient descriptive terms given are “species parvula”. A full description was later provided by Maximowicz (1886), who also validated the name. Apart from the revision by Mears (1982), the species was accepted in *Flora of Japan* (Ohwi 1965) and *Flora of China* (Bao & al. 2003). In GBIF (<https://doi.org/10.15468/39omei> – accessed 6 Apr 2020) there are 46 records spanning the Ōsumi-Shotō Islands, Ryukyu Islands, Nansei-Shotō, Okinawa-Islands to the south of Taiwan. The species does not occur in Australia (the three specimens in L are incorrectly attributed).

Acknowledgements

This investigation was carried out in partial fulfilment of a doctoral thesis of T.O.L. at Freie Universität Berlin. We thank the Dirección General de Biodiversidad, La Paz, Bolivia, for granting permits. We are grateful for the support of Stephan Beck, Rosa Isela Meneses (both La Paz), and of the Museo Nacional de Historia Nacional of Bolivia (MNHN). John Wood (Oxford) collected several relevant samples for the study. Vanessa Di Vincenzo (Berlin) provided support in illustrating the BEAST results with her R script. Nick Turland (Berlin) provided valuable insights regarding nomenclature and typification. The help of Bettina Giesicke, Kim Govers, Christine Grüber (all Berlin) during lab work is appreciated. We further appreciate the constructive comments of two anonymous reviewers. We acknowledge funding from Deutsche Forschungsgemeinschaft (BO1815/1-1 to T.B. and BO1815/1-4 to T.B. and T.O.L.).

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Willdenowia

Open-access online edition bioone.org/journals/willdenowia



Online ISSN 1868-6397 · Print ISSN 0511-9618 · 2019 Journal Impact Factor 0.887

Published by the Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin

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Appendix 1. Specimens used in phylogenetic analysis and reconstruction of ancestral character states including voucher information and EMBL/GenBank accession numbers for sequences. All sequences that were published in previous papers are cited with a superscript number corresponding to the respective source immediately after the accession number: ¹from Müller & Borsch 2005; ²from Sánchez-del Pino & al. 2009; ³from McCauley & Ballard 2007; ⁴from Borsch & al. 2011; ⁵from Sage & al. 2007; ⁶from Hammer & al. 2015; ⁷from Di Vincenzo & al. 2018; ⁸from Borsch & al. 2018. Ind. = Individual; for *matK-trnK* and ITS in several cases population samples with several individuals in the same gathering and corresponding to the same herbarium voucher were collected and in this case a letter is appended to the code, e.g. “AC1053b” (these are mentioned in Fig. 2 and 3). DB numbers refer to the corresponding accession at the DNA bank at the BGBM. In cases where material was taken from a herbarium specimen, the exact duplicate is indicated by underlining the herbarium code.

Code	Ind.	DB no.	Taxon name	Field/garden origin	Voucher	<i>rpl16</i>	<i>trnL-F</i>	<i>matK-trnK</i>	nr-ITS
AC0016		DB 35496	<i>Froelichia floridana</i> (Nutt.) Moq.	B.G. Bonn 03615-90	<i>Thiel s.n.</i> (BONN)	–	–	AY514799 ¹	LS452939 ⁸
			<i>Froelichia floridana</i> (Nutt.) Moq.	U.S.A.	<i>Fryxell 1847</i> (NY)	EF688680 ²	EF688751 ²	–	–
AC0461		DB 35941	<i>Gomphrena agrestis</i> Mart.	Brazil, MG de 7 km Itacambira	<i>Stannard, Oliveira, Kawasaki & Harley 36152</i> (B, K, LPB)	–	LR828663	LR828626	LR828552
AC0183		DB 35663	<i>Gomphrena bicolor</i> Mart.	Bolivia, Cochabamba	<i>Borsch & Ortuño 3558</i> (B, LPB)	–	–	LR828603	–
AC0453		DB 35933	<i>Gomphrena bicolor</i> Mart.	Bolivia, Cochabamba, Arani	<i>Borsch & Ortuño 3580</i> (B, LPB)	–	–	LR828622	LR828548
AC0454		DB 35934	<i>Gomphrena bicolor</i> Mart.	Bolivia, Cochabamba, Arani	<i>Borsch & Ortuño 3581</i> (B, LPB)	–	–	LR828623	LR828549
AC1053	b	DB 37264	<i>Gomphrena bicolor</i> Mart.	Bolivia	<i>Borsch, Ortuño & Fuentes 3961</i> (B, LPB)	–	–	LR828660	LR828587
AC0140		DB 35620	<i>Gomphrena boliviana</i> Moq.	Bolivia	<i>Borsch & Ortuño 3577</i> (B, LPB)	–	–	LR828599	LS452947 ⁸
			<i>Gomphrena boliviana</i> Moq.	Bolivia	<i>Fortunato & Adelqui 5526</i> (NY)	EF688683 ²	EF688754 ²	–	–
AC0998		DB 36476	<i>Gomphrena brachystylis</i> F. Muell. subsp. <i>brachystylis</i>	Australia, Timber Creek	<i>Evans 3118</i> (DNA, BRI, CANB, K, NSW)	–	–	LR828651	LR828578
AC0988		DB 36466	<i>Gomphrena canescens</i> subsp. <i>erythrina</i> J. Palmer	Australia, Fortescue Botanical District	<i>Short 4273</i> (AD, BRI, CANB, MEL, NSW, PERTH)	–	–	LR828650	LR828577
AC0460		DB 35940	<i>Gomphrena cardenasii</i> Standl. ex E. Holzh.	Bolivia, Santa Cruz, Chiquitos	<i>Wood 18813</i> (B, K, LPB)	–	–	LR828625	LR828551
AC1027		DB 36505	<i>Gomphrena cardenasii</i> Standl. ex E. Holzh.	Bolivia, Santa Cruz, Chiquitos	<i>Wood 20678</i> (B, LPB)	–	–	LR828655	LR828582
AC0932			<i>Gomphrena celosioides</i> Mart.	South Africa, Gauteng	<i>Müller 882</i> (B, PRE)	LT995243 ⁷	LT993038 ⁷	LT992585 ⁷	LT992985 ⁷
AC1095		DB 36573	<i>Gomphrena celosioides</i> Mart.	Ethiopia	<i>Wondafraash 2215</i> (B, ETH)	–	–	–	LR828588
AC1182		DB 36660	<i>Gomphrena celosioides</i> Mart.	Kenya	<i>Di Vincenzo, Kamau, Wondafraash, Mbale 317</i> (B, EA, ETH)	–	LR828671	LR828661	–
AC0893		DB 36371	<i>Gomphrena demissa</i> Mart.	Brazil, Bahia, Rio de Contas	<i>Harley 26991</i> (B, CEPEC, K, SPF)	–	–	–	LR828574
			<i>Gomphrena elegans</i> Mart.	Bolivia	<i>Nee 34257</i> (NY)	EF688684 ²	EF688755 ²	–	–

