Systematics and evolution of *Gomphrena* (Amaranthaceae) *w*ith an emphasis on the species in Bolivia

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Extinction is the rule. Survival is the exception

Carl Sagan

To my beloved family

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Summary

The dissertation investigates *Gomphrena* L. and allied genera with morphological and molecular data in order to test the phylogenetic relationships and to better understand the evolutionary history of this linage. An emphasis is on the actual *Gomphrena* clade and as well the diversity in Bolivia. *Gomphrena* (Gomphrenoideae) is the largest genus of the Amaranthaceae with an estimated number of 120 species. The areas of main diversity of this genus comprise South America with about two thirds of the species, Central and North America (about 15%), and Australia (about 20%). This genus largely grows in tropical climates. Some of the species are used as medicinal plants, and a few are cultivated as ornamental plants exhibiting attractive pigmentation in their tepals.

The first chapter presents the state of knowledge and a general introduction into *Gomphrena*. It is important to note that previous molecular phylogenetic studies revealed that *Gomphrena* in the widely used circumscription of Schinz (1934) is a polyphyletic group. These past studies included only few species of *Gomphrena* and distinguished two main clades. The first clade includes the type species of the genus, *G. globosa* L., and certain Australian and American species, plus the allied genera *Gossypianthus* Hook., *Lithophila* Sw., and *Philoxerus* R.Br. (= *Blutaparon* Raf.) with not fully understood relationships. This group of *Gomphrena* s. str. is here called "*Gomphrena* clade" whereas the second group that includes *G. elegans* Mart., *G. mandonii* R.E.Fr. and others is part of a lineage called *Pfaffia* clade (not studied here). In addition, the first chapter presents the complex taxonomic history of *Gomphrena*.

The second chapter focuses on the morphological characteristics of the *Gomphrena* clade. As a result 22 vegetative and floral morphological characters were defined with their respective states and assessed for 27 representative samples. The photosynthesis type (absence or presence of C_4 photosynthesis) was coded in the form of a single trait including morpho-anatomical characteristics.

For chapter three a combined data set of chloroplast sequences (*matK-trnK* + *trnL-F* + *rpl16*) of the *Gomphrena* clade (including the allied segregate genera) and outgroups from Gomphrenoideae was analyzed with parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI) methods. The 22 morphological characters were optimized on the Bayesian Maximum clade credibility tree using Bayes Traits. The results show that most vegetative characters including the annual life form have evolved multiple times, whereas some floral character states were identified as synapomorphies. An important result reveals that many of the nine characters defined for the androecium, most of which were used historically for the pre-phylogenetic delimitation of *Gomphrena* and other genera, appear homoplastic. The presence of a fused stamen tube without stamen tube appendages (but with lateral filament appendages in some species) is confined to the Gomphrenoid clade (*Gomphrena* clade plus *Froelichia,*

Xerosiphon, and the *Pfaffia* clade) whereas the Alternantheroid clade (here represented by *Pedersenia*) differs by the presence of stamen tube appendages. The important character is the difference between inner and outer tepals showing that all members of the newly found core C_4 *Gomphrena* clade have a difference in the size of the two inner tepals. To the contrary, all other species present five tepals of similar size. Another interesting result is the detection of pseudanthia, acting as a visual attractant for pollinators. The pseudanthial leaves are typical for a "Mostly Andean clade". But pseudanthial leaves also were derived two more times independently in *G. boliviana* and allies and *G. meyeniana* and allied.

The combined plastid tree also shows with high support that the species of *Philoxerus, Lithophila* and *Gossypianthus* are nested within the core C_4 *Gomphrena* clade. For this reason, it is proposed here to include the three genera into *Gomphrena* and a respective treatment is provided.

The extended taxon sampling for *matK-trnK* (80 samples) and nrITS (82 samples) show that most of the major lineages are congruently resolved between plastid and nuclear data with one exception in the early branching *G. mollis - rupestris* clade (that is C3). It is sister to all C_4 species of *Gomphrena* in the nrITS tree whereas it appears as a second branch after the *G. prostrata - Guilleminea* clade in all plastid trees. Ancestral character state reconstruction shows that C_4 photosynthesis arose in the common ancestor of the *Gomphrena* clade plus *Froelichia* but reversed back to C_3 in the lineage of *G. mollis* and *G. rupestris*.

The age of the crown group of the core C_4 *Gomphrena* clade plus *Froelichia* is inferred as 18 Ma (10.2-28.4, 95% HPD), which corresponds to the mid-Miocene climatic optimum (c. 18-16 Ma) when an increase in temperature and aridity and later drop in concentrations of CO_2 occurred. This result is also consistent with the emergence of C_4 photosynthesis in Chenopodiaceae and Poaceae. The core *Gomphrena* clade stands out by being a C_4 clade that diversified at least twice into high elevation Andean environments. Species such as *G. fuscipellita* (growing at elevations of 3600-4300 m) and *G. meyeniana* Walp. (3200-4700 m) constitute at the moment the highest populations of any herb C_4.

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. 95% HPD). The majority of the species from the inter Andean dry valleys, Prepuna and Puna ecoregions in the extensively sampled *matK-trnK* and ITS trees are included in two major subclades of the "Mostly Andean clade". The molecular time divergence estimate concurs with the maximum Andean mountain upheaval that occurred at 5 Ma, which created new habitats through the geomorphological and climatic modifications. The dry climates led to the recent and multiple evolution of annual species such as *G. phaeotricha*, *G. pallida* or *G. umbellata*.

The sister of the Mostly Andean clade is the Australian clade., The results of this thesis (chapter 3) show with high support that the disjunctly distributed Australian species are closely related to the coastal species of *Lithophila* and *Philoxerus*. The latter is distributed on the Pacific coast of central America includes morphologically similar species that are endemics on the Galapagos islands. the same applies to *Lithophila* with one widely distributed Caribbean species and Galapagos endemics. The species of *Lithophila* and *Philoxerus* present adaptations to live in high concentrations of salt such as fleshy leaves, adventitious roots allowing vegetative reproduction from broken-off stems. The current distribution of *Philoxerus vermicularis* is restricted to the west coast of tropical Africa, and the species has not further extended into Africa, which decreases the possibilities for dispersal between Africa and Australia. The stem age of the clade comprising *Lithophila*, *Philoxerus* and the Australian *Gomphrena spp.* 10 Ma (5.7-16.9 95 % HPD). This confirms that the disjunction occurred recently so that Gondwanan vicariance is not possible a tectonic. It is therefore hypothesized that the dispersal to Australia involved long distance dispersal (LDD). Ancestors of *Lithophila* or *Philoxerus* -like plants came across the Pacific Ocean, perhaps even from Galapagos that acted as a stepping stone through marine currents such as the South Ecuatorial Current, which then leads over into the East Australian current and which were present since about 6 Ma.

The chapter four provides a taxonomic treatment for the species of the core C_4 *Gomphrena* clade in Bolivia, including keys for identification detailed morphological descriptions and distribution maps. In the introductory part to this chapter dot distribution maps are presented, which are layed over by maps with environmental data in order to better standardize the habitat types of the species for the descriptions of their respective ecology. The results are based on extensive field and herbarium studies and now recognize 30 species of core *Gomphrena* in Bolivia, which is an increase in eight over the state of knowledge in the Catálogo de Plantas Vasculares de Bolivia that was published in 2014 with 22 species of core *Gomphrena*. These eight species represent discoveries new to science.

Zusammenfassung

Diese Dissertation untersucht *Gomphrena* L. und verwandte Gattungen mit morphologischen und molekularen Merkmalen, um die phylogenetischen Beziehungen zu rekonstruieren und um die Evolutionssgeschichte dieser Pflanzengruppe besser zu verstehen. Der Schwerpunkt liegt bei dem eigentlichen *Gomphrena* Clade und bei der Artenvielfalt in Bolivien. *Gomphrena* (Gomphrenoideae) ist die größte Gattung der Amaranthaceae mit geschätzt rund 120 Arten. Das Hauptverbreitungsgebiet der Gattung liegt in Südamerika mit ca. zwei Drittel der Arten, Zentral- und Nordamerika beherbergen ca. 15% und Australien ungefähr 20% der Arten. Die Gattung kommt vor allem in tropischen Klimagebieten vor. Einige der Arten sind Medizinalpflanzen, und ganz wenige werden als Zierpflanzen wegen der attraktiven Pigmentation ihrer Tepalen angepflanzt.

Das erste Kapitel beleuchtet den gegenwärtigen Kenntnisstand und gibt eine allgemeine Einführung zu *Gomphrena*. Es ist interessant zu vermerken, dass vorangegangene molekular-phylogenetische Untersuchungen zeigen, dass *Gomphrena* in der weitläufig benutzten Umschreibung von Schinz (1934), eine polyphyletische Gruppe ist. Die vor dieser Arbeit vorliegenden Untersuchungen beinhalten nur wenige *Gomphrena* Arten und unterscheiden zwei Haupt- Clades. Der erste Clade umfasst die Typusart der Gattung, *G. globosa* L., und bestimmte australische und amerikanische Arten, sowie die Gattungen *Gossypianthus* Hook., *Lithophila* Sw. und *Philoxerus* R.Br. (= *Blutaparon* Raf.) mit unklaren, nicht vollständig verstandenen verwandtschaftlichen Beziehungen. Diese Gruppe von *Gomphrena* im engeren Sinne wird hier "*Gomphrena* clade" genannt und ist Thema der Dissertation. Demgegenüber ist die zweite Gruppe mit *G. elegans* Mart., *G. mandonii* R.E. Fr. und weiteren Arten Teil eines *Pfaffia* Clade (nicht hier untersucht). Zusätzlich beinhaltet das erste Kapitel eine Darstellung der komplexen taxonomischen Geschichte von *Gomphrena*.

Das zweite Kapitel konzentriert sich auf die morphologischen Charakteristika des *Gomphrena* Clades. Als Ergebnis werden 22 vegetative und blütenmorphologische Merkmale mit ihren entsprechenden Merkmalsausprägungen definiert und für 27 repräsentative Samples erhoben. Der Photosynthese Typ (Fehlen oder Vorhandensein von C_4 Photosynthese) wurde in Form eines einzigen Traits kodiert, der die morphologisch-anatomischen Merkmale einschließt.

Für Kapitel drei wurde ein kombinierter Datensatz der Chloroplasten Sequencen (*matK-trnK* + *trnL-F* + *rpl16*) des *Gomphrena* Clades (inklusive der Segregatgattungen) sowie Aussengruppen der Gomphrenoideae analysiert mit den Baumrekonstruktions-Methoden Maximum Parsimonie (MP), Maximum Likelihood (ML) und Bayesian inference (BI)". Die Evolution der 22 morphologischen Merkmale wurde mittels des Bayesian Maximum Clade Credibility Baumes unter Verwendung von Bayes Traits rekonstruiert. Die Ergebnisse belegen, dass die meisten vegetativen Merkmale, inklusive die annuelle Lebensform, sich mehrfach entwickelten.

Demgegenüber zeigten einige Blütenmorphologische Merkmale Synapomorphien. Ein wichtiges Ergebnis ist, dass viele der neun blütenmorphologischen Merkmale, die für das Androecium kodiert wurden, und die historisch gesehen für die prä-phylogenetische Abgrenzung von *Gomphrena* und anderen Gattungen benutzt wurden, homoplastisch sind. Das Auftreten von einer fast komplett fusionierten Filamentröhre ohne Filamentröhren-Anhängsel (aber mit lateralen Filamentanhängseln bei einigen Arten) ist begrenzt auf den Gomphrenoid Clade (*Gomphrena* Clade plus *Froelichia, Xerosiphon*) und den *Pfaffia* Clade. Hingegen unterscheidet sich der Alternantheroid clade (hier repräsentiert durch *Pedersenia*) durch das Vorhandensein von Filamentröhren Anhängsel. Ein wichtiges Merkmal ist die Verschiedenartigkeit von inneren und äußeren Tepalen, für das sich zeigte, dass es alle Mitglieder des neu gefundenen Kern C_4 *Gomphrena* Clades aufweisen. Im Unterschied dazu haben alle anderen Arten fünf Tepalen ähnlicher Größe. Ein weiteres interessantes Ergebnis ist, dass zum ersten Mal Pseudanthien beschrieben werden, die als visuelle Anziehungselemente für die Bestäuber dienen. Die Pseudanthien sind typisch für einen "Mostly Andean clade". Aber Pseudanthien entstanden noch zwei weitere Male, unabhängig in *G. boliviana* und Verwandten und in *G. meyeniana* und Verwandten. Der kombinierte Plastiden-Baum zeigt mit hoher statistischer Stützung der relevanten Knoten, dass die Arten von *Gossypianthus, Lithophila und Philoxerus* innerhalb des Kern-C_4 *Gomphrena* Clades stehen. Aus diesem Grund wird vorgeschlagen, die drei Gattungen in *Gomphrena* zu integrieren; eine entsprechende taxonomische Bearbeitung wird vorgelegt.

Der Bäume mit dem umfangreicheren Taxon-Sampling für *matK-trnK* (80 Proben) und nrITS (82 Proben) zeigen, dass die meisten Evolutionslinien kongruent basierend auf den Plastiden und Kern-Sequenz Daten gefunden werden. Eine Ausnahme ist der früh abzweigende *Gomphrena mollis – G. rupestris* Clade (mit C_3 Photosynthese). Dieser ist eine Schwestergruppe von allen C_4 Arten von *Gomphrena* im nrITS-Baum, während er als zweiter Ast nach dem *Gomphrena prostrata – Guilleminea-* Clade in allen Plastiden-Bäumen erscheint. Die Rekonstruktion der Merkmalsevolution zeigt, dass C_4 Photosynthese im gemeinsamen Vorfahren des *Gomphrena* Clade plus *Froelichia* entstand, aber in der Linie von *G. mollis* und *G. rupestris* zu C_3 revertiert ist.

Das Alter der Kronengruppe des Kern-C4 *Gomphrena* Clade plus *Froelichia* wird mit Hilfe einer molekularen Uhr auf 18 Ma (10.2-28.4, 95% HPD) eingeschätzt. Dies entspricht dem klimatischen Optimum des Mittleren Miozän (c. 18-16 Ma), als eine Zunahme der Temperatur und Trockenheit passierte, später gefolgt von einer Absenkung der CO_2 Konzentrationen. Dieser Zeitraum stimmt mit dem der Enstehung von C_4 Photosynthese bei Chenopodiaceen und Poaceen überein. Der Kern-*Gomphrena* Clade erweist sich als C4 Clade, der zumindest zweimal in hoch andinen Lebensräumen diversifizierte. Arten wie *G. fuscipellita* Ortuño & Borsch (wächst auf Höhen über dem Meeresspiegel zwischen 3600 und 4300 m) und *G. meyeniana* Walp. (3200-4700 m) gelten gegenwärtig als die am höchsten vorkommenden Populationen jeglicher C_4 Pflanzen.

Der “Mostly Andean Clade” divergierte um 8 Ma (4.0-13.6, 95 % HPD) von Tiefland-Vorfahren, hingegen hat die Kronen Gruppe ein Alter von gerade einmal 4.3 Ma (1.8-10.3. 95% HPD). Die Mehrheit der Arten aus den interandinen Trockentälern gehören zu zwei größeren Subcladen des “Mostly Andean clade”. Die Ergebnisse der Altersberechnung mittels der molekularen Uhr zeigt, dass deren Differnzierung zeitrlich mit der maximalen Auffaltung der Anden zusammen fällt, die vor 5 Ma durch die geomorphologischen und klimatischen Modifikationen neue Habitate entstehen ließ. Das trockene Klima führte zu der mehrfachen Entwicklung von annuellen Arten wie *G. phaeotricha, G. pallida* und *G. umbellata*.

Die Schwestergruppe des “Mostly Andean clade” ist der Australische Clade mit *Lithophila* und *Philoxerus*. Die Ergebnisse dieser Doktorarbeit (Kapitel 3) zeigen mit hoher Signifikanz, dass die disjunkt verbreiteten australischen Arten nahe verwandt sind mit den Küstenarten *Lithophila* und *Philoxerus*. Letztere ist verbreitet an den Küsten des Pazifiks auf der Höhe von Mittelamerika, sowie der Karibik. Philoxerus umfasst außerdem morphologisch ähnliche Arten die endemisch auf den Galapagos Inseln sind. Das Gleiche gilt für *Lithophila* mit einer weit verbreiteten karibischen Art und Endemiten auf Galapagos. Die Arten von *Lithophila* und *Philoxerus* zeigen Anpassungen für das Leben bei hohen Salzkonzentrationen, wie fleischige Blätter, Adventiv-Wurzelbildung, die eine vegetative Vermehrung durch abgebrochene Triebe erlauben. Die altweltliche Verbreitung von *Philoxerus vermicularis* begrenzt sich auf die Westküste des tropischen Afrikas; die Art hat sich in Afrika nicht weiter verbreitet, was die Möglichkeit einer Ausbreitung über Afrika nach Australien nicht wahrscheinlich macht. Das Stamm-Alter des Clades, der sich aus *Lithophila, Philoxerus* und den australischen *Gomphrena* spp. zusammensetzt ist 10 Ma (5.7-16.9 95 % HPD). Das bestätigt, dass die Disjunktion erst relativ kürzlich verlief, sodass eine tektonische Gondwanana Vikarianz nicht möglich ist. Deswegen wird ein “long distance dispersal” (LDD) für die Verbreitung nach Australien angenommen. Vorfahren von *Lithophila* oder *Philoxerus* –ähnliche Pflanzen kamen über den pazifischen Ozean, vielleicht von Galapagos, das als Trittbrett diente, durch die Meeresströmungen wie den South Ecuatorial Current, der dann in den “East Australian Current” mündet, und seit ca. 6 Ma. vorhanden war.

Kapitel 4 präsentiert eine taxonomische Bearbeitung der Arten des Kern C4 *Gomphrena* Clades in Bolivien mit Schlüsseln zur Bestimmung, detaillierten morphologischen Beschreibungen und Verbreitungskarten. In dem Einführungsteil zu diesem Kapitel werden Punkt-Verbreitungskarten vorgestellt, die auf Karten mit Umweltdaten projektiert wurden, zu einer besseren und einheitlichen Beschreibung der Habitat Typen führen, die bei der Beschreibung der Ökologie der Arten genannt werden. Die Ergebnisse beruhen auf umfangreichen Feld- und Herbarstudien. Damit werden jetzt 30 Arten des C_4 Kern *Gomphrena* Clades in Bolivien anerkannt, eine Zunahme von acht Arten im Vergleich zum Kenntnisstand im “Catálogo de Plantas Vasculares de Bolivia”, publiziert 2014 mit 22 Arten des C_4 Kern *Gomphrena* Clade. Diese acht Arten repräsentieren neue Entdeckungen.

Contents

Chapter 1

Introduction

1.1. Diversity and phylogeny of the Amaranthaceae

Amaranthaceae is a family comprised of approximately 840 species within 77 genera (Eliasson 1988, Townsend 1993, Müller & Borsch 2005a). The family is most diverse and richly represented in arid and semiarid habitats in the Neotropics, and tropical and southern Africa and Australia (Townsend 2003, Müller & Borsch 2005a, Sánchez del Pino et al. 2009). It has a nearly cosmopolitan distribution but is absent from arctic areas and is rare or lacking in alpine regions; most the genera growing in the Africa regions with one or two species, in 25 genera (Eliasson 1987). It is possible to find some genera and species in warm and humid areas of the tropical rainforest. It grows in a broad spectrum of ecological habitats from desert to evergreen rainforest, and it has evolved in a high variety of different life forms including trees, shrubs, lianas, perennial and annual herbs (Kadereit et al. 2003). The Amaranthaceae are highly variable in overall morphology of pollen morphology (Borsch 1998), and physiology having a highly number of species with C_4 photosynthesis (Kadereit et al. 2003, Sage et al 2007).

The family belongs to the order Caryophyllales. The lineage is considered to have a great ecological and evolutionary interest because it shows multiple origins of specialized morphological, anatomical and biochemical traits (Hernández et al. 2015), possesses the next highest diversity of species with C_4 photosynthesis after the grasses C_4 (Sage et al, 2011). The lineage was traditionally recognized by the syndrome of centrospermous embryological characteristics, such as the campylotropous, bitemic, crassinuclear ovule, food curved or spiraled around the central perisperm, the presence of betalain pigments replacing anthocyanins (except in Caryophyllaceae and Molluginaceae that produce anthocyanins) and sieve-element plastids with a subperipheral ring of proteinaceous filaments (Behnke, 2012).

Following the concept based on molecular phylogenetic studies and line proposed in Hernandez et al. (2015), the family Amaranthaceae is part of 39 familias of the Caryophyllales forming a well supports linage together with Chenopodiaceae (Cuénoud et al. 2002, Kadereit et al. 2003, Brockimgton et al. 2009). In the strict sense (excluded Chenopodiaceae) Müller & Borsch (2005) confirmed as a monophyletic family in the sense of Schinz (1893) was upheld by Townsend (1993) to be para or polyphyletic.

Several species of the family Amaranthaceae are economically important, as the cultivated food Amaranthus, which is consumed in different countries of the word including China, India, Kenya, Poland, Thailandia, Argentina, Bolivia, and Mexico. They are used also as traditional medicine (e.g. in Africa (*Achyranthes aspera*, *Cyathula prostrata*, *C. officinalis*), Europe (= naturalized neotropical ssp. *G. globosa*) and in Sud America in Brasil (and Bolivia (*G. meyeniana*)), and is cultivated as ornamental plants in different gardens around the world (*Amaranthus*, *Gomphrena globosa*, *G. macrocephala*, *Celosia, G. flaccida*). This drives different research in different scientific fields.

Major phylogenetic analyses of the Amaranthaceae converged on recognizing the Gomphrenoideae as monophyletic as characterized by the presence of unilocular anthers (Müller and Borsch 2005a; Sánchez del Pino et al. 2009). Additionally, the core of the clade (Gomphrenoideae except *Iresine*; Müller and Borsch 2005) was supported by the presence of metareticulate pollen (Borsch 1998, Borsch & Barthlott 1998), which was recognized as a synapomorphy. While Kadereit et al. (2003) Müller and Borsch (2005) and Sánchez del-Pino et al. (2009) showed that most of the entities recognized at the tribal and subtribal levels in the pre-phylogenetic classification system of the Gomphrenoideae (Townsend 1993) do not reflect natural groups, the study of Sánchez del Pino et al. (2009) advanced through considerably increased taxon sampling and the use of *trnL-F* and *rpl*16 sequence data resulting in high support for most of the inferred nodes. The authors depicted three subclades, informally called Gomphrenoids, Alternantheroids and Iresinoids.

1.2. Phylogenetic position and circumscription of *Gomphrena*

The Gomphrenoids contained species of *Gomphrena* in two different clades: the first includes *Blutaparon*, *Lithophila* and *Gossypianthus* along with most species of *Gomphrena*, including *G. globosa* as the type species of the genus, here considered as *Gomphrena s.str.* or core *Gomphrena*; the second is composed of *Xerosiphon*, *G. vaga*, *G. elegans*, *Hebanthe*, and *Pfaffia*. A third lineage contains the two species of *Xerosiphon* that was recently recognized as being different from *Gomphrena* (Pedersen 1990), also supported by phylogenetic analysis of *matK-trnK* sequence data (Sage et al. 2007).

Interestingly, the recognition of two different lineages containing species of *Gomphrena* (Kadereit et al 2003, Sánchez del Pino et al. 2009) is also supported by pollen characters. The lineage constituted by *Gomphrena* s. str, *Blutaparon*, *Lithophila* and *Gossypianthus* is characterized by metareticulate pollen with strongly reduced tectum; whereas the others including *Hebanthe*, *Pfaffia*, and two species of *Gomphrena* (*G. elegans* and *G. vaga*) has metareticulate pollen with the tectum completely covering the mesoporia and possessing just small perforations or foveolae

(Borsch 1998, Borsch & Barthlott 1998) and belong to the pollen *Pfaffia* type (Borsch 1998, Ortuño & Borsch 2006).

According to Sánchez del-Pino et al (2009) *Blutaparon* and *Lithophila* are resolved within *Gomphrena* s. str. as sister to the Australian *Gomphrena flaccida* with high confidence. The relationship between *Blutaparon* and *Lithophila* has low support, however, they share morphological characters like the staminal tubes being shorter than the pistil (Mears 1982; Townsend 1993) and both are tropical coastal plants. The *trnLF* plus *rpl16* analysis of Sánchez del Pino et al. (2009) placed *Gossypianthus* as sister of *Gomphrena boliviana,* albeit with low support. Thus, it remains to be seen if *Gossypianthus* is a derived lineage within *Gomphrena* or sister to the remainder of species of the *Gomphrena* s.str. clade. On the other Hand, *Guilleminea* (= Brayulinea) as member of the tribe Gomphreneae, (together with and Tidestronia) defined per Schinz (1934) and supported from *rbcL* data in previous studies (Kadereit et al. 2003), Standley (1917) described and separated the tribe Brayulineae based on the presence of perigynous stamens and protruding to ascending habit with flowers solitary in the axil of caulinar leaves, which is accepted by Schinz (1934) and followed by Townsend (1993), but more deeper relations between the lineage *Guilleminea* and *Gomphrena* s.str. and the related species are yet to be resolved. To clarify the position of *Blutaparon*, *Lithophila, Gossypianthus and Guilleminea* with respect to *Gomphrena* is it necessary to both increase the taxon sampling and to explore additional genomic regions the organellar and nuclear genomes with high phylogenetic utility (Korotkova et al. 2011).

1.3. Taxonomic history of *Gomphrena* and allies

Rheede tot Draakenstein (1689-1669) was the first person to described one specimen of the currently species belong to *Gomphrena*, under the name Wadapus published in Hortus Indicus Malabaricus (vol 9-10. pl. 73. 21-73), were include the first design of *G. globosa,* and describe the plants with oblong leaves, the white indumentum denser in the nodes, the flowers grouped in glomerulus with intense color purple, during the floriation's the filament stick out of the flowers, in stellate shape, contrary to the internal gynoecium, which has only one dark seed per flower, *G. globosa* was use as a plant medicinal. Later Linneaus (1747, 1756, 1762) describe officially the genus *Gomphrena* cited in most of his publication Rheede tot Draakenstein works, using this genus as synonymous of *Gomphrena* concept.

Carl von Linné (1738 in Hortus Cliffortianum) was the first to establish the genus *Gomphrena*: The name apparently was based on the Flora's dictionary Wirt (1837), the origin of the name *Gomphrena* is adopted by Linnaeus, from Dalechamp. Linnaeus probably made an allusion to Gomphos, a nail, wedge, or club applied to the round head of flowers.

Linneaus, described two species of *Gomphrena*: *G. globosa* and *G. flava* (= *Alternanthera flava* (L.) Mear), following in the next publication, first edition of Species Plantarum-(1753) and fifth edition of Genera Plantarum (1754). Linnaeus, include nine species. Since them, and added one further species for this genus in Centuria II plantarum Uppsala 1756 and one more in species Plantarum II Stockolm 1762. However, he transferred four species originally included under *Gomphrena* L. to a new genus Illecebrum L. (Sp.Pl.1: 206.1753). The Linnaean concept of *Gomphrena* based on inflorescence characters more than to number of stamens and stigma. The Linnaean species of *Gomphrena* were considered to belong to four genera by later authors: apart from *Gomphrena* to *Blutaparon* Raf. In New Fl. 4. 45 183-86 (= *Philoxerus* R. Br; Prodr. Fl. Nov. Holland. 416. 1810), *Froelichia* Moench and *Alternanthera* Forssk. (Mears 1980).

The consistent characteristic of the species of *Gomphrena* recognized by Linnaeus (1747, 1753,1756, 1762) are the absence of corolla, charthaceous sepals, and more or less condensed, globose terminal inflorescences, erect caule. Linnaeus divided the genus *Gomphrena* into two groups, one he considered to have "floribus terminalibus caule erecto" [with terminal flowers and an erect stem] and the other "floribus lateralibus caule diffuso" [lateral flowers on branched stems], since *Gomphrena* was described as a genus of Linnaeus' section *Pentandria Digynia* and *Illecebrum* of *Pentandria Monogynia*. Mears (1980), to preserve the current concept of the genus, Hitchcock and Green (1929) lectotypified the genus with *G. globosa* L., the 1762 transfers suggest a re-examination of floral parts, and designed as lectotype of *Gomphrena globosa* a specimen in Clifford's herbarium. Currently follow the Linnaean Plant name Typification Project in Jarvis (2005), the type of *Gomphrena* is *G. globosa*, was designated by Standley (N. Amer. Fl. 21: 147. 1917), but that was done under the so-called "American Code" so it was arguably not effective according to Art. 10.5(b), but was affirmed (e.g. designated again with the same species name), by Hitchcock (Prop. Brit. Bot.: 137. 1929) that is effective typification.

The valid lectotype of *Gomphrena* was designated by Townsend in Nasir & Ali, Fl. W. Pakistan 71:46 (1974), and corresponds to the specimen of *G. globosa*, Herb. Linn No 319.1 (LINN), Fig xx. Palmer (1998, Farr 1986, Jarvis 1992, 1993, 2005) indicates a specimen in the Clifford Herbarium (BM) as the lectotype, following Townsend (1985 in Fl. Trop. E. Africa Amaranthaceae: 129). It is important to remark then, the first author who effectively designates a lectotype must be followed (Art. 9.19), so Townsend's took precedence.