Code	Ind.	DB no.	Taxon name	Field/garden origin	Voucher	rpl16	tml-F	matK-trnK	nrITS
AC0444		DB 35924	<i>Gomphrena ferruginea</i> Pedersen	Argentina, Salta	<i>Borsch, Ortuño & López 3743</i> (B, LPB)	–	–	LR828617	LR828543
AC0446	b	DB 37173	<i>Gomphrena ferruginea</i> Pedersen var. <i>ferruginea</i>	Argentina	<i>Borsch, Ortuño & López 3751</i> (B, LPB)	–	–	LR828619	LR828545
AC0143		DB 35623	<i>Gomphrena ferruginea</i> var. <i>rustica</i> Pedersen	Bolivia, Tarija	<i>Borsch & Ortuño 3650</i> (B, LPB)	–	–	AM887524 ⁵	LR828526
AC0092		DB 35572	<i>Gomphrena flaccida</i> R. Br.	Australia	<i>Jacobs 8830</i> (NSW)	–	–	LR828596	LR828520
AC0095		DB 35575	<i>Gomphrena flaccida</i> R. Br.	Australia	<i>Jacobs 8776</i> (NSW)	–	–	LR828597	LR828521
AC0138		DB 35618	<i>Gomphrena flaccida</i> R. Br.	Australia	<i>Fryxell & al. 4748</i> (NY)	EF688685 ²	EF688756 ²	–	–
AC0138		DB 35618	<i>Gomphrena fuscipellita</i> T. Ortuño & Borsch	Australia	<i>Courtney 203</i> (PERTH)	–	–	–	KP875879 ⁶
AC0141		DB 35621	<i>Gomphrena haenkeana</i> Mart.	Bolivia	<i>Borsch & Ortuño 3594</i> (B, LPB)	–	–	AM887525 ⁵	LR828524
AC0141		DB 35621	<i>Gomphrena haenkeana</i> Mart.	Bolivia, Cochabamba, Tapacari	<i>Borsch & Ortuño 3572</i> (B, LPB)	–	–	LR828600	–
AC0487		DB 35967	<i>Gomphrena haenkeana</i> Mart.	Bolivia, Santa Cruz, Caballero	<i>Borsch & Ortuño 3627</i> (B, LPB)	–	–	LR828631	LR828558
AC1051	c	DB 37259	<i>Gomphrena haenkeana</i> Mart.	Bolivia, Cochabamba, Tapacari	<i>Borsch, Ortuño & Fuentes 3963</i> (B, LPB)	–	–	LR828658	LR828585
AC1029		DB 36507	<i>Gomphrena haenkeana</i> Mart.	Bolivia	<i>Nee & al. 52178</i> (NY)	EF688688 ²	EF688754 ²	–	–
AC1029		DB 36507	<i>Gomphrena kanisii</i> J. Palmer	Australia		–	–	–	KP875880 ⁶
AC0099		DB 35579	<i>Gomphrena lanigera</i> Pohl	Bolivia, Santa Cruz	<i>Wood 19964</i> (B, K, LPB)	LS451006 ⁸	LS453411 ⁸	LS451270 ⁸	LS452986 ⁸
AC0495		DB 35975	<i>Gomphrena mandonii</i> R. E. Fr.	Bolivia	<i>St Beck 18170</i> (B, LPB)	–	–	AY514801 ¹	LR828522
AC0495		DB 35975	<i>Gomphrena martiana</i> Mart.	Bolivia, Santa Cruz, Andrez Ibañez	<i>Borsch & Coimbra 3535</i> (B, LPB)	–	–	LR828636	LR828563
AC0913		DB 36391	<i>Gomphrena martiana</i> Mart.	Bolivia, Chuquisaca, Sud Cinti	<i>Fuentes 120</i> (B, LPB)	–	–	LR828648	LR828575
AC0436		DB 35916	<i>Gomphrena meyeniana</i> Walp.	Argentina, Jujuy, Yavi	<i>Borsch, Ortuño & López 3726</i> (B, LPB)	–	–	–	LR828537
AC0492		DB 35972	<i>Gomphrena meyeniana</i> Walp.	Bolivia, Tarija, Mendez	<i>Borsch & Ortuño 3663</i> (B, LPB)	–	–	LR828634	LR828561
AC0184		DB 35664	<i>Gomphrena meyeniana</i> var. <i>flaccida</i> Pedersen	Bolivia, Cochabamba, Tapacari	<i>Borsch & Ortuño 3561</i> (B, LPB)	–	–	LR828604	–
AC0786	b	DB 37215	<i>Gomphrena meyeniana</i> var. <i>flaccida</i> Pedersen	Bolivia, La Paz a Cochabamba, Japo	<i>Borsch & Ortuño 3955</i> (B, LPB)	–	–	LR828643	LR828569