Martius (1826) made a trip to South America to investigate the most important provinces of Brazil by order of the Academy of Sciences of Bavaria, recognized 19 species of *Gomphrena* Published in "Beitrag zur Kenntnis der natürlichen Familie der Amaranthaceae" this work is an important base study for the family Amaranthaceae. According to Cavaco (1962) the first morphological concept of *Gomphrena*, for Martius was the two Bracteoles and one bracts form a calyx, and the five tepals form the corolla, in a similar concept than in Polygala, after he change and suggest the bracteoles and bract form the corolla in the family Amarantaceae and Calyx in Chenopodiaceae, now it is not possible to use these analogies, because is accepted than *Gomphrena* do not have a really corolla (Vrijdaghs et al. 2014, see chapther two). In strict sense for Martius he main character to recognized the species of the genera *Gomphrena* was the corolla pentapetala, with petals base few connected, the anther unilocular, five stamens united into a tube, with two or three fringes (or denominated here filament appendages), where the anthers are attached in the middle fringes., the gynoecium has one style with two cylindrical stigmas, and the ovary produce only one utricule monospermus.

Rafinesque (1836), described the genus *Ninanga* in addition to *Gomphrena* based on the type of *Gomphrena perennis* L.; his differential character was the androecium unitd in a tube with five teeth between which the anthers are inserted, two stigmas and one utricle: He also mentioned in this document also the name "*Gomphrena arborescens* L., for him was another specie of the genus *Wadapus* Raf. (= *G. globosa* L.), but is not clear if for him the genus *Wadapus* is the same that described by Rheede tot Draakenstein (1689-1669) in Hortus Indicus Malabaricus (vol 9-10. pl. 73. 21-73).

Endlicher (1837) considerably enlarged the genus concept of *Gomphrena* by including the genera *Serturnera* Mart., *Pfaffia* Mart., *Hebanthe* Mart., the four of which were classified at the level of sections within *Gomphrena*. The characters used for the descriptions of section *Gomphrena* are very similar to Martius (1826). He only added the character of the "three filament lobes of the tube of the androceum from which the laterals are bigger than the middle", in this case he describes the characters currently call pseudostaminoidea or apical filament appendices' (Eliasson 1988; see chapter two). Stigma characters were not used. These are very different in the three Martian genera. Endlicher's (1937) concept was only used by Moquin Tandon (1848), Seubert (1875), but modern authors largely came back to treating them independently under *Pfaffia*, *Hebanthe* was re-established by Borsch & Pedersen (1997).

Moquin-Tandon (1849) presented the most complete treatment of the genus after Martius (1825, 1826) and described *Gomphrena* in widely sense as Endlicher (1837), separating 5 sections: Seccion 1. *Serturnera*, Engl. Gen. p.301, 1958. (= *Serturnera* Mart. Nov. Gen. Sp. Pl. p. 36-38 1826). Seccion 2. *Hebanthe* Engl., gen.p. (= *Hebanthe* Mart. Nov. Gen. Sp. Pl. p. 42 1826). Seccion 3. *Pfaffia* Engl.p.302, . (=*Pfaffia* Mart. Nov. Gen. Sp. Pl. p. 20 1826).
Section 4. *Wadapus* (= *Gomphrena* Mart. Nov. Gen el spec. bras, p1; *Schultesia* Schrad. On Goetting Anz. Non Mart. (1) nec Roth (2), nec Spreg (3). *Bragantia* Vandelli in Roem, script p. 50, non Lour. (4). *Gomphrena* sect. *Gomphrena* Endl. Gen p.302. Wadapus et *Ninanga* Rafin. Fl Tell.n 723. Section 5 Xerosiphon Turcz. (with 3 species).

The section 4, corresponding to Wadapus (currently Gomphrena) have been as distinctive characteristics the free sepals, elongate androecium, connate in a tube with filaments with two lateral lobes, ligulate form, capitula globosa, or spiciform aphylla or with leaves. Moquin- Tandon differentiated entities within *Gomphrena*. **Group 1**: 13 species with the subglobose or spherical capitula, flowers with two lateral bracteoles not crested (*Cristula destituta*), without leaves under the inflorescence ("Capitula aphylla", e.g. *G. prostrata* Desf., *G. mollis* Mart., *G. vaga* Mart., *G. elegans* Mart. 2). **Group 1-2**: 17 species with bracteoles not prominent crested ("sursum") and just under the inflorescence with leaves (e.g. *G. umbellata* Remy, *G. flaccida* R. Br., *G. canescens* R. Br., *G. martiana* Gillies *ex* Moq. and *G. perennis*). **Group 2**: 27 species with lateral orientation of bracteoles, crested in the apical dorsal part and with leaves under the inflorescence (e.g. *G. agrestis* Mart., *G. lanigera* Pohl, *G. macrocephala* A. St.-Hil., *G. haenkeana* Mart., *G. oligocephala* Remy). **Group 4**: 9 other species with enough marks for included in the mentioned groups (*G. meyeniana* Walp., *G. lanuginosa* Span.

Seubert (1875) essentially used the concept of Moquin-Tandon (1849), maintained the sections *Serturnera* Mart., *Hebanthe* Mart., and *Pfaffia* Mart., but divided the section *Wadapus* into the sections *Gomphrenula* Seubert, *Cristularia* Seubert, *Xerosiphon* (Turcz.) proposed by Moquin (1849), but added a new section named *Stachyanthus* Seubert. The section *Gomphrenula*, 20 species, with the filaments were described as fused into a tube, with free lateral lobes ("lobis lateralibus integris"), bracteoles without crest, divided in two group without leaves, (a.i. *G. prostrata* Moq., *G. vaga* Mart., *G. mollis* Mart.,) and the second group with leaves under the capitula, a.i. (*G. duriuscula* Moq.,*G. pohlii*. The section *Cristularia* with 27 species was characterized to possess flowers with crested bracteoles and leaves under the capitula (e.g. *G. perennis L.*, *G. agrestis*, *G. globosa* L., *G. celosioides* Mart.). In this section, the filaments were considered to be fused from the base into an elongated tube, with lateral appendages the intermedium sub null, two filiform stigma, lateral bracteole in middle nerve, menbranaceae with crest. Section *Stachyanthus* Seubert, with a spike-like elongated inflorescence, bracteoles with reduced cristae, a curved filament tube, and the two filiform stigma lobes branching from a cylindrically elongated style contained only *G. graminea*. Section *Xerosiphon* (Turcz.) was maintained as in Moquin-Tandon (1849).

Standley (1917) in his study of the Amaranthaceae of North America, used the same genus concept of *Gomphrena* like Bentham & Hooker (1880), and refined the genus description as follows: Flowers with five sepals, stigma subulate-filiform, stamen-tube the 2 at 5, with broad and entire lobes, usually 3-lobed, dentate or lacinate, no pseudostaminodia.

Fries (1920-1921) in his study of the *Gomphrena* species of South America kept the concept of the genus *Gomphrena* of Seubert. He thus divided the genus in three sections but in addition separated different informal groups in *Gomphrenula*. These were the groups of

Gomphrena elegans Mart., the "*Platycephala*"-group, and the "*tomentosa* group (="*Chnoanthus*" group). Fries, R. (1920 a) performed critical and comparative morphological studies of the South American species collected mainly by Glaziou (1816 - 1895), given high importance to the distributions of the specimens analyzed. He followed Standley, Uline and Urban work's for the species of Central and North America, and especially the Brazilian classification made by Seubert, in consideration of the specialized level of detail he gives to the floral morphological character works.

Fries (1920) focus his works in observations in the floral morphological characters. In *Gomphrena*, clarifying and study species distributed in Argentina and Bolivia, and organized them, in natural groups, inside sections previously described by other authors (Martious 1826, Seubert 1875). The relevant groups are:

G. elegans group, include *G. elegans* Mart., *G. vaga* Mart. *G. holocericea* Moq., *G. mandonii* R.E.F., with androecium with filaments, lateral lobes, and in the middle filaments linear-triangular acute, stylus short, thick stigma bilobed.

The platycephala group, include *G. platycephala* R.E.F., *G. lanceolate* = *G. boliviana* fo. robusta Pedersen, and *G. glutinosa* R.E.F. = *G. martiana* Pedersen, with the inflorescences, which are supported at the base of green and well-developed leaves. The bracteoles conical membranous, tepals (perigonion blaters) the outer ones woolly hairy, slightly above the base extended, from there uniformly or towards the top gradually narrowed, two- lobed surrounded in a short stylus. For the group typist the androecium is the following: comparatively longer in uniform and one band – shaped. Both last groups are allocated in the sections Gomphrenula Seub. Fries (1920).

Choanthus groups, corresponds to a new section established by Fries based on new specie describe by ñ, and include *G. tomentosa* (Griseb.) R.E. Fr. and *G. discolor*, the characteristic of this species was the rounded margin bracteoles, without a crest, or spatula-shaped, the stems woolly hairy with contracted leaves.

Fries, R. (1920 b) also established the genus *Pseudogomphrena* based on in the description of the *G. scandens* (R.E. Fr.) J.C. Siqueira, this new genus was mainly created based on the structure of the androceum, and how the anther as inserted in the basal part of the united tube of the androceum between one complete "staminodio". This of the point of view of Fries (1920b) (also follow by Siqueira 1992), this character seems for one way very different than usually of "Gomphrenen" (Fries 1920:34 p). They are, on the other hand, homologous formations to the interstices between the anthers, in the *Froelichia* species, although the filaments are divided in this genus simply shape, and not fork-shaped. Therefore the "staminodia" in Pseudog*omphrena* can be derived from those of the Gomphrenen, in the manner that the filaments would have grown along the edges, forming two "lobes" to almost the pointed ones. If this interpretation is correct or not, the new generic system is systematically situated near the *Gomphrena*, which emerges from the flowering of the rest, especially from the long filiform styles.

Schinz (1934-1893) prepared a detailed treatment of the Amaranthaceae for the second edition of Engler & Prantl´s Pflanzenfamilien. He organized the species in subfamilies, tribes and genera. He divided the subfamily Gomphrenoideae with unilocular anthers into the tribes i) Brayulineae with perigynous flowers and short stigma) and ii) Gomphreneae with hypogynious flowers, spiciform, capituliform, sometimes axillar, compressed, flowers, and bilobed stigma. He included *Gomphrena* in tribe Gomphreneae and cited *G. globosa* the type of the genus. Schinz also recognized four sections: *Gomphrenula*, *Stachyanthus*, *Cristularia* (=*Wadapus*) and *Xerosiphon* Turcz.

Holzhammer (1955;1956) presented a revision of the American species of *Gomphrena*. She followed the classification system of Seubert (1875), and included five sections and refined their morphological descriptions: **Section *Stachyanthus*** Seubert with one species; flowers in terminal and axillary, petiolate, spike-likes inflorescences often more than 1 cm long, with crested bracteoles; inflorescence supported by a pair of leaves. **Section *Gomphrena*** Holzhammer [= *Cristularia*] i (with 41 species, distinctive characters are individual flowers, terminal or axillary, sometimes petiolate or sessile. Flowers arranged in heads that are spherical, hemispherical, ovoid or cylindrical by in outline and supported involucral leaves, bracteoles with crests. **Section *Gomphrenula*** Seubert, forty-two species, bracteoles without crests. Lanceolate, linear/lanceolate or linear tepals more or less tapered at the apex, sometimes obtuse, narrowed at the base; style often short; the free part of filaments rectangular shaped, two broadband shaped linear or lanceolate, apex acute or obtuse rarely rounded, free part of filaments shortly lobed with the apex rounded or smoothly truncated). **Section *Chnoanthus*** (Philippi) R.E. Fr. Four species, bracteoles without crest, spatulate tepals, rounded at the top, just below the middle contracted into a narrower part, forming a kind of bottle around the ovary; the free part of the filaments are triangular lobes or narrow bands, without laterals lobes). **Section *Xerosiphon*** Türczan, (3 sp., the distinctive character are the fused tepals in their lower part).

Cavaco (1962) has proposed new classifications based on floral morphology and inflorescences survey of African and Madagscarean Amaranthaceae. He raised the four tribes in Schinz’s system and older classification. Proposed the subfamilies Celosioideae, Amaranthoideae, Brayulinecoideae. Gomphrenoideae. The morphological criteria, on which the taxa were based, are the same as those used by Shinz (1934). Gomphrenoideae are characterized by a solitary ovule, campylotrope without a sterile flower and unicular anthers, this was divided into two tribes Tidestromeae, and Gomphreneae. Flower in the apex or false-capitate (head). This is subdivided in two subtribes the first is Froelichiinae with capitate stigma and penicillin not divided into branches elongated shape and ending in a point. The presence of candelabres trichomes. The second subtribe Gomphrenineae with subdivided stigma. The presence of smooth wall trichomes hair (poils). The represented genus in Africa are *Philoxerus* and two species of *Gomphrena* in the range of the genus in America and Australia are: *Woehleria*, *Dicraurus, Psedogomphrena*, *Iresine* and *Lithophila.*

Siqueira (1992) studied the species of *Gomphrena* L, from Brazil and used the same classifications of Seubert and Holzhammer but included the genus *Pseudogomphrena* R.E. Fr. as a further section *Pseudogomphrena* (R.E. Fr.) Siqueira.

Eliasson (1986-1988) mostly accepted the system proposed by Schinz (1934), specifically underscoring that *Guilleminea* (Brayulineae) belongs to the same tribe Gomphrenoideae, and he thought that perigynous flowers are probably a secondary feature, whereas floral characters and pollen sculping are very similar. Eliasson (1988) further considered that *Guilleminea* Moq. and *Gossypianthus* are closely related.

According to the concept of Eliasson of *Gomphrena* it has a spike-or head-like inflorescences with long pointed bracteoles that have the tendency of being curved at the tip. The genus has like most Amaranthaceae five stamens, the filaments fused all along their length or almost so, the anthers are unilocular; the pseudostaminodes have very long staminal tubes. The gynoecium has two filiform stigma lobes, united almost to the apex and with anthers attached in the sinuous between the apical lobes, the ovary is uniovulate, with solitary ovules and. In comparison to that, Eliasson (1988) described *Blutaparon* Raf. and *Lithophila* Sw. as having two filiform stigma lobes quite similar to those of *Gomphrena*, but both without the presence of pseudostaminal structures. While *Blutaparon* Raf. was found to develop five stamens equal to *Gomphrena* L., *Lithophila* Sw. was observed to have only two fertile stamens, whereas in the species of the Galapagos *Lithophila* the missing third stamen is present as teeth on the filament base cup and is interpreted as staminodia.

Pedersen (1967-2000- 2016) performed the morphological studies in Amaranthaceae genera, especially distributed in South America in five papers published in different journals. With the comments, descriptions and nomenclatural revision have improved the compression of the genus *Gomphrena*. Pedersen (1976) clarifies the species of *G. haenkeana* Mart. respect of *G. pulchella* Mart., using the characters of annual or perennial habit, and floral characters as the presence or not the crest in the bracteoles. Described species of *G. ferruginea* Pedersen (+ *G. ferruginea* var *rustica* Pedersen); *G. pallida* Pedersen (+ *G. pallida* ssp. *pallida* Pedersen*, G.pallida* ssp. *pallida* fo. calva Pedersen), *G. phaeotricha* Pedersen, *G. radiata* Pedersen. All these species are distributed mainly in the North of Argentina, and South of Bolivia, his work include keys for these species e.g. *G. martiana* Gillies ex Moq. and *G. boliviana* Moq. key, usually difficult to distinguish. Pedersen used for this propose the relation of the size between bract and bracteoles, and including in this group the new species for *G. spissa* Pedersen from Bolivia. He also proposes new varieties of *G. tomentosa* (Griseb.) R.E. Fr. and new combinations for the complex species of *G. celosioides* Mart. Pedersen works with highly morphological details. He do not follow the section established by other author, in mostly of his works revisions identify species an infrageneric level, and he created complex confusions nomenclatural describing trinomials at different rank, as for example the he case of *G. meyeniana* Walp that is treated vol. III of his studies of Sud American Amaranthaceae (1990). which includes a key practically based on characters of tepals, constituting in essential character for determination of these species and essential basis for this work focus in Bolivian's species Ramella et al. (2016) based on the Pedersen works published the flora of Amaranthaceae of Paraguay in this work are included several species of *Gomphrena* that growing also in Bolivia.

[Australia relatives *Gomphrena*] Robert Brown (1810) described the first four Australian species of *Gomphrena, based on morphological character of* perianth five, stamina five united in a tube cilindrical, ovario with one stylus and two stigma, Anther unicular (*G. lanata*, *G. humilis*, *G. flaccida*, *G. canescens*), and also described two species in a new genus, *Philoxerus* R.Br. Prodr. Fl. Nov. Holland. 416. 1810 (= *Blutaparon* Raf. (New Fl. 4. 45 183-86)) with the morphological difference than the anther are connate tube but the apical part without toothed. Opposite leaves, terminal spikes, tribracteate. *P. conicus*, *P. diffusus* and near *Lithophila* only different number of anthers.

Poiret (1816) transferred Brown's four *Gomphrena* L. species to *Philoxerus* R. Br. placing them in section *Philoxerus* R.Br.

Sprengel (1824) transferred Brown's two Australian *Philoxerus* R. Br. species to *Gomphrena*.L (*G. conica* Spreng. Syst. Veg., ed. 16 1: 824. 1824 and, *G. diffusa* (R.Br.) Spreng. Syst. Veg. ed 1 1824. In De Candolle's 'Prodromus', Moquin-Tandon (1849) considered that *Iresine* Browne (1810) was a more appropriate genus for some of the Australian taxa, resulting in one *Gomphrena* species being transferred to *Iresine* and the description of three new *Iresine* species.

Von Mueller (1862) described four new species of *Gomphrena*. (*G. maitlamdi* F. Muell., *G.brachystylis* F. Muell. G. breviflora F. Muell, G. firma F. Muell.).

Bentham & Hooker (1880) in 'Flora Australiensis', where 14 species were treated, including three new combinations in *Gomphrena* for some of those species previously included under *Iresine* and *Philoxerus* and, including four new species. Excluded the sections *Hebanthe*, *Pfaffia* and *Serturnera* from *Gomphrena* but classified all these genera to constitute the Tribe Gomphreneae, along with the genera *Guilleminea* Kunth, *Cladothrix* Nutt.(= *Tidestromia* Standl.), *Pfaffia* Mart., *Mogiphanes* Mart. (= *Alternanthera* Forsk.), *Telanthera* R. Br. (=*Alternanthera* Fosck), *Alternanthera* Forsk., *Gossypianthus* Hook , *Woehleria* Griseb. *R. Br.* (=*Blutaparon Raf.*), *Gomphrena* L.

The mains characters in *Gomphrena* L., are the capitule, rare spikes, with or not basal leaves. Perianth not equal or subequal, tepals concave, rare planes. The androecium are fused in long or short tube with the apical part can be vary: in one entire fringe (2 fidis - with two emarginate apex (oblong to linear) anther attached in the senus the emarginated fringe, or one fringe (locule) lineal, anther attached sessile in the apex, or entire fringes, anther attached in alternate bridges. The androecium never as a cup, as *Philoxerus* R.Br. this species is different of *Gomphrena* because the tube size, and for the other characteristic seems very similar, for this reason consider than *Philoxerus* R. Br. is congeneric to *Gomphrena,* and mention than in his work do not f ollow the rules of Moquin's Tandon (1849). Bentham & Hooker (1880) considers also, that the sizes of the stigma shaped is it most important, difference between the American and Australian species.

Kuntze (1891) resurrected *Xeraea* L. as an earlier name for *Gomphrena* and transferred all the Australian and American species to the *Xeraea* genus, the argued of this drastically changes were based on in a concept of Kuntze *Xeraea* was the first name given by Linneus, but *Xeraea* was published prior to 1753 and has no status under the 'International Code for Botanical Nomenclature'. Over the following 120 years, four new *Gomphrena* taxa were described. However, Lopriore (1902) synonymized again *Xeraea* with *Gomphrena.*

Farmar (1905) two species, Ewart (1913) one species and Domin (1921) one species. Shinz (1934), in a treatment of the whole family, informally included all the Australian species under *Philoxerus* although he mentions that some species should remain as *Gomphrena* but further study was required.

Palmer (1998), realized a taxonomic revision about thirty-three species from Australia, most the Australian species, not have correspondence with the sections recognized in the Americans treatment realized by author as Holzhammer (1955) and Siqueira (1992), only eleven species can be allocated between these section *Pseudogomphrena* (R.E.Fr.) J.C. Siqueira (1-6 sp.) and *Gomphrenula* Seubert (five sp.). The species of Australia, vary to respect the Americans having filaments united for only part of their length, so that the anthers are positioned on the free filament portions rather than being sessile, or the filaments fused in a tube in different way positioned is less than or about equal, in relations of the fruit. Many species have much longer styles than the American species. That mean, to understanding the relationships between the

Australian and American taxa it is necessary created a new formal infrageneric system. For this reason, Palmer (1998), include 4 groups of *Gomphrena* follow Bentham & Hooker (1880) criterion arrangement of taxa based mainly on the length of the filament tube relative to the fruit length, and in the presence or absence of pseudostaminodes between the free filament portions e.g. *G. canescens* R. Br. have pseudoestaminodes present between the free filament portion. In addition, Palmer (1988), follow the Bentham & Hooker (1890) the concept respect to *Philoxerus* R. Br. accepted in this treatment than *Gomphrena* L. and *Philoxerus* are congeneric.

Townsend (1993) presented in Kubitzki´s families and Genera of Vascular Plants a more detailed morphological analysis of the family Amaranthaceae and a brief treatment of all accepted genera. Townsend (1993) included in the Gomphreneae, Endl. Froelichiinae Schinz *Guilleminea* Kunth with *Brayulinea* Small and *Gossypianthus* HooK. as synonyms (according to Mears (1967) and also *Pfaffia* Mart., in the subtribe Gomphreninae the monotypic genera *Irenella* Suesseng., *Pseudogomphrena* R.E.Fr., and *Woehleria* Griseb., besides *Blutaparon*, *Iresine*, *Lithophila* Sw. and *Gomphrena* L. but without mentioning *Hebanthe* Mart. This means he used the genus concept Schinz (1893). The most recent generic level classification of the Caryophyllales (Hernández-Ledesma et al. 2015), which includes the Amaranthaceae, has still maintained the genus concept of *Gomphrena* as in previous to see the resold in this study. Townsend (1993), respect to the near relationship about Australia and the American neotropical species of the genus follow he idea than the morphological variation in the floral character like the androecium, not seem possible to divided the species in Australian or American, because

Gomphrena had highly similarities morphological like in tepals form, gynoecium, etc. than above are inseparable there seems no option but to include all within a single genus, but of course in the future probably is will be necessary to propose a deeper new classification. In *Gomphrena* Townsend found than the androceum, shows more variations tan in any other in the family, the variations being entirely due to the Australias species, the staminal tube in such Species as *G. conica* Spreng, and *G. leptoclada* Nemth, is virtually identical to those of American species, and the same wavy hairs are present on the perianth. In *G. humilis* R.Br. it remains long-tubular but the free parts of the filaments are subulate; in G. *brownii* Moq. Are fused to about half ways with distinct, large pseudostaminodes.

1.4. Distribution and diversity of *Gomphrena*

The majority of the species of *Gomphrena* are adapted to drier and markedly seasonal environments. Around 104 species, with ca. 42 % of endemism, occur in the semi-deciduous forest of south-eastern Brazil or even the semi-arid north-eastern Brazilian “Caatinga and Cerrado” (based on Flora de Brasil Senna, Marchioretto, Senna & Siqueira 2010), and 45 spp. occur in dry forest (Inter-Andean forest), Prepuna, Bolivian-Cerrado, dry forest Chiquitano, Xeric Puna, Bolivian-Tucuman forest region, and the Chaco Boreal of northern in Bolivia, Argentina and western slopes of the Andes. Of these 45 species, the Flora del Cono Sur mentions 34 species, without varieties (Zuloaga, Morrone & Belgrano 2008); and the Bolivianvascular plant catalogue, 31 spp. (Borsch, Ortuño & Nee 2014). In Bolivia, most of the paraphyletic species of *Gomphrena*, such as *G. elegans, G. vaga,G. mandonii,* occur in more open vegetation in moister habitats, such as Amazonian Forest, Flooded savannas, Yungas, but also occur less commonly in Inter-andean forest, while the majority of species of *Gomphrena* s.str. are restricted to the southern west of Bolivia in dry forest or Puna. Of these *Gomphrena* s.str., only *G. celosioides* lives in a wider spectrum of habitats.

Patterns of species distribution and endemism support the hypothesis that the genus arose in the Neotropical seasonal “Dry Forest or Tropical Seasonal Forests and tropical savannas (SDTF)”, suggesting one radiation that happened during the Pliocene and Pleistocene, according to the dry diagonal or open formation hypothesis, previously called “Pleistocenic Arc Hypothesis” (Prado & Gibb 1993, Pennington, T. et al. 2000, Pennington, Lewis & Ratter 2006, Fiaschi & Pirani 2009).

The distribution of coastal species from North and Central America show that migration was possible in two directions, from south to north or vice versa. Based on the present distribution of these species, we can postulate two hypotheses: i) the first is in accordance with the SDTF distribution and with the dry diagonal or open formation, and was caused by the expansion/contraction of the humid forest during the Plioceno and Pleistocene (Prado & Gibb 1993, Prado 2000, Pennigton, Lewis & Ratter 2006, Fiaschi & Pirani 2009); ii) the alternative hypothesis explains that during the Oligocene and Middle Miocene (33-35- to 12-11 Ma), sea level raised and there were marine incursions which caused the migration of species to migrate into the Amazon basin and sea level changedof high position in the sea level and/or the connectionbetween the Caribbean and the Amazon basin by the area of lake Maracaibo or the Pacific (Hoorn et al. 1995, Hooghiemstra & Van der Hammen 1998, Iturralde-Vinent M. 2004). Both the expansion/contraction of the humid forests and the narine incursions may have fostered the migration of ancestors of *Gomphrena* (*Froelichia* or *Guilleminea*). Phylogenetic studies will allow datation of the time these migrations happened.

The distribution of *Gomphrena* and that of SDTF in the Neotropics (Pennigton, Lewis & Rattes 2006) can be seen in Fig. 1. The match between *Gomphrena* and SDTF distributions is related to the dry diagonal open formations proposed by Bucher (1982), who employed another term (tropical savannas) in a more general sense integrating all the dry areas, which span from north-eastern Caatingain Brasil to the Chaco in the northern Argentina, are isolated by a savanna corridor, sandwiched between the coastal and the Amazonian rainforest, known as Cerrado or campos Cerrados. Thought the Chaco, this diagonal of open formations, affords access and trans-connections of xeric areas from the west has connections with the xeric areas from the west, north west, and south (the Mont desert, Andean shrub formations and Patagonian Desert).

The term "tropical savanna" proposed by Huntley & Walker (1982) includes not only America, but also Australia, and Africa. That is why this term can be used to generalize the reference to *Gomphrena* distribution across continents (that way, we do not have to use multiple local names). Tropical savannas in the sense of these authors are characterized by a vegetation structure of vegetation where there is prevalence of spinescent and succulent plants, beside the known grass and heliophytic herb cover. This type of vegetation is common in the Caatinga, Chaco, Andean dry valleys and Prepuna in South America, and also in Africa and Australia. Australia has 33 species of *Gomphrena*, most of them indigenous and only two naturalized species from the South America (Palmer 1998). African Gomph*renas*pecies are only represented by a low (2 or 3) number of naturalized species but the family Amaranthaceae has a large number of genera (Cavaco 1962).

Furthermore, the main distinctive kind the species in all these communities of tropical savanna are Kranz syndrome or C4 grasses (Bucher 1982). *Gomprhena* s. str. have also the kranz anatomy, and this characteristic is deeply linked with the arid or semiarid environments (Kadereit 2003, Sage et al. 2007). Savannas have a wide range of precipitations which fall mainly in summer, and very high radiation most of the year. Most have no frost season, but this is not the case for the Chaco and mountain regions, where several degrees below zero are attained most of the winters.

1.5 Flora and vegetation of Bolivia

[Andes] The diversification of the lineages of *Gomphrena* and related genera are strongly influenced by several geologic and climatic processes occurring during the early Oligocene to the Pleistocene. These processes changed the biota of South America (Graham 2010). One of the most important events was the orogeny of the Andes, which was a gradual process. Most authors agree that the most intense period of mountain building occurred between 10 to 6 Ma (Gregory-Wodzicki 2000, Zachos 2001, Mc Quarrie et al. 2005, Blisniuk et al. 2005, Jiménez et al. 2009, Garreaud 2009, 2010, Graham 2010), in which one of the topographic effects was the rising of ridges which created microclimates with wet/dry slopes. This uplifting was of paramount importance in the appearance of the arid diagonal of South America (SAAD Rain-shadow effect) which began to form 16 Ma and which reinforced aridity in western South America (Blisniuk et al. 2005, Garreaud et al. 2009, 2010, Chacon et al. 2012, Graham 2010). Gentry (1982, 1993) was one of the first to hypothesize that the uplift of the Andes fostered rapid diversification, and this is supported by recent phylogenetic analyses (e.g. Hughes 2006, Luebert 2010, Lagomarsino 2016).