Code	Ind.	DB no.	Taxon name	Field/garden origin	Voucher	rp116	trnL-F	matK-trnK	nrITS
AC0783	a	DB36261	<i>Gomphrena meyeniana</i> Walp. var. <i>meyeniana</i>	Bolivia, La Paz a Cochabamba, Japo	<i>Borsch & Ortuño 3952</i> (B, LPB)	LR828593	LR828667	-	-
AC0783	b	DB 37195	<i>Gomphrena meyeniana</i> Walp. var. <i>meyeniana</i>	Bolivia, La Paz a Cochabamba, Japo	<i>Borsch & Ortuño 3952</i> (B, LPB)	-	-	LR828640	-
AC0783	c	DB 37196	<i>Gomphrena meyeniana</i> Walp. var. <i>meyeniana</i>	Bolivia, La Paz a Cochabamba, Japo	<i>Borsch & Ortuño 3952</i> (B, LPB)	-	-	-	LR828566
AC0784	a	DB 36262	<i>Gomphrena meyeniana</i> Walp. var. <i>meyeniana</i>	Bolivia, La Paz a Cochabamba, Japo	<i>Borsch & Ortuño 3953</i> (B, LPB)	LR828594	LR828668	-	-
AC0784	c	DB 37200	<i>Gomphrena meyeniana</i> Walp. var. <i>meyeniana</i>	Bolivia, La Paz a Cochabamba, Japo	<i>Borsch & Ortuño 3953</i> (B, LPB)	-	-	LR828641	LR828567
AC0785	d	DB 37207	<i>Gomphrena meyeniana</i> Walp. var. <i>meyeniana</i>	Bolivia, La Paz a Cochabamba, Japo	<i>Borsch & Ortuño 3954</i> (B, LPB)	-	-	LR828642	-
AC0785	e	DB 37208	<i>Gomphrena meyeniana</i> Walp. var. <i>meyeniana</i>	Bolivia, La Paz a Cochabamba, Japo	<i>Borsch & Ortuño 3954</i> (B, LPB)	-	-	-	LR828568
AC0455		DB 35935	<i>Gomphrena mizqueensis</i> T. Ortuño & Borsch	Bolivia, Cochabamba	<i>Borsch & Ortuño 3584</i> (B, LPB)	-	-	LR828624	LR828550
AC0462		DB 35942	<i>Gomphrena mollis</i> Mart.	Brazil, Bahia, Paramirin	<i>Harley 27179</i> (B, K)	LR828590	LR828664	LR828627	LR828553
AC0463		DB 35943	<i>Gomphrena mollis</i> Mart.	Brazil, Bahia, Paramirin	<i>Harley 27021</i> (B, K)	-	-	LR828628	LR828554
AC0496		DB 35976	<i>Gomphrena nitida</i> Roth.	Mexico, Oaxaca	<i>Borsch & al. 3773</i> (B, MEXU)	-	-	LR828637	LR828564
AC0250	c	DB 37132	<i>Gomphrena oligocephala</i> J. Rémy	Bolivia, Chuquisaca, Yamparaez, Candelaria	<i>Borsch & Ortuño 3760</i> (B, LPB)	-	-	LR828606	LR828531
AC0432	b	DB 37153	<i>Gomphrena pallida</i> (Suess.) Pedersen	Bolivia, Potosí, Nor Chichas	<i>Borsch, Ortuño & López 3719</i> (B, LPB)	-	-	-	LR828534
AC0432	c	DB 37154	<i>Gomphrena pallida</i> (Suess.) Pedersen	Bolivia, Potosí, Nor Chichas	<i>Borsch, Ortuño & López 3719</i> (B, LPB)	-	-	LR828609	-
AC0435	b	DB 37158	<i>Gomphrena pallida</i> (Suess.) Pedersen	Bolivia, Potosí, Nor Chichas	<i>Borsch, Ortuño & López 3724</i> (B, LPB)	-	-	LR828611	LR828536
AC0449	i	DB 37194	<i>Gomphrena pallida</i> (Suess.) Pedersen	Bolivia, Potosí, Saavedra	<i>Borsch, Ortuño & López 3755</i> (B, LPB)	-	-	LR828621	LR828547
AC0788	b	DB 37229	<i>Gomphrena pallida</i> (Suess.) Pedersen	Bolivia, Sucre, Sorona	<i>Ortuño, López & Rios 1217</i> (B, LPB)	-	-	LR828645	LR828571
AC0142		DB 35622	<i>Gomphrena perennis</i> L.	Bolivia, Cochabamba, Mizque	<i>Borsch & Ortuño 3590</i> (B, LPB)	-	-	LR828525	-
AC0485		DB 35965	<i>Gomphrena perennis</i> L.	Bolivia, Cochabamba	<i>Borsch & Ortuño 3618</i> (B, LPB)	-	-	-	LR828557