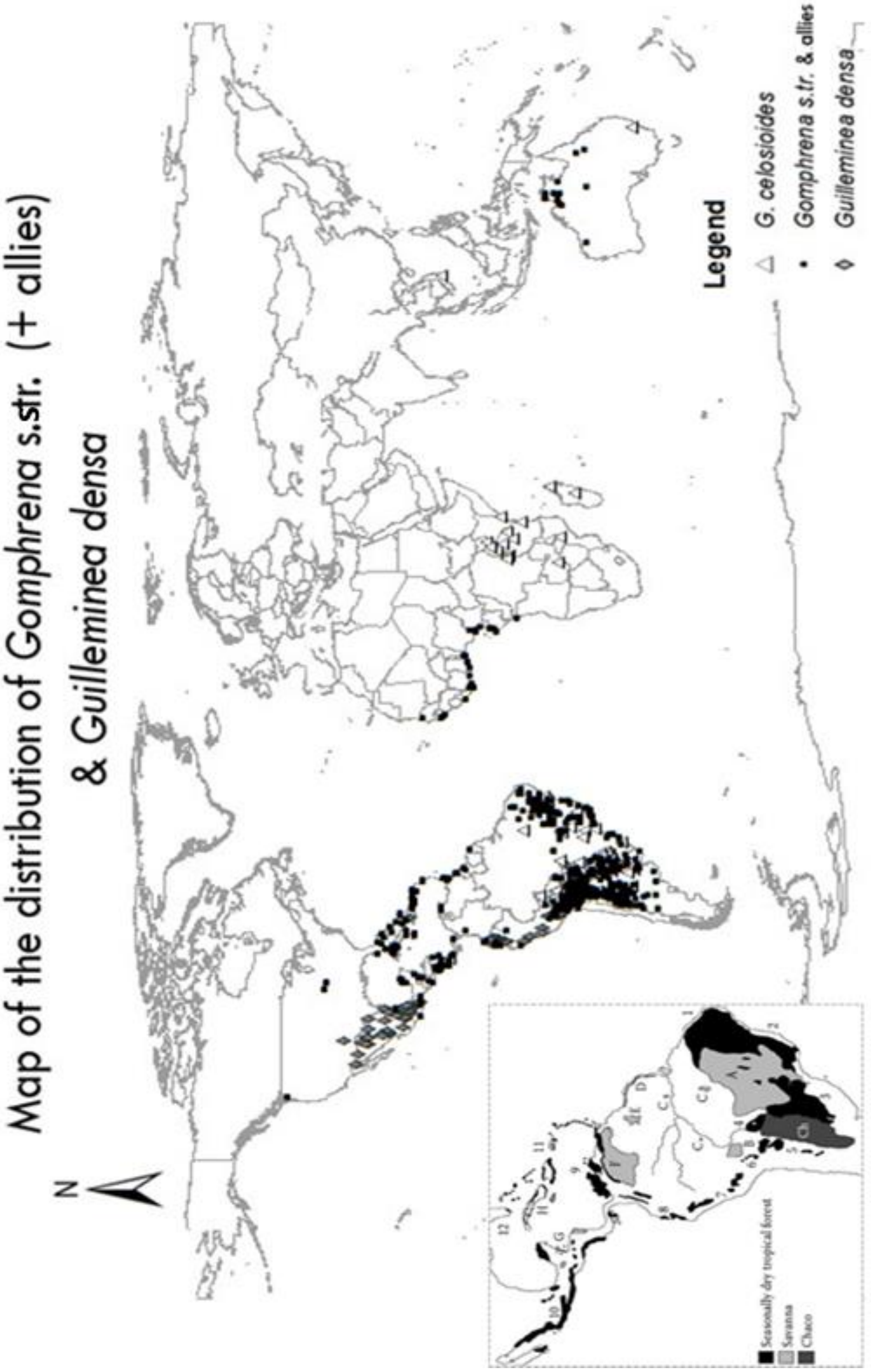


Fig. 1-1. Maps of the distributions of *Gomphrena* and species allies. A) Distributions od *Gomphrena* s.str. plus *Lithophila*, *Gossypianthus*, and *Blutaparon* species. Elaborated in this work based on 1800 data base records, with verified georeferences B) The distributions of seasonally dry vegetation in the neotropic. Seasonally dry Forest 1. Caatinga. 2. Misiones nucleus. 3. Bolivian Chiquitano region. 4. Piedmont coastal Ecuador. 5. Bolivian and Peruvian Inter Andean valleys. 6.Pacific coastal Ecuador. 7. Colombian InterAndean valley. 8. Caribbean coast of colombia and Venezuel. 9. Central América. 10. Antilles. Savannas: Ce, Cerrado. LlLanos. Ru. Rupununi. Ch. Chaco. Extracted from Pennigton et al. (2000).

Gomphrena species extend south up to the Andes of northern Argentina. The high number of species and endemism suggests a high radiation of *Gomphrena* (Ortuño and Borsch, 2005; 2006). The rugged topography of the Andes limits the migrations of species, giving way to the formation of various endemisms, and creates the conditionsfor great speciation (Gentry 1982, Hughes & Easwood 2006, Luebert 2010), and also serves as a bridge for species of cold climates of the north to the south. The Andes are characterized by having mountains with high elevations, strong wings, high radiation, low temperatures, and a daily thermal regime (Garreaud et al. 2003, Körner 2003). In a short distance over a few kilometers, the elevation and topography can vary a lot, contributing to a great diversity of habitats, with exclusive characteristic microclimatics.

The Andes in Bolivia comprises the region of the Eastern Cordillera delimited in the northwest by the peruvian border (13°40'S, 69°W), and in the south with the Argentine border in Bermejo Heights (22°40' S, 64°25' W). The region having widely range of altitude between 1.000 to 3.500 m, in short distance from few kilometers the elevation and topography and microclimate can vary in high levels. There is high radiation, strong winds, a daily thermal regime (Garreaud et al. 2003, Körner 2003, Blisniuk et al. 2005, Jorgensen et al. 2014, Garreaud 2009, 2010, Zachos 2001), the average annual temperature is 9-20 °C, and rainfall ranges from 300 > 6,000 mm per year, presents 0-10 dry months. The major diversity of the flora in country are saved in the Oriental slopes of Andes of Bolivia, these regions comprise six ecoregions: the dry valley, Bosque serrano Chaqueño, Paramo yungueño, Ceja de Monte Yungas Bosque Tucumano con ca. 12.427 sp. (Jorgensen, et al. 2014 p. 74).

Currently, the number of species register in Bolivia are 15.345 species, of which 12.165 are native and 2342 are endemic, in total of 286 families listed follow the APG III classification system based on a recent publication of the Catalogue of the Vascular Flora of Bolivia (Jorgensen et al. 2014). This work was a united effort of 44 of the Botanist of the all Herbariums from Bolivia, and the contribution of 221 specialists and 53 reviewers' international herbarium (e.g. MO, K, BGBM, SI, NY). This played an important role because the botanical exploration of Bolivia during the last two centuries did not leave a botanical legacy in the country. Only at the end of the 20 th century Bolivia implemented biology as a career at the universities and consequently, the foundation of its own herbaria. The "Herbario Nacional de Bolivia" (LPB) was created in 1972, actually it has near 360000 collections ranging, follow by the "Herbario Oriente Boliviano" (USZ) with 160000 collections, "Herbario Nacional Forestal" (BOLV.) 60.000 specimens, and the "Herbario del Sur de Bolivia" (HSB) with 40000 collections (Jorgensen, et al. 2014).

After the publication of the "Catalog the Bolivian of vascular plants". The Herbariums from Bolivia, and international botanical specialist in different groups of the Bolivians plants, started the project "Flora of Bolivia", which was fundamental to allow the country to documents its natural patrimony, and as a guideline for sustainable use of plants resources.

In Meneses et al. (2013, 2015), all the herbarium of Bolivia and allied institutions, planned the strategies to develop this project. Most efficiently are planned an electronic, open access publication with international participation, employed modern tools for the taxonomy and morphological data sets (e.g. Edit, Xpers2, Tropicos, etc.), increase the collections in gaps places, and start with groups currently studies, also the molecular phylogenetic studies is the priority currently the participants established jointly a preliminary format for the taxonomic treatments. Currently, the Museum and Botanical Garden of Berlin (BGBM) offers an important support to this project. For instance, one of the most relevant activity was the organization of the first workshop of flora in La Paz- Bolivia with the participation of national and international specialists. Recent (2014 to 2017) promote exchange between the technical team of informatics and curators, as well as the participation of students and botanic specialists of high level to elaborate dataset for specific group of species, and support a PhD student working in punctual groups, thinking on the contributions Flora. All these activities contributing a positive challenge by the Bolivia botanical community. The advance in the project and improve the Knowledge of the circumscription taxa, focus in accessible document will be have repercussions in different levels in the society, in area scientific with information used by ecological, project, but mainly in a political level to have a rea tools for environmental conservation.

1.6. Evolution of the photosynthesis pathways

In the past decade there have been increased studies related with the phylogenetic studies with photosynthetic systems (C3-C4. C3 or C4) type due to the interest and the emergence of interesting evolutionary questions that have arisen from the results of research on photosynthetic pathways C4 showing that these have higher rates of production and water efficiency in relation to the species of the C3 pathway, the C4 species have undergone numerous modifications to anatomical, physiological and biochemical levels, the C4 characteristic will only be fully manifested when this three levels of characteristics are present. On the other hand, it is known that the species via C4 belong almost exclusively to the group of angiosperms, which led to think of a monophyletic origin within this group, with the complexity of these can be found both in monocots (Poaceae, Cyperaceae and Hydrocharitaceae) and dicotyledons (Chenopodiaceae, Amaranthaceae, Euphorbiaceae, etc.) making a total 18 families with this feature.

Advances in the understanding of the phylogeny of angiosperms indicate so far that the photosynthetic pathway C4 evolved independently in each family and in some of them had multiple origins, also independent (Giussani et al., 2001; Sage, 2004), studies of the fossil record, isotopic analysis of paleosoil suggest that the appearance of the C4 pathway is recent and that could take place between the middle Oligocene to Miocene (10 to 20 million years), and during this period of time the Continent of South America was highly influenced by multiples geologic, climatic event, that definitely change the biota of their continent (Grahan 2011), crossing genetically species C3 species C4 observed that the anatomical characteristics (anatomy kranz) segregate independently of physiological (Ascon-Bieto & Tacon, 2008, Sage, 2004). The C4 character would be helped off the ancient C3 to better adaptations in high temperature conditions.

More specific studies in the family of Chenopodiaceae Amaranthacea show that the C4 photosynthesis pathways has been interpreted as evolutionary adaptation to the extremes and variables changes in their originals hábitats (Kadereit 2003, Sage 2007, Sage 2011). Most of these studies are focused on understanding the evolutionary origin of the C4 photosynthesis within the family, it is through the identification of the phylogenetic positions of the intermediary C3-C4 species between C3 and C4 species (Kadereit 2003,. Sage et al. 2007) provided carbon isotope ratios of 607 species of Amaranthaceae and mapped into the phylogeny (*matk-trnk)* found that C4 species occur in 10 genus, one of them was *Gomphrena* with 109 (89%) of the 122 species of *Gomphrena* with C4 photosynthesis pathway (the sampled including all the natives species of Australia) the other has C3.

Amaranthaceae have five independent origins for the C4, the clade *Gomphrena* s. str., include: *Gossypianthus*, *Guilleminea*, *Froelichia* and *Blutaparon,* all C4 photosynthesis. And all the paraphyletic G*omphrena*, with C3 photosynthesis, was recovered as unrelated to *Gomphrena* s. str. and the genus Xerosiphon (a C3 species) and *Froelichia* (a C4 species), is the sister of this clade. In this case would be interesting to see with additional samples and the different marker if all the considered group of plants considered *Gomphrena* s. stric. Has a photosynthesis pathway any phylogenetic studies could answer the times of appearance of these lineages and give us the answer on ancestral relation

1.7 Approaches to molecular phylogenetics of flowering plants and selection of markers for this thesis

For the phylogenetic molecular study in *Gomphrena* s.str. and genus allied, a distribution samples and optimal marker was select. For first instance, the data sampling was reduced (27 species) focus in made a combined three, expected arrive a high support values in a delimitation a genus level.

The chloroplast genome, having a high number of copies for reproducing in work laboratory. Usually, does not present problems of heterogenetic or recombination for the haploid conditions. The latter related to a number of genes, usually less than in nuclear marker, so in theory it must have problems with the maintenance of ancestral polymorphisms and lineage sorting. However, only represents the history of one lineage (mother) and there may also be interspecific introgression problems, that may confound the results obtained (Schaal et al. 1998), although the mutation rates are high vary according to the region and no information is available on the evolution of these (Shaw et al. 2005).

Previous studies in Amaranthaceae with rpl16 (Group II-intron) and trn-F plastidial regions (group I intron in trnL and trnl-F spacer) resolved useful the delimitation of the Gomphrenoideae subfamilies and certain linages. Proven the interspecific variability and the yield good phylogenetic signal between closely related taxa compared to other plastic markers in the same taxon set (Löhne et al. 2007, Sánchez del-Pino et al. 2009, Korotkova et al. 2011). The matK- trnK markers region (group II intron and exon respectively) have a high number of informative characters, even at low taxonomic level (Hilu et al. 2003, Barniske et al. 2012). It has been used in previous e.g. delimitation linages of clades C3/C4 species of the family Amaranthaceae (Sage et al. 2007), and the genus *Ptilotus* (Hammer et al. 2015). Further sampling of the plastid genome combined Rpl16 and matk-trnK provides potential for improving phylogenetic resolution within also other groups as Campanula (Jones 2017).

In a second instance, numbers samples increasing (ca. 80 samples)-especially in the Andean species- for resolved the linages between *Gomphrena* s. str. and distinguishes certain pattern of distribution related to clades, and using datation tools for planted a preliminary hypothesis about when occurs the mainly clades in broad sense. In the large data set analysis phylogenetic, the cloroplastidial regions used was the trnK-matk, and in addition the nuclear region ITS. The latter is commonly used for phylogenetic reconstructions due to several advantageous as high sequence variability, evolution under near neutrality, and biparental inheritance (Álvarez & Wendel 2003, Feliner. N. et al. 2007). This last one allows to insights into possible reticulate events at the species level, hybrid speciation, and parentage of polyploids.

A disadvantage of ITS is that it has been proved to be polymorphic within species, or even within individual plants, suggesting that concerted evolution has not completely homogenized the repeats (Bailey et al. 2003, Álvarez & Wendel 2003, Feliner et al. 2007). The effects in ITS evolution like homogenization, hybridisation, lineage sorting, recombination can involve the generation of orthologoues, derived from speciation events, and paralogoues, derived from gene duplication events. Also, in the ITS regions, can be pseudogenes, (Mayol & Roselló 2001). The pseudogenes, the originated in multiple loci accumulating mutations, may have non-functional these continue to exist and evolve independently at a different mutacional rate than the functional gene, because they not have any functional constrain anymore. (Álvarez & Wendel, 2003, Nieto Feliner et al. 2007).

During process of the aliments, can be distinguished the orthologues, paralogues and pseudogenes (Nieto Feliner et al. 2007). And sampling all ITS copies independently the number is recommended, can be showing complex patterns of interpretation but are useful property for identifying reticulation and when examines together with the distributions of repeat across geographic areas and species, it can be effective to discard the possibility of linage sorting (Feliner et al. 2007).

ITS nuclear marker was use in several previous studies in the family Amaranthaceae most with useful result clear example the molecular to test the monophyly of Ptilotus and planted the first robust infrageneric classification (employed in additions the trnK-matK and morphology data). Other different case was planted by Mc Cauley. R. (2002) indicates the difficulties in aligning the ITS2 region in a small molecular phylogenetic study in *Froelichia* complemented with morphological data.