Code	Ind.	DB no.	Taxon name	Field/garden origin	Voucher	rpl16	trnL-F	matK-trnK	nrITS
AC0494		DB 35974	<i>Gomphrena perennis</i> L.	Bolivia, Santa Cruz, Andrez Ibañez	Borsch & Ibsch 3529 (B, LPB)	-	-	LR828635	LR828562
AC0787	c	DB 37225	<i>Gomphrena perennis</i> L.	Bolivia, Sucre, Morochata	Ortuño, López & Ríos 1211 (B, LPB)	-	-	LR828644	LR828570
AC0790		DB 36268	<i>Gomphrena perennis</i> L.	Bolivia, Chuquisaca, Camargo	Ortuño, López & Ríos 1236 (B, LPB)	-	-	-	LR828573
AC0249	c	DB 37130	<i>Gomphrena potosiana</i> Suess. & Benl.	Bolivia, Potosí, T. Frias	Borsch & Ortuño 3716 (B, LPB)	-	-	LR828605	LR828530
AC0251	b	DB 37139	<i>Gomphrena potosiana</i> Suess. & Benl.	Bolivia, Potosí	Borsch & Ortuño 3672 (B, LPB)	-	-	LR828607	LR828532
AC0168		DB 35648	<i>Gomphrena</i> cf. <i>phaeotricha</i> Pedersen	Bolivia, Tarija	Borsch & Ortuño 3648 (B, LPB)	-	-	LR828602	LR828528
AC0489		DB 35969	<i>Gomphrena</i> cf. <i>phaeotricha</i> Pedersen	Bolivia, Tarija	Borsch & Ortuño 3647 (B, LPB)	-	-	LR828632	LR828559
AC0491		DB 35971	<i>Gomphrena</i> cf. <i>phaeotricha</i> Pedersen	Bolivia, Tarija	Borsch & Ortuño 3657 (B, LPB)	-	-	LR828633	LR828560
AC0441	b	DB 37169	<i>Gomphrena phaeotricha</i> Pedersen	Argentina, Salta	Borsch, Ortuño & López 3738 (B, LPB)	-	-	LR828615	-
AC0441	e	DB 37172	<i>Gomphrena phaeotricha</i> Pedersen	Argentina, Salta	Borsch, Ortuño & López 3738 (B, LPB)	-	-	-	LR828541
AC0465		DB 35945	<i>Gomphrena prostrata</i> Mart.	Brazil, Bahia, Agua Quente	Harley 26995 (B, K)	LR828592	LR828666	LR828630	LR828556
AC0007		DB 35487	<i>Gomphrena pulchella</i> A. St. Hil.	Paraguay	Zardini 45564 (B)	-	-	AY514802 ¹	-
AC0443		DB 35923	<i>Gomphrena pulchella</i> A. St. Hil.	Paraguay	Schinini & Dematteis 33318 (NY)	EF688689 ²	EF688760 ²	-	-
AC0445		DB 35925	<i>Gomphrena radiata</i> Pedersen	Argentina, Salta	Borsch, Ortuño & López 3740 (B, LPB)	-	-	LR828616	LR828542
AC0464		DB 35944	<i>Gomphrena rupestris</i> Nees	Brazil, Bahia	Borsch, Ortuño & López 3749 (B, LPB)	LR828589	LR828662	LR828618	LR828544
AC0167		DB 35647	<i>Gomphrena tomentosa</i> (Griseb.) R. E. Fries	Bolivia, Tarija	Harley 26990 (B, K)	LR828591	LR828665	LR828629	LR828555
AC0433		DB 35913	<i>Gomphrena tomentosa</i> (Griseb.) R. E. Fries	Bolivia, Potosí, Nor Chichas	Borsch, Ortuño & López 3722 (B, LPB)	-	-	LR828601	LR828527
AC0793		DB 36271	<i>Gomphrena tomentosa</i> (Griseb.) R. E. Fries	Bolivia, Sucre	Ortuño, López & Ríos 1235 (B, LPB)	-	-	LR828647	-