1.8 Context in which this thesis was elaborated

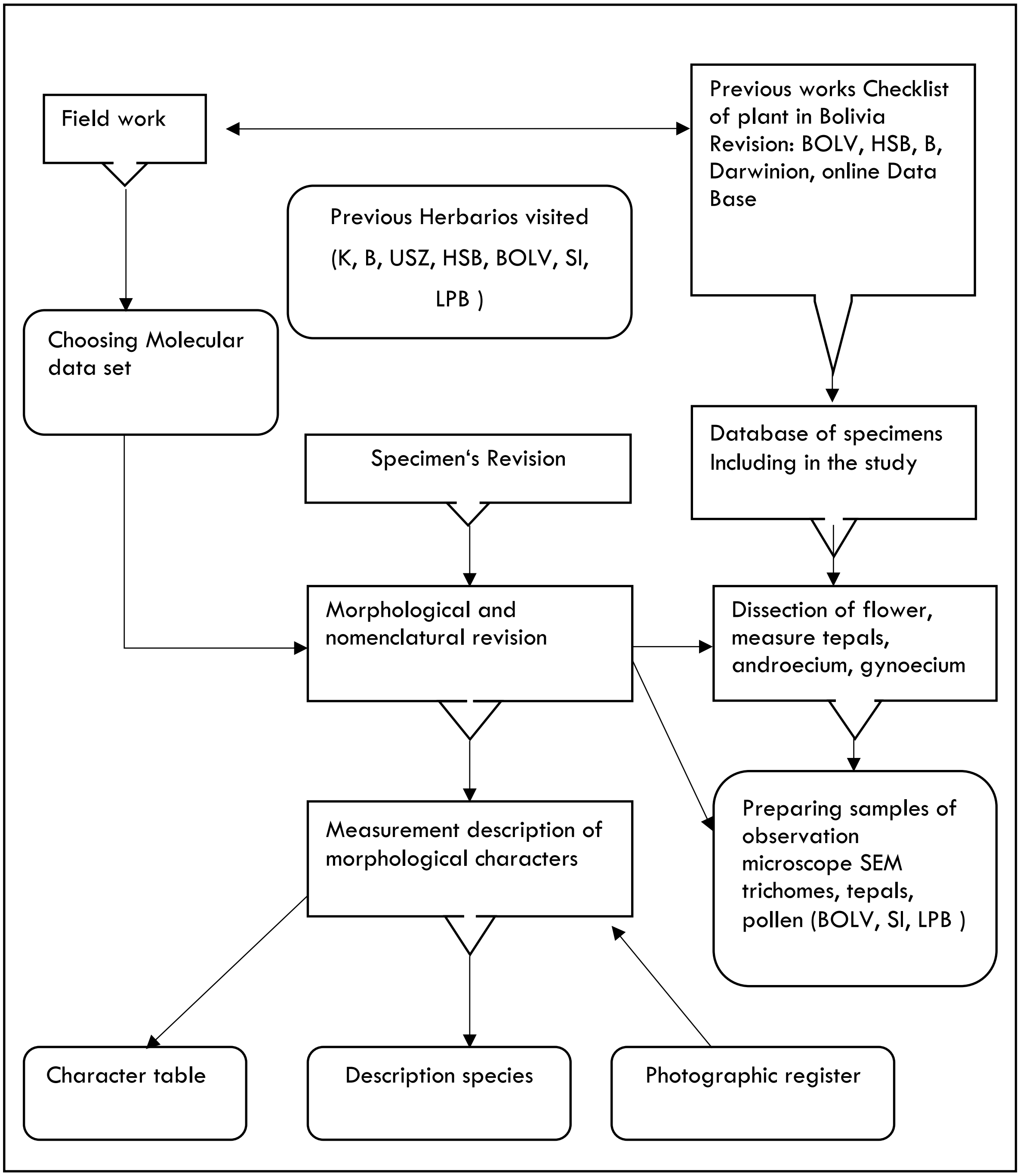
The last fifteen years are established a deeper cooperation between Bolivia and Germany, through the different projects elaborated by the Prof. Thomas Borsch. The cooperation between Germany and Bolivia began within the Botanical Garden University of Bonn, and currently continues with the support of the Botanical Garden, and Botanical Museum (BGBM) and the "Freie Universität Berlin". The Bolivian institutions with official agreements are the Herbarium National of Bolivia (LPB), and the Museum History Natural of Bolivia (MNHN). Under these agreements, the work started with the “Systematics and Diversity of Amaranthaceae” project (supported by DFG, German Research

Foundation) and continued over the last years with the support of the Botanical Garden, and Botanical Museum (BGBM) and the Freie Universität Berlin.

Respect to the fieldwork, in four trip was planning for collected in different ecoregions in Bolivia and Argentina, building on this material between 2010-2016, I have complemented the collections with samples of sites and species not yet covered in the earlier years. Currently the areas more interesting of *Gomphrena* distributions comprise Southeaster of the central Andes of Bolivia, sixty-seven percent of the species growing in these places. The thirty eight percent of the species of the *Gomphrena* are in the Dry valley (Borsch, Ortuño & Nee 2014). The last fifteen years, several botanic researches were as implemented in these regions (López & Ortuño 2008, López, Larrea & Ortuño 2009, Meneses et al. 2010, Wood et al. 2010). All the research focus in have base information to support conservation plan and strategies in the places, one example important advance was the included one new species of Gomphrena in the Red Book of the threatened Flora of Bolivia, of the Andean Zone (Ortuño, Atahuachi & Borsch 2012). Tree new species was described in the context of project of "Systematics and Diversity of Amaranthaceae" (Ortuño & Borsch, 2005; 2006) And the numbers increasing in this work, curiously most the species growing in around these areas in isolated places.

This work pretends to integrate objectives at different levels: the highly and general is the advancement and contribution of the Flora of Bolivia (Chapter 2 and 4). The second level, the revision of the species of Bolivian *Gomphrena* s. str. based on "systematics and evolution", because both concepts are deeply related. The Systematic are based on morphological (> 20 characters defined), of each specimen using as a voucher in the molecular study, with the aims to arrive support the new groups (sections) of *Gomphrena* s. str. based on phylogenetic the Andean lineages (Chapter 3), further more corroborated with the morphological character a generic level and specie level in the case of the Bolivian species (chapter4). The third level is to clarify the relation between *Gomphrena* s.str. and allied genus (*Blutaparon*, *Gossypianthus*, *Lithophila*) and inferring a preliminary hypothesis of the historical distribution of the genus, for arrive a preliminary concept of when the different lineages occur based on obtain the dictation phylogeny through the molecular clock tools.

1.9 General approach of the thesis



Chapter 2

Morphology

This chapter reviews the current state of knowledge on phenotypic characters in *Gomphrena* and also in relation to the Amaranthaceae and presents definitions of the characters and states as well as the respective terminology used in the following chapters (Chapter 3 dealing with phylogenetic relationships and Chapter 4 providing species descriptions). Therefore, it delivers a robust base for the morphology and terminology in support of the treatment of *Gomphrena* for the Flora of Bolivia. For consistency, the numbers of characters and of characters' states included in the reconstruction of ancestral characters using a set of 27 specimens of *Gomphrena* and related genera (Chapter 3) are maintained in this chapter. However, the morphological information that is needed to arrive at a description of the species of Bolivia required including not only more taxa but also more characters. Many of these characters are variable at species level or include quantitative measurements, which were not included to study the phylogetic relationships of *Gomphrena* and the genus concept. Since these characters will not be used at this time for any evolutionary reconstruction of ancestral character states, these characters do not have any numbering (character numbers to be used in a matrix). But since these characters belong to different plant parts (e.g., vegetative morphology, flower morphology), they are inserted into the overall list of characters that is structured into groups characters belonging to the respective different plant parts.

2.1. Overview of previous studies on morphology and other phenotypic characters in the Amaranthaceae and in Gomphrena.

The first morphological descriptions of the genus were made for Gomphrena globosa by Rheede tot Draakenstein In 1689 -1669 Hortus Indicus Malabaricus (vol 9-10. pl. 73. 21-73), (Rheede tot Draakenstein, 1689-1669) which was later formally described by Linnaeus (1753). Eliasson (1988) studied the floral morphology of the Gomphrenoideae. He mentions that Gomphrena differs from other genera of the subfamily Gomphrenoideae in having two slender stigma branches associated with a long filament tube with the anther attached in the sinuses between apical filaments lobules. Townsend (1993) prepared the treatment of the family Amaranthaceae for the families and also summarized the studies so far available on morphology and anatomy.

Between the earlier and the current studies of the species in Gomphrena the character base was increased little by little using a spectrum of macroscopic features (Standley 1917, Holzhammer 1955, 1956, Pedersen 1976, 1990, 1999, Eliasson 1987, Siqueira 1992, Palmer

1998). More detailed comparative studies of individual morphological characters were just carried out by Eliasson (1988). However, the terminology of the characters and hypotheses of homology for the definition of morphological characters are in several cases not fully resolved (such as the characters of the Between the earlier and the current studies of the species in Gomphrena the character base was increased little by little using a spectrum of macroscopic features (Standley 1917, Holzhammer 1955, 1956, Pedersen 1976, 1990, 1999, Eliasson 1987, Siqueira 1992, Palmer 1998). More detailed comparative studies of individual morphological characters were just carried out by Eliasson (1988). However, the terminology of the characters and hypotheses of homology for the definition of morphological characters are in several cases not fully resolved (such as the characters of the androeceum). This is linked to the fact that certain aspects such as ontogeny still remain poorly studied and much the modern studies only include a few widely distributed or easily accessible species (Behnke & Mabry 2012, Acosta et al. 2009, Vrijdaghs et al. 2014). No doubt detailed comparative studies including a more representative selection of species have increased the past years such as Carolin (1983) for trichomes, Borsch (1998) for pollen, Acosta et al. (2009) for inflorescences.

Below some more detaild information on certain kinds of characters but also autecological features (pollination biology) are provided. After this, the methodology is explained that was used to develop a comprehensive list of characters for species of *Gomphrena* but also close relatives. These definitions of the characters and their states were used for the reconstructions of some ancestral characters (characters 1-22) based on molecular trees (chapter 3) part and also for the description and taxonomic treatment (chapter 4) of the Bolivian species of *Gomphrena*. For the descriptions a much more extensive set of characters, many of them quantitative, was used than for examining the generic limits of the genus *Gomphrena*.

2.1.1. Vegetative anatomy.

Stem anatomy. Based on the summary of Townsend (1993) the stem of Amaranthaceae is frequently angular or round, and shallowly sulcate between the highly collenchymatous ribs with collenchyma also present as a ring between the epidermal cells and the usually three to seven layers of isodiametric cells of assimilatory tissue. Cork is occasionally present with increased age. The pericycle usually includes small strands, and is occasionally fibrous. The vascular system normally exhibits anomalous secondary thickening as in the other members of the Amaranthaceae and Chenopodiaceae. The ring or arc of pericyclic meristem producing a succession of collateral vascular bundles embedded in parenchymatous or prosenchymatous ground tissue, which may be in concentric circles or irregularly distributed according to the disposition of the cambium (whether forming a ring or an arc). This is the most specialized feature of the family (Townsend (1993). Wood in the family has uniformly small to medium-sized vessels with simple perforations; rays are high and broad when present, but normally absent and replaced by radial sheet of parenchyma, the parenchyma being paratracheal. Studies carried out by Rajput (2002) were investigating secondary xylem in seventeen species from nine genera of Amaranthaceae, including the two species *G. celosioides* and *G. globosa*. The author found that these species have a radial growth in the main stem, which was achieved by the formation of cambial variants. One segment of cambium produces elements of the xyleme and phloem in fascicular segments (cambium outside of phloem), and other producing axial parenquima in the interfascicular (conjunctive tissues in another segment of cambium), this variation occurs in alternant times, staggered according to the different cambium rings Rajput (2002). In the case of both *Gomphrena* species, the interfascicular regions of the cambium differentiated into thick-walled conjunctive tissues on the side of the xylem and thin walled parenchyma on the phloem side (Rajput (2002). All these species accumulated scanty secondary xylem, which was composed of vessel elements, tracheids, fiber and axial parenchyma while xylem rays were absent at least in the early stages of secondary growth. The cambium in *Gomphrena* is producing thick-walled conjunctive tissues toward the xylem and development of a new cambium ring is observed only after the cessation of cell divisions in the previous cambium. The study of Rajput (2002) showed the thin-walled upright ray cells as well as libriform fibres, and at least the beginnings of rays are evident in the transection of *Gomphrena globosa.* Rays play an important role in radial transport of reserve materials, water and storage. An additional function of rays is compartmentalization from wounding, in which rays participate by forming radial walls of compartments (Shigo 1984). Despite all these roles, a part of dicotyledons is devoid of rays (Carlquist 2003, Rajput 2002).

Leaf anatomy. The presence of "Kranz anatomy" is a structural characteristic that occurs in many Amaranthaceae, some of the genera reported are *Amaranthus*, *Gossypianthus, Lithophila Alternanthera*, *Guilleminea*, *Tidestromia*, *Gomphrena* and *Froelichia* (Welkie and Caldwell 1970; Carolin et al. 1978, Sage et al. 2007). The species with specialized studies in Kranz anatomy are *G. connica*, *G. flaccida* by Carolin et al. (1978), *G. macrocephala*, *G. prostrata* by Estelita-Teixeira & Handro (1984), *G. macrocephala*, *G. prostrata, G. hermogenesii*, *G. lanigera* by Fank-de-Carvalho et al. (2010), *G. arborecens* by Antonucci (2010). The published results indicate that the anatomical details within the genus *Gomphrena* are very similar also in species such as *Guilleminea* (Filippa & Espinar 1993) and *Blutaparon vermiculare* (Do Carmo de Oliveira et al., 2009), the majority of them, except G. *connica* and G. *hermogenesii*, are including in the molecular analysis Chapter 3, in all the this species it is possible to distinguish a closed bundle sheath around the vascular bundles surrounded by non-kranz mesophyll cells or a chlorophyllous palisade layer. The physiology and functions of the Krany anatomy have a tissue complex and is related with the C4 photosynthesis. This anatomical type was described as "*Gomphrena* type" C4 anatomy by Kadereit et al. (2003). It differs from the "Amaranthus type" C4 anatomy that is found in the genus *Amaranthus* (subfamily Amaranthoideae) by a higher number of Kranz cells around the bundle sheaths. And currently in several studies improve in more specific areas the knowlend. (e.g. Sage et al. 2004, Fank-de-Carvalho et al. 2010).

Karyology The haploid chromosome number in *Gomphrena*, varies in number from $x^2 = 8$ to $x^2 = 9$, $x^2=10$, $x^2=11$(found also in Cactaceae), and $x^2=13$ this probably dysploid derivatives from ancestral relatives with base number of $x= 12$, this data are based in 10 species counted, 5 are polyploid (Turner, B. in Behnke & Mabry 2012 pp. 30). The genus with the highest number in Amaranthaceae is *Philotus* with $n = 27\text{-}29$ (Townsend 1993, Turner, B. in Behnke & Mabry 2012).

2.1.2. Dispersal

In the majority is of the genus of Amaranthaceae the highly number of seems producing and the sizes of the fruit are small, helping for the dispersions seems by the wind most than for animals or insect. In *Gomphrena* case the fruit is one utricule (c.1 mm), the perianth in the madurity in general are indurate and compressed cover the fruit, also the majority of the cases are completely cover with lanate trichomes, all this characteristic helping to conclude than the wind are the mainly dispersal of the seeds.

Wind dispersal occurs in species, which grow in Cerrado ecosystems. They are affected by fire, for example *G. macrocephala* (Coutinho 1982, Siqueira 1992, Fank-de-Calvalho et al. 2015) and can after natural fires be dispersed more easily. The passage of the fire burns the grasses and other herbaceous plants and helps dispersal of *G. macrocephala*, *G. pohlii* Moq., *G. virgata* Mart (Coutinho 1982 Fank-de-Calvalho et al. 2015). *Gomphrena macrochepala* is a native Cerrado plant which behaves the same way than other plants in this habitat. After pollination parts of the inflorescences grow to enclose the fruits during maturation and after that, the shoot inclines towards the soil and the inflorescence structure can release the dispersal units to the soil (Coutinho 1982, Siqueira 1992, Fank-de-Calvalho et al. (Coutinho 1982, Siqueira 1992, Fank-de-Calvalho et al. 2015).

In the case of the costal species as *Blutaparon* ssp. Studies recent showing highly capacity to regeneration and high survival capacity to the marine habitat, with some time storms and high tides, one strategy is the reproduction with rhizomes fragment showing the study of Cordazzo (2003) where high percentage of the species showing regeneration ability, this vary seasonally with high sprouting of buds during winter, when the highest nitrogen is content in rhizome, was also found, B. portulacoides has two different reproduction strategies which warrants its persistence on backshore areas. In areas of low shoot density, clonal growth and regeneration of fragmented rhizomes represent a good mechanism on unstable southern Brazilian backshores, while, under high shoot densities of the plants, the species invests more into sexual reproduction, which warrant a good dispersion and a maintenance of genetic diversity on the population. The other mainly factor to help in the dispersal and survival capacity strategy is the tolerance to high concentrations of salt of this species, especially in places with sandy soil are deeper (Cordazzo 2007).

2. 1.3. Pollination

Most the species on *Gomphrena* are reported anemophylus (see dispersal) as that is most norms in Amaranthaceae, reported in *G. agrestis* Mart., *G. graminea, G. macrocephala, G. virgata* (Tannus, J. 2006). However, entomophily seem also play an undoubted part, particularly per bees and butterflies in a new species describing by Barret & Palmer (2015) in Australia, *G. splendida* is reported tha is commonly visited by butterflies and other potential pollinators that obtain small amounts of nectar from the flowers. The most common visitor is the *Fuscous Swallowtail* (*Papilio fuscus* subsp. *canopus* Westwood.

In the Bolivian species we observe, in the field work the new specie (Gomphrena Spec. 7) near to *G. phaeotrichia,* this species has a dark yellow color in the upper part of the Apical leaves subtended the inflorescent and this specie is visited by a *Dipthera* with long prosboscis (in this study). And *G. trollii* we observe than flowers give off very strong odor in general this is associated with attraction to insects; also, the color of its flowers is striking purple.

Ibarra & Sendoya (2016) showing and proving the ant pollination in *Blutaparon portulacoide*, this plant species has most of the traits favorable for and pollination, such as short and aggregated inflorescences, and synchronized blooming as well as growing in an environment where ant pollination is likely to occur, ants are the most abundant visitors throughout the day and that there is no effect of ant integument on pollen germination. Furthermore, the flower visitor exclusion experiment showed that ants have a role in the pollination of *B. portulacoides* by promoting seed formation. Ants can have an important part in the pollination of *B. portulacoides* in a scenario where winged insects are absent or scarce.

Fig. 2-1. *Pollination. A) Flowers of Blutaparon portulacoides visited by an ant (Foto from Ibarra & Sendoya 1016). B) Gomphrena sp. nov. (Spec. 7) [voucher: Ortuño et al. 1677 (LPB, B)] visited by Diptera (Foto T. Ortuño). C) G. splendida pollinated by butterflies (*Foto from Barret & Palmer *2015).*

2.1.4. Pigments

The most striking phytochemical characteristic of the Amaranthaceae is that, in common with Chenopodiales, the family contains betalain pigments, both the yellow betaxanthins and purple betacymins are found, the main betacyanins features by Amaranthaceae are amaranthin (Also present in Chenopodiales) and betamin (replaced by phyllocactin Chenopodiaceae). True alkaloids have not yet been detected in the family (Townsed 1993, Cronquist & Thorne 1994). Betalian pigmentation is much related with the type of dispersal and pollination attraction and indirectly with the evolutions of the perianth in the diferent of family of caryophlyllales tant including Amaranthaceae and Chenopodiaceae (Brockington et al. 2009).

Clement & Mabry (1996) presented the controversy existing about the possible historical factors that have led to the suppression of the anthocyanins and favoured betalain distribution in different families of Caryophyllales including the Amaranthaceae (but see also paragraph above on pollination). Several studies exist that examine the evolution of the pigments in Caryophyllales. One of most recient studies was made by Brockington et al. (2011) with a focus on the biosynthetic pathway of betalain pigments and their biosynthetic distinctness from anthocyanins. Two key enzymes within the betalain synthesis pathway have been identified: 4, 5-dioxygenase (DODA) that catalyzes the formation of betalamic acid and CYP76AD1, a cytochrome P450 gene that catalyzes the formation of cyclo-DOPA. In summary the study concluded that betalain pigmentation arose once early in the evolution of the Caryophyllales, and then was lost in anthocyanic lineages Molluginaceae and Caryophyllaceae.

Specific studies in *Gomphrena* show that *G. globosa* presents in its inflorescences several betalains such as betaxanthins (yellow-orange) and mainly betacyanins (red-violet; Heuer 1992, Kugler 2007). However, the profile of its phenolic compounds is presently less known, and only one flavonoid has been described from the inflorescences (Dinda et al. 2006). More recent research by Ferreres (2011) using metabolite profiling with liquid chromatography-diode array detection/electrospray ionization multi-stage mass spectrometry (HPLC-DAD/ESI-MSn) found 24 phenolic compounds including p-coumaricand ferulic acids, quercetin, kaempferol, isorhamnetin, and hydroxylated 6,7-methylenedioxyflavone derivatives, as well as their aglycones, in the species. Other studies in the genus *Gomphrena* were made by Harrison (2010) on the Australian species *G. flaccida* (red-purple flowers). This species only has betacyanine (betalaine) compounds such as amaranthin, celosianin I, celosianin II, Isocelosianin II, but no betaxanthins were present. As mentioned by Ferreres (2011) and Harrison (2010) is necessary to implement analysis of pigments with a broader set of samples representing different taxa.

2.1.5. Other secondary metabolites

The biochemical composition of species of the genus *Gomphrena* is the focus of several recent studies. Many of the compounds in *Gomphrena* are interesting in terms of ecological interactions of the species in their natural habitats but also for practical applications in pharmacy, agriculture etc. The following Table 2-1presents a summary of the principal components found in some species of *Gomphrena*. Some species, such as *G. globosa* and *G. macrocephala* therefore have an economic importance, being horticultural and pharmaceutical. But also in traditional use, *Gomphrena spp.* has significance as medicinal plants (Ghaffar et al. 2007, Tranam 2014, Fank-de-Carvalho 2012). The taproots of the cerrado species *G. macrocephala* and *G. marginata* were studied with respect to their content of fructo-polysaccharides and accumulated fructans (Fank-de-Carvalho 2012, Viera et al. 1993, Shiomi 1996). The authors suggested that these secondary compounds are part of a crucial physiological strategy of these species as its main reserve carbohydrates, as part of their strategy for survival in environments with a long dry period (Viera et al. 1993, Shiomi 1996).

Table 2-1. Summary of the principal components found in the bibliographic revisions in species of *Gomphrena* including in this study.

SUBSCHRUB	**Summary report on secondary metabolites in *Gomphrena* species**	**Summary main biological activities reported for** Gomphrena	**Traditional User**
Gomphrena mollis Mart.			Folk medicinal plants, used as tonic and carninative (Fank-de - Carvalho 2012).
Gomphrena celosioides Mart.	Ecdysterone, Saponine. (Viera et al. 1994). Aurantiamides (Domosu et al. 2014).	Antimicrobial activity (Bacteria, Plasmodium falciparum); Anticancer properties; Analgesic activity (Salvador et al. 2012). Antibacterial activity in root extracts (Botha & Gerritsma in Domosu et al. 2014).	Urinary problems, skin diseases in Nigeria (Tranam 2014), Analgesic effect (Oladele 2009).
Blutaparon portulacoide (A.St.-Hil.) Mears		Antibacterial componunds, tripanocidal, leismaniacidad. (Salvador et al. 2012). anti-inflammatory activity (Pereira et al. 2009).	Medicinal plant, used to combat leukorrhea (Fank-de - Carvalho 2012)
Gomphrena globosa L.	Betacianins (gomphrenen), Gomphrenin I, II, III Isogomphrenin I, II, III Sinapoyl-isogomphrenin I flavonol (Ferreres et al. 2011). Phytoecdysteroids (Viera et al. 1994).	Antimicrobial activity; Anticancer properties; cytotoxic activity (Salvador et al. 2012, Kugler 2007).	High colesterol and Urinay problem in Latinoamerica and Caribben (Ghaffar 2007, Tranam 2014). Ornamental plants.
Gomphrena macrocephala A.St.-Hill	Betalains Ecdysterone, Saponins (chikusetsu saponin) (Viera et al. 1994).	Molluscicidal (Biomphalaria glabrata) and cytotoxic against Artemia salina (Salvador et al. 2012). Tapoots with storage fructan-rich (Fank-de-Carvalho 2012, Viera et al. 1993, Shiomi 1996).	Antimalarian in Brasil- India (Tranam 2014)., Used as tonic, to reduce fever and against respiratory deseases in Brasil; Ornamental plant (Fank-de-Carvalho 2012).
Gomphrena agrestis Mart.	Aurone aurantiamide acetate, and tiliroside, was isolated from the ethanolic extract, the structural determination of 1 was based on spectroscopic and spectrometric data. (Ferreira et al. 2004)	Active mainly Staphylococcus aureus, Staphylococcus epidermidis and Pseudomonas aeruginosa. (Ferreira et al. 2004)	

SUBSCHRUB	**Summary report on secondary metabolites in *Gomphrena* species**	**Summary main biological activities reported for Gomphrena**	**Traditional User**
Gomphrena meyeniana Walp.	Flavonoides (Viera et al. 1994).	Antimicrobial activity; Anticancer properties; cytotoxic activity (Salvador et al. 2012).	Wound healing in Bolivia Tradicional knowlend.
Gomphrena nitida Rothr.	Betalains (Kimber et al. 1970).		
Gomphrena perennis L.	Protoalkaloides (Viera et al. 1994).	Antimicrobial activity; Anticancer properties; cytotoxic activity (Salvador et al. 2012).	
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Gomphrena canescens R.Br.	Ecdysteroid in seeds (Savchenko 1998)		
Gomphrena flaccida R. Br.	Betacyanins (Betalains) fragment in Amarantin, Celosianin I,II Isocelosianin II, but no present Betaxanthins (Harrison et al. 2010).		
Gomphrena haenkeana Mart.	Terpenoides (Viera et al. 1994).	Antimicrobial activity; Anticancer properties; cytotoxic activity (Salvador et al. 2012).	
Gomphrena boliviana Moq.	Terpenoids, Flavonoids, protokaloides, Glycoside (Viera et al. 1994).	Antimicrobial activity; Anticancer properties; cytotoxic activity (Salvador et al. 2012).	
Gomphrena martiana Gillies ex Moq.	Glycoside, sterols, triterpenoids, ecdysteroids, flavonoids, Betacyanins (Viera et al. 1994).	Antimicrobial activity, Anticancer, properties; cytotoxic activity (Pomillo 1992, Salvador et al. 2012).	Diuretic, laxative and emollient propities (Pomillo 1992).

2.2. Material and methods

2.2.1. Documentation of material

In case specific specimens were examined for individual characters, the same material was used as for the taxonomic treatment (see voucher information in Chapter 4). In those cases only the collector and number are provided here. However, since the purpose of this chapter mainly is to define the characters and their states it often just provides illustrations with mentioning the species that serves as exemplar.

2.2.2. Analysis and description of macromorphological characters

Measurements were usually taken in dry plant specimens based on herbarium material. Macro- morphological observations were mades using in certain cases a stereo microscope, with 20 – 50 X magnification, the measurement was taken with a normal ruler. Solitary flower was taken for dissection from the herbarium specimens; each part of the dissection was made a humid flower- moistened with water-, and different part of the flower was taken in slides and fixed by coverslip with sticker clay. The measurement was taken by a millimeter ruler using the stereo microscope 10-50X, the bract, bracteoles, tepals, androecium and gynoecium was drawing by hand, taking care of the proportions and take note the sizes. Below, we present the quantitatively measured characters. The data of measures for scpecie was introduced in the Xper2 program, distinguished the main chatarter (or descriptors) with the respective character's states for most of the species of chapter 4 (Items).

2.2.3. Micromorphology of trichomes

Gomphrena s. str., the alliend (+ out group species), used in the phylogenic and macro-morfology studies, (most focus in the Bolivians species) was deeper observe using scanning microscope (SEM), the michomorphological observations was focus in the trichomes of the stems, cauline leaves and apical leaves subtending the paracladia (abaxial and adaxial surface), Further more the tepals tissue were review in the apical part, and in general view for see the indumentum. For some observatios and photographic registres was using the light microscope. In the ligth microscope was used the 400X and 800X magnifications.

In this case the sample are prepared in slides we do for each part of the plant trichomes one slides, only Scraping with stiletto and fixing the sample with the help of an object covers. We used plasticine to fix the cover object, and take care of the sample.

For prepared dissection of the samples using material herbarium dry leaves and tepals, dissection for take the tepals samples requires dexterity and care because the flowers are smaller and was made using stereo-microscope, we separated, external, intermedian and inner tepal, usually in the dorsal, ventral and lateral position. The caulinar leaves was cutting in square form for the lower part of the leaves, and in the form of a triangle for upper part. The pieces were take into small aluminium stubs covered with a Leit-Tab (Plano GmbH, Marburg, Germany). The data of measures for specie are introduced in the Xper2 program, distinguished the chatarter with the respective character state.

2.2.4. Micromorphology of pollen

The pollen resgiters form some species was obtained using the scanning electron microscope the samples need to bring under to sputtering or vacuum evaporation process, which physically removes portions of a coating target material, here gold, by shelling with energetic ions (mostly inert gases like argon). The struck-out atoms condensate on the substrate and build a thin layer. A direct current-gas discharge (DC-sputtering) serves as ionic source. The reason for sputtering is that the substrates are often not conducting. In order to have a standard for comparison, of the photos scanned it is used the
two magnification, the first of the 10- 20 µm, and for the secong with detail and 100-200 µm, also the photos were keeping only in one system because the high number of them, the rename include the data of the photo, voucher collector, include the number, accession COD, and the name of plants. I some samples as *G. lanigera* we using the acetolisis modification the Edman methodology for complement the reference information.