Code	Ind.	DB no.	Taxon name	Field/garden origin	Voucher	rpl16	trnL-F	matK-trnK	nrITS
AC1052		DB 36530	<i>Gomphrena tomentosa</i> (Griseb.) R. E. Fries	Bolivia, Potosí, Sud Chichas, Tupiza	Beck 33662 (B, LPB)	–	LR828670	LR828659	LR828586
AC0789	b	DB 37238	<i>Gomphrena trollii</i> Suess.	Bolivia, Potosí, Nor Chichas	Ortuño, López & Ríos 1255 (B, LPB)	–	–	LR828646	LR828572
AC0171		DB 35651	<i>Gomphrena umbellata</i> J. Rémy	Bolivia, Potosí	Wood 10741 (K, LPB)	–	–	–	LR828529
AC0437		DB 35917	<i>Gomphrena umbellata</i> J. Rémy	Argentina, Jujuy	Borsch, Ortuño & López 3727 (B, LPB)	–	–	LR828612	LR828538
AC1025		DB 36503	<i>Gomphrena umbellata</i> J. Rémy	Bolivia, Oruro, Jirira	Acho 2 (B, LPB)	–	–	LR828654	–
AC1050		DB 36528	<i>Gomphrena</i> spec. 2	Bolivia, Potosí, Charcas, Toro Toro	Wood 22662 (B, K, LPB)	–	–	LR828657	LR828584
AC1028		DB 36506	<i>Gomphrena</i> spec. 3	Bolivia, Chuquisaca, Cerro Chataquilla	Wood 22568 (B, K, LPB)	–	–	LR828656	LR828583
AC0252	d	DB 37148	<i>Gomphrena</i> spec. 4	Bolivia	Borsch & Ortuño 3766 (B, LPB)	–	–	LR828608	LR828533
AC1013		DB 36491	<i>Gomphrena</i> spec. 6	Bolivia, Potosí, Torotoro	Huaylla 3647 (B, LPB)	–	–	–	LR828580
AC1007	b	DB 37248	<i>Gomphrena</i> spec. 7	Bolivia, Potosí, Sud Chichas, Tupiza	Ortuño 1677 (B, LPB)	–	–	LR828652	–
AC1007	d	DB 37250	<i>Gomphrena</i> spec. 7	Bolivia, Potosí, Sud Chichas, Tupiza	Ortuño 1677 (B, LPB)	–	–	–	LR828579
AC0438		DB 35918	<i>Gomphrena</i> spec. 8	Argentina, Jujuy	Borsch, Ortuño & López 3731 (LPB)	–	–	LR828613	LR828539
AC0439	b	DB 37163	<i>Gomphrena</i> spec. 8	Argentina, Jujuy	Borsch, Ortuño & López 3733 (B, LPB)	–	–	LR828614	LR828540
AC0447	d	DB 37181	<i>Gomphrena</i> spec. 9	Argentina	Borsch, Ortuño & López 3753 (B, LPB)	–	–	LR828620	LR828546
AC1199		DB 36677	<i>Gossypianthus brittonii</i> Standl.	Cuba, Villa Clara	Castañeda (UCLV)	LT999993 ⁷	LT999882 ⁷	LT999994 ⁷	LT999992 ⁷
AC0051		DB 35531	<i>Guilleminea densa</i> (Willd.) Moq.	U.S.A., Texas	Borsch & al. 3437 (B, ISC)	–	–	AY514803 ¹	–
AC0931		DB 36409	<i>Guilleminea densa</i> (Willd.) Moq.	South Africa, Gauteng	Mitller 881 (B, PRE)	LR828595	LR828669	LR828649	LR828576
AC1214		DB 36692	<i>Guilleminea densa</i> (Willd.) Moq.	Ethiopia	Di Vincenzo & Hailu 180 (B, ETH)	LT992957 ⁷	LT993061 ⁷	LT992611 ⁷	LT993010 ⁷
			<i>Guilleminea densa</i> (Willd.) Moq.	Mexico	Flores Olvera & al. HF 02-24 (MEXU)	EF688764 ²	EF688693 ²	–	–
AC0365		DB 35845	<i>Guilleminea densa</i> (Willd.) Moq.	Mexico	McCauley 167 (BHO, MEXU)	–	–	–	AY173411 ³
			<i>Hebanthe grandiflora</i> (Hook.) Borsch & Pedersen	Mexico, Chiapas	Borsch & al. 3882 (B, MEXU)	–	–	–	LS452964 ⁸

Code	Ind.	DB no.	Taxon name	Field/garden origin	Voucher	rpl16	trnL-F	matK-trnK	nrlITS
AC0008	DB	35488	<i>Hebanthe occidentalis</i> (R. E. Fr.) Borsch & Pedersen	Paraguay	Zardini 45377 (B, MO)	-	-	AY514798 ¹	-
AC0677	DB	36157	<i>Hebanthe occidentalis</i> (R. E. Fr.) Borsch & Pedersen	Bolivia	Nee & Saldias 47054 (NY)	EF688679 ²	EF688748 ²	-	-
AC0154	DB	35634	<i>Lithophila muscooides</i> Sw.	Cuba	Greuter & al. 26915 (B, HAJB)	-	-	LR828639	LR828565
AC0105	DB	35585	<i>Lithophila muscooides</i> Sw.	Turks and Caicos Islands	Corell 43425 (NY)	EF688710 ²	EF688780 ²	-	-
AC1023	DB	36501	<i>Pedersenia volubilis</i> Borsch, T. Ortuño & Nee	Bolivia	Borsch & Coimbra 3537 (B, LPB)	LS450969 ⁸	LS453374 ⁸	FR870371 ⁴	LS452948 ⁸
AC1024	DB	36502	<i>Pjaffia fruticulosa</i> Suess.	Bolivia	Borsch 3522 (B, LPB)	-	-	AM887492 ¹	-
AC0053	DB	35533	<i>Pjaffia gnaphalioides</i> Mart.	Bolivia	Wood 22738 (B, LPB)	-	-	-	LS452985 ⁸
AC0674	DB	36154	<i>Pjaffia tuberosa</i> (Moq. ex DC) Hicken	Uruguay	Pedersen 1010 (NY)	EF688717 ²	EF688786 ²	-	-
AC0040	DB	35520	<i>Philoxerus portulacoides</i> A. St.-Hil.	U.S.A., Texas	Beck 33571 (B, LPB)	-	-	LR828653	LR828581
AC0101	DB	35581	<i>Philoxerus vermicularis</i> (L.) J. E. Sm.	Argentina	Borsch & al. 3444 (B, ISC)	-	-	AY514798 ¹	LR828519
AC0040	DB	35520	<i>Philoxerus vermicularis</i> (L.) J. E. Sm.	Cuba	Greuter & al. 26916 (B, HAJB)	-	-	LR828638	-
AC0101	DB	35581	<i>Philoxerus vermicularis</i> (L.) J. E. Sm.	Brazil	Liogier 34352 (NY)	EF688676 ²	EF688748 ²	-	-
AC0040	DB	35520	<i>Pseudoplantago friesii</i> Suess.	Argentina	Pedersen 15792 (C, CTES)	-	-	-	LR828518
AC0101	DB	35581	<i>Xerosiphon aphyllus</i> (Pohl ex Moq.) Pedersen	Brazil	Splett 701 (B)	-	-	LR828523	LR828598
AC0101	DB	35581	<i>Xerosiphon aphyllus</i> (Pohl ex Moq.) Pedersen	Brazil	Fonseca & al. 1303 (NY)	EF688729 ²	EF676100 ²	-	-

Appendix 2. List of morphological characters and their states

Habit and vegetative morphology (Characters 1–6)

1. Life cycle. Character 1

Annual herbs in *Gomphrena* and allies complete their life cycle in a single year and survive the dry season as seeds. Perennial herbs, subshrubs, shrubs, lianas or vines live for many years.

States: annual (0), perennial (1)

2. Type of root. Character 2

Annual herbs have a slender primary root with short lateral roots (such “simple” roots exist for example in *Gomphrena haenkeana* and *G. radiata*). Perennial herbs have taproots, with a strongly developed main root. Such taproots are often thickened as in *Guilleminea densa* (Henrickson 1987), *G. meyeniana* and *G. tomentosa*. Adventitious roots appear from the nodes of usually decumbent stems, different to the primary root system. They are present in the perennial herbs *Philoxerus portulacoides* and *P. vermicularis*.

States: simple root (0); taproot (1), taproot and adventitious roots (2)

3. Basal leaves. Character 3

Basal leaves clustered into a rosette growing at a reduced main axis are present in species of *Guilleminea*, *Gossypianthus* (Henrickson 1987) and also *Gomphrena meyeniana*. Pedersen (1990) described this character as “scapose flowering stem”. The basal leaves are bigger than the cauline leaves but otherwise similar.

States: absent (0), dense rosette in prostrate or decumbent plants (1), rosette with few leaves in erect plants (2)

4. Orientation of growth of stems. Character 4

Several modes of growth are present in the plants. They are procumbent, when the stems grow spreading on the ground for their lifetime; decumbent when stems initially spread on the ground but later grow upward. Upright stems are called “erect”. In the case of *G. meyeniana* the main axes appear to be condensed (coded as erect) and synflorescences are at the tip of decumbent to ascendant branches.

States: procumbent (0), decumbent (1), erect (2)

5. Vegetative branching system. Character 5

Species of *Gomphrena* and allies have different branching systems. In some of them erect stems are unbranched, although a plant can develop several stems from a rootstock. Unbranched stems are only present in perennial plants. But many annual and perennial species have stems branched from near the base.

States: only with unbranched principal stems (0), with secondary and tertiary stems (1)

6. Determinate vs. indeterminate growth of stems. Character 6

The term “determinate growth” is used in the sense to characterize the main axes as stem formed by an apical meristem. This meristem may abort after some period of functioning or it may transform into a specialized structure such as a flower or inflorescence, impeding its further extension capacity (Barthélémy & Caraglio 2007). Here “determinate” growth is understood to be present in those species of *Gomphrena* in which all stems (principal but also secondary or tertiary) terminate in inflorescences, such as in *G. flaccida*, *G. haenkeana* and *G. meyeniana*. In contrast, indefinite extension refers to an axis on which an apical meristem indefinitely maintains its growth potential (Barthélémy & Caraglio 2007). This is found in species with procumbent stems such as *G. tomentosa* or *Guilleminea densa*.

States: indeterminate (0), determinate (1)

Inflorescence morphology (Characters 7–10)

7. Shape of paracladia. Character 7

The flower unit in *Gomphrenoideae* is solitary with flowers subtended by one bract and two bracteoles. Considering that *Amaranthaceae* have a cymous inflorescence architecture, the partial florescences are reduced to a solitary flower in *Gomphrenoideae* (Borsch & Pedersen 1987; Acosta & al. 2009). These paracladia have been described as globose heads, subglobose or short to elongate capitate or glomerate spikes by some authors (Standley 1917; Eliasson 1988; Henrickson 1987; Borsch 2001). This includes lateral (co-florescences) and terminal (main florescences).

States: globose to subglobose with flowers densely adjacent (0), elongate to cylindrical with flowers not densely aggregated (1)

8. Arrangement of paracladia (synflorescence structure). Character 8

Gomphrena and other *Gomphrenoideae* exhibit very complex synflorescence structures, part of which were described by Borsch & Pedersen (1987) for the thyrsoid structures in *Hebanthe* and by Acosta & al. (2009) in their wider analysis of the *Amaranthaceae*. This character includes the arrangement of the paracladia (= partial florescences) and therefore, it defines the different structures of the branching system that is constituted by the axes bearing paracladia.

States: paracladia solitary and terminal on the main vegetative axes (0); paracladia solitary on main axes as well as on lateral branches (1); paracladia on the axes of one of the opposite cauline leaves, and in terminal parts of

major branches of the plant on elongated or very reduced axes appearing in one of the leaf axils (2); paracladia arranged on strongly condensed axes in a way that multiple paracladia appear in a terminal whorl-like structure with a terminal partial florescence surrounded by usually 5 (3–6) paracladia without visible axes (3); paracladium with a regular asymmetric arrangement arising from the axillary bud of a large cauline leaf and a very condensed branching structure with multiple branching orders and smaller paracladia arising from axillary buds of smaller cauline leaves that usually appear only on one side of the stem (4); 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 (5)

9. Apical leaves subtending paracladia. Character 9

In the case of synflorescences with condensed axes bearing partial florescences (paracladia; character 8 state 3), there may be specialized cauline leaves that subtend the paracladia. For these leaves that are morphologically deviant in shape and size but also often in indumentum and texture from the cauline leaves we propose the term “apical leaves subtending paracladia”. In the case of the pseudanthium in *Gomphrena*, the number of subtending apical leaves is reduced to one per paracladium (= partial florescence). Alternatively, leaves subtending partial florescences can be completely absent, so that partial florescences appear pedunculate.

States: absent (0), two oppositely arranged and unspecialized, similar to cauline leaves (1), broadened, (4–)5(–6) and stellately arranged in a whorl (2), 5–10, irregularly arranged, similar in texture to cauline leaves but very distinct through their narrower shape (3)

10. Cauline leaves supporting branches in synflorescence. Character 10

The paracladia may appear in a complex branching system (synflorescence) where the respective cauline leaf organs are not just reduced in size but considerably modified and differ from the other normal photosynthetic cauline leaves also in texture and anatomy (Acosta & al. 2009). With the presence of such scales, an inflorescence appears leafless.

States: cauline-like (0), membranous scales (1)

Photosynthesis (Character 11)

11. Photosynthesis of C₃ and C₄ type. Character 11

The photosynthesis type is here understood as a complex character syndrome corresponding to either C₃ with unspecialized anatomy or C₄ with visible specialized Kranz anatomy. The complex character syndrome also includes characteristic $\delta^{13}\text{C}$ values for C₃ and C₄ (following the broad assessment of *Amaranthaceae* by Sage & al. 2007).

States: C₃ photosynthesis (0), C₄ photosynthesis (1)

Floral morphology (Characters 12–13)

12. Morphology of sepals. Character 12

The morphology of the inner two sepals differ in shape, size and texture. The character is here defined as complex trait (composite coding; see Torres-Montúfar & al. 2018) with three states as further analysis will require detailed microscopic work that goes beyond the scope of this study.

States: all five tepals equal in shape and texture (0), inner two tepals distinctly smaller than the outer three, strongly compressed and carinate in fruit (1), inner two tepals smaller than the outer two but equal in texture (2)

13. Perigynous vs. hypogynous flowers. Character 13

In *Gomphrena* and most related genera flowers are hypogynous with sepals and androecium tube attached to the axis below the ovary. This feature is different in the species of *Guilleminea* where the androecium is adnate to the perianth and the flowers are perigynous (Mears 1967; Eliasson 1988).

States: perigynous (0), hypogynous (1)

Androecium (Characters 14–21)

The members of *Gomphrena* and related genera have five functional stamens, with the exception of *Lithophila*, which has two stamens (Eliasson 1988). The filaments are united only basally into a cup or to higher degrees into an elongate tube, with an usually small free portion of filaments (Eliasson 1988; Sánchez-del Pino & al. 2019). In some taxa, stamen tube appendages develop from the tubular meristem and then alternate with filaments. The free portion of the androecium tube can be a simple extension of the filament or possess lateral appendages on each side. The characters and states describe these qualitative features of the androecium and also the proportions.

14. Length of androecial tube. Character 14

Due to gradual variation five size classes for the length of the tube are distinguished. Measurements are from the connection to the floral axis (proximal) to the distal tip of the filament where it is connected to the anther.

States: 0.6–4.2mm (0), 4.3–5.9 mm (1), 6–7 mm (2), 8.1–10.2 mm (3), > 30 mm (4)

15. Fusion of androecial tube. Character 15

This character exhibits gradual variation and stands for the relation of the total size of the androecium as in character 14 to the free part measured from the deepest point between two stamens or between the stamen and the adjacent androecial tube appendage to the distal tip of the filament. Six ranks for the degree in percent of the free part are differentiated.

States: 0.6–6 (0), 7–30 (1), 31–50 (2), 51–60 (3), 61–75 (4), >75(5)

16. Shape of androecial tube. Character 16

States: broadly cup-shaped with distinctly spaced linear filaments (0), more or less broadly cup-shaped with V-shaped connection between gradually narrowing filaments (1), more or less broadly cup-shaped with U-shaped connection between more or less abruptly narrowing filaments (2), filaments broadly linear with narrowly U-shaped connection between filaments (3)

17. Androecial tube appendages. Character 17

The androecial tube appendages were called “pseudo-staminodia” and transitions to stamen appendages have been described (Townsend 1993). Considering that either such pseudostaminodia or stamen appendages on both sides of the filament were found, both were considered to represent modifications of one character (Townsend 1993; Eliasson 1988). Here we define the androecial tube appendages as an own character that is not homologous to lateral filament appendages following Vrijdaghs & al (2014) and Sánchez-del Pino & al. (2019).

States: absent (0), present (1)

18. Shape of androecial tube appendage. Character 18

States: broadly rounded to truncate (0), narrowly oblong and obtuse at apex (1), linear with cleft apex (2)

19. Filament appendages. Character 19

States: absent (0), present (1)

20. Length of filament appendages. Character 20

This is a quantitative character, for which four size classes are distinguished.

States: 0.1–0.2 mm (0), 0.3–0.5 mm (1), 0.6–1.0 mm (2), 1.1–1.5 mm (3)

21. Shape of filament appendages. Character 21

States: lanceolate-acuminate apex (0), lanceolate with rounded apex (1), falcate (2), narrowly acute (3)

Appendices S1–S12

The following Appendices are published electronically under Supplemental content online (see <https://doi.org/10.3372/wi.50.50301>).

Appendix S1. Sequence data of the *matK-trnK*, *rpl16*, *trnL-F* dataset A. Includes the multiple sequence alignment with hotspots annotated, the sequence matrix used for tree inference, the list of indels and the indel matrix.

Appendix S2. Sequence data of the *matK-trnK* dataset B-1. Includes the multiple sequence alignment with hotspots annotated, the sequence matrix used for tree inference, the list of indels and the indel matrix.

Appendix S3. Sequence data of the ITS dataset B-2. Includes the multiple sequence alignment with hotspots annotated, the sequence matrix used for tree inference, the list of indels and the indel matrix.

Appendix S4. Sequence data of the *matK-trnK* dataset C. Includes the multiple sequence alignment with hotspots annotated and the sequence matrix used for tree inference.

Appendix S5. Sequence data of the *matK-trnK* dataset D-1. Includes the multiple sequence alignment with hotspots annotated and the sequence matrix used for tree inference.

Appendix S6. Sequence data of the ITS dataset D-2. Includes the multiple sequence alignment with hotspots annotated and the sequence matrix used for tree inference.

Appendix S7. Matrix of morphological characters.

Appendix S8. Ancestral states of morphological characters 7 and 10 in *Gomphrena* and allies reconstructed over the 27-taxon tree (dataset A).

Appendix S9. Ancestral states of morphological characters 15, 18, 20 and 21 in *Gomphrena* and allies reconstructed over the 27-taxon tree (dataset A).

Appendix S10. Complete tree of the BEAST analysis based on the extended dataset C depicting node ages with confidence intervals of the *Amaranthaceae–Chenopodiaceae*, supplemented by a tree showing all nodes numbered through and a supplementary table with the precise ages and HPDs of these nodes.

Appendix S11. Ancestral states of C₃ and C₄ photosynthesis (character 11) in the extended *matK-trnK* dataset (dataset D) as inferred using BayesTraits under an MCMC model and an ML model.

Appendix S12. Ancestral states of C₃ and C₄ photosynthesis (character 11) using the extended nrITS dataset (dataset D) as inferred using BayesTraits under an MCMC model and an ML model.