2.3. Description and discussion of characters and states (Table 2-1)

The explanation and definition of the main characters used in chapters 3 and 4 are present below. The Twenty Two characteres employed in the phylogenetic reconstruction are organized in the next subtitles (small tree, see chapter 3, with number 1-22). The characters used in Chapter 4.

2.3.1. Vegetative morphology

Life cycle. Character 1

The annual herb completes its life cycle in a single year; any aboveground shoots, whether vegetative or reproductive, die back at the end of an annual growth season (Simpson, 2010). Perennial herbs, subshrubs, shrubs, lianas or vines in Amaranthaceae live for many years.

Life cycle: annual (0), perennial (1).

Complementary information, of the life cycle, the “life form” categorization was distinguishing in *Gomphrena* and allied species. The perennial life form, as in subshrubs, presents a long period of life usualy with woody stems; persistent lignified, especially in the basal part, the upper more thin and ascendant erect stems. The perennial species also having a tuberous taproot, for example in the *G. stellate* and *G. cardenassi cases;* having a tuberous root (xylopodium) for water-use efficiently or carbohydrates storage because these species are adapted to a highlight, hot, arid conditions, to the dry period during part of the year, because are endemic from the Dry valley and Cerrado Chiquitano boliviano. In the case *G. cardenassii* Cerrado species, to discontinuous burning, persisting this species regenerating again from the bud's cells apical in the roots (Wood J.R. 2011), also reported in species of the subshrubs *G. mollis* growing campo rupestris Brazil (Fank de Carvalho et al. 2012), *G. macrocephala*, *G. celosioides* in the savannas de Chaco-Paraguay (Mereles 2005).

The vast majority of the species of Gomphrena studies are herbaceous perennials, or hemicriptophytic perennials. The lasts, with innovation buds at or near ground level producing new leaves and stems during the environmental conditions are good, most the Bolivian species are adapted to a Puna, Prepuna, Inter Andean Dry valley conditions tropical seasonality of the year, with a six-month period dry in winter time with low temperatures and six humid but with Low annual precipitation averages. One the most extreme species is *G. meyeniana* this species grown in widela distribution in the high ecoregion "altoandina" of the Andes, refers to an high altitude between ca. 4100-5000 m (Navarro 2011, Sage et al. 2007), this species has an acaule stems. Cover in the apical part with buds zone protected by dense trichomes, in this acaule stems it is possible observe the scar of the older renovations one for year near a ring, this proving that these species can reach long living than more than 10-15 year (Meneses et al. 2015). The annual, the maturity of the plant is rapid, producing a lot of seeds in a short period of time, in Bolivia the species emergen especially during the wet season and present a fibrous root and vegetative part less development, e.g. *G. umbellata* and *G. pallida* this growing in isolated places of the arid.

Puna were the climatic conditions are more streams (less pp 300 mm), in the second case the seems was founded in "seems bank in the soil" in ecological works in Jirira Salar Uyuni (Acho 2009) showing strategy for surviving to the next humid station. However, the annual species are not only small herbs. Exist also species with vegetative parts developed greatly as *G. perennis*, *G. martiana* and *G. boliviana,* were the plants can be measured more than 1 a 1.5 m growing in the ecoregions of Chaco, Inter Andean dry forest, below showing a Table 2.2 with the list of the species *Gomphrena* categorized by a form of life also including, phenological information.

Table 2-2. List of species of *Gomphrena* including in this study, categorized by form of life including also, information of vernacular name and 36 honological information.

SUBSCHRUB	**VERNACULAR NAME**	TYPE ROOT	FLOWERING	FLOWER COLOR
Guilleminea densa (Humb. & Bonpl. ex Schult.) Moq.	Ojo de pollo (Argentina)	Taproot	Ene-Abr	white
Gomphrena prostrata Mart.		Taproot - woody	All the year	white
Gomphrena mollis Mart.	Erva -mole, herva rosa (in Brasil)	Taproot	All the year	White- pale pink
Gomphrena rupestris Nees		Taproot	All the year	White- pale pink
Gomphrena celosioides Mart.		Taproot		White, Pink, Yellow
PERENNIAL HERB	**VERNACULAR NAME**	TYPE ROOT	FLOWERING	FLOWER COLOR
Lithophyla muscoides Sw.			only records in Jan.	White
Gossypianthus brittonii Standl.		Taproot		White
Blutaparon verniculares Raf.		Taproot	oct-feb or Ago.	White -Ligth yellow
Blutaparon portulacoides (A.St.-Hil.) Mears		Taproot	All the year	White -Ligth yellow
Gomphrena lanigera Pohl		Taproot	Dic- Abr. (after burnig)	yellow-ligth brown
Gomphrena cardenasii Standl. ex Holz.		Taproot	All the year	White
Gomphrena macrocephala A. St. Hill	"Perpétua, perpétua-do-campo, perpétua-domato, paratudo-do-campo, paratudoerva, raiz-do-padre" (in Brasil)	Taproot	Ene- Apr.	White, Red,
Gomphrena stellata T. Ortuño & Borsch		Taproot	Ene -Apr.	white
Gomphrena meyeniana Walp.	La peregrina (Bolivia)	Taproot	Dic -Apr	White, androcum, red, pink
Gomphrena tomentosa (Griseb.) R.E.Fr.		Taproot	Dic -Apr	white- ligth yellow
Gomphrena perennis L.	"infalível, paratudo, paratudinho, paratudo-amarelinho" (Brasil).	Taproot	Dic -Apr	white
Gomphrena potosiana Suess. et Benl.		Taproot	Dic -Apr	white
Gomphrena agrestis Mart.		Taproot	All the year	white rosado claro ao rubro,
Gomphrena bicolor Mart.		Taproot	Dic -Apr	white-bract dark brown

Gomphrena oligocephala Remy		Taproot	Dic -Apr	White
Gomphrena sp. nov (Spec.3) Ortuño & Borsch		Taproot	Dic -Apr	White tepals, androceum dark yellow
Gomphrena fuscipellita Ortuño & Borsch		Taproot	Dic -Apr	White trichomes ligth brown
Gomphrena stolonifera Ortuño & Borsch		Taproot	Dic -Apr	white
Gomphrena trollii Suess.		Taproot	Dic -Apr	Purple

ANNUAL HERB	**VERNACULAR NAME**	TYPE ROOT	FLOWERING	FLOWER COLOR
Gomphrena canescens R.Br.		Fibrous -simple	Jan-Jun	Magenta, mauve, purplish pink, pink or white
Gomphrena flaccida R. Br.		Fibrous -simple	Jan-Jun	Pink-purple
Gomphrena brachystylis F. Muell.		Fibrous -simple	Jan-Apr.	White
Gomphrena radiata Pedersen		Fibrous -simple	Dic -Apr	White
Gomphrena umbellata Remy			Dic -Apr	White
Gomphrena mizqueensis Ortuño & Borsch		Fibrous -simple	Dic -Apr	White- Trichomes yellow -ligth Brown
Gomphrena sp. nov. (Spec. 2) Ortuño & Borsch		Fibrous -simple	Dic -Apr	White
Gomphrena sp. nov. (Spec. 7) Ortuño & Borsch		Fibrous -simple	Dic -Apr	White the apical leaves subtentend paracladia upper part dark yellow
Gomphrena nov. comb. (flexuosa) Ortuño & Borsch		Fibrous -simple	Dic -Apr	White
Gomphrena phaeotrichia (Suess.)Pedersen		Fibrous -simple	Dic -Apr	White
Gomphrena haenkeana Mart.		Fibrous -simple	Dic -Apr	Dark-Pink
Gomphrena boliviana Moq.		Fibrous -simple	Dic -Apr	White
Gomphrena martiana Gillies ex Moq.		Fibrous -simple	Dic -Apr	White
Gomphrena globosa L.		Taproot	Feb-Abr	White, Red, Purple
Gomphrena nitida Rothr.		Fibrous -simple		white

Type of Root. Character 2

Annual herbs have a few "development roots" distinguish in *G. haenkeana*, *G. radiate and G. umbellata.* The perennial herbs have taproots, with a strongly developed of main root, its appearance is indurate and thickened. The taproots are present in *G. tomentosa*, *Guilleminea densa* (Henrickson 1987), in *G. meyeniana* (Meneses et al. 2015), this case is broad, fleshy and can reach considerable sizes and depths to more 25 cm in *G. meyeniana* and more than one meter, in *G. macrocephala*. In this last species and also *G. marginata*, are founded in tissue tuberous root storage fructans (non-structural carbohydrates) these species belong to the dry environment of the Cerrado and Chaco of sub-America this characteristic is crucial for survival the plants the long periods of seasonality dry climate (see chapter 4). In *G. cardenasii* and *G. stellata* the taproot is more lignified especially near the surface of the soil and present woody root, development a secondary cambium atopical reported also in in *G. globosa*, *G. albiflora* (Rajput et al. 2002, Jauregui et al. 2014).

The adventitious root characterized for growing from any structure of the plant, in other structure of plant different to the primary root herb, *Blutaparon verniculare* and *B. portulacoides* when the adventitious root sprout in the stems nodes (Cordazzo 2003, 2007). At the moment only in one species have a stolon root this is system. Besides, these are present in the perennial a new species, growing in the dry forest interandean of the department Chuquisaca, Cochabamba and Santa Cruz of Bolivia, the stolon is slender horizontal branch serving to propagate the organism, is a slender stem that grows horizontally along the ground, giving rise to roots and aerial (vertical) branches at specialized points called nodes.

Currently, only one species that al examined have this type of root,). are describing below is the voucher the "simple root" (0); taproot (1), taproot and adventicious root (2).

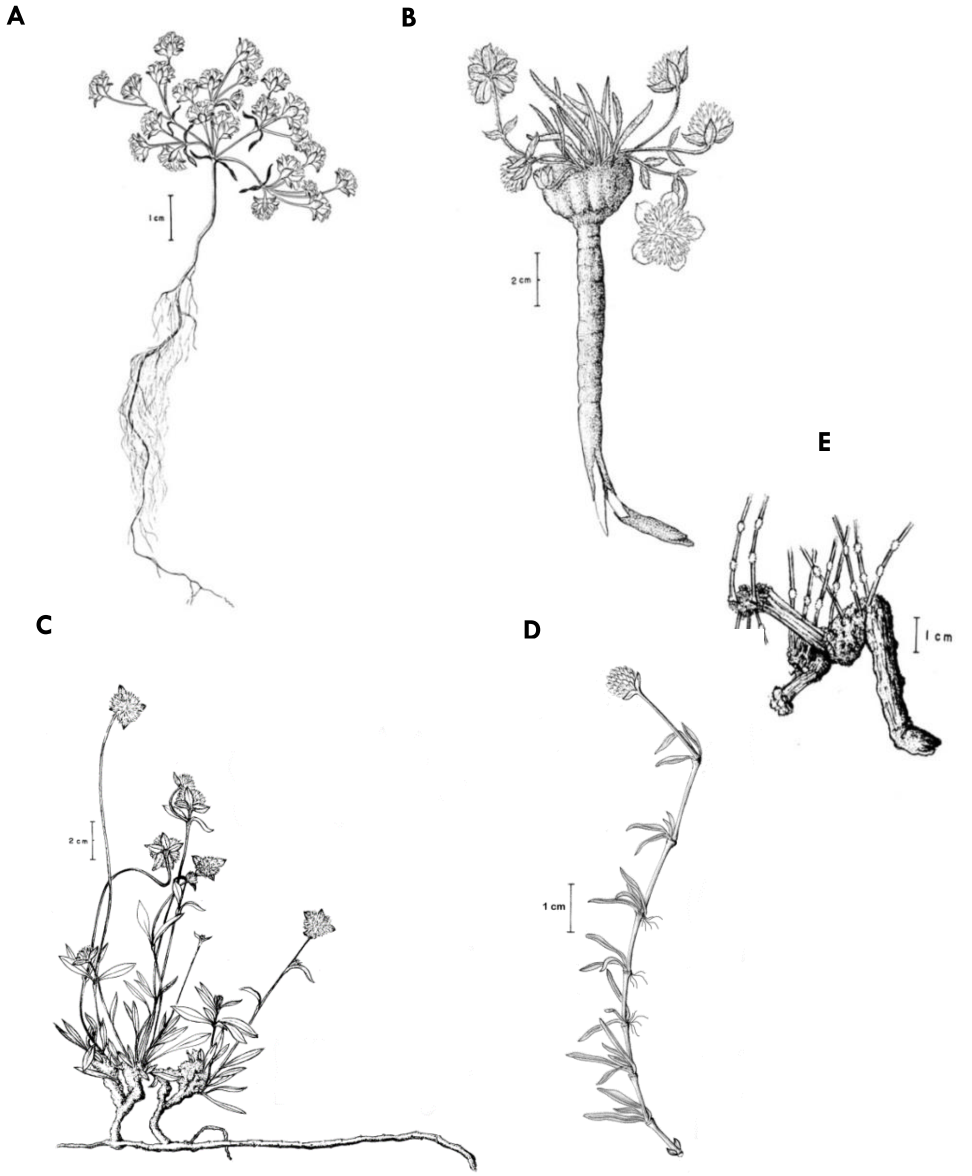


Fig. 2-2. *Type root. A) G. umbellata herb annual with simple root. B) G. meyeniana* herb perennial with taproot. C) *Gomphrena nov. sp.* with stolon. *D) Blutaparon vermiculare* with adventitious root. *E) G. cardenasii* with woody root.

Radical leaves. Character 3

Plants with radical leaves clustered into a rosette growing in reduced main axis. Radical or basal rosette is present in species of *Guilleminea densa*, *Gossypianthus brittonii* (Henrickson 1987) and *Gomphrena meyeniana* (Fig. 2.3). In these species Pedersen (1990) described the character such as "Flowering stem scapose". The basal leaves are biggest than the stemlike leaves but usually are almost similar. The phyllotaxis can be different depending the species in general opposite decussate but *G. meyeniana* has alternated and spiral phyllotaxis.

Radical leaves not present (0), present in prostrate or decumbent plant (1), present in erect plants (2).

Orientation of growth of the stems. Character 4

Several modes of growth are present in the plants: procumbent, when the branch grows spreading along the ground for all their lifetime as *G. tomentosa*. Decumbent, the stems initially spreading is horizontally but then it is growing upwards as *G. potosiana*, *G. pallida*, *G. mizqueensis*. Erect, the stems grow held at right angles to the surface; perpendicular to the surface of the ground as *G. haenkeana*, *G. trollii*, *G. ferruginea*, *G. perennis* (Fig. 2-.4).

Fig. 2-3. Radical leaves. A) *Guilleminea densa* deciduous radical leaves. B) *Gossypianthus brittonii* permanent radical leaves (Cuba). C) *G. tomentosa* permanent radical leaves. D) *G. meyeniana* seasonal radical leaves.

Procumbent (0), decumbent (1), erect (2).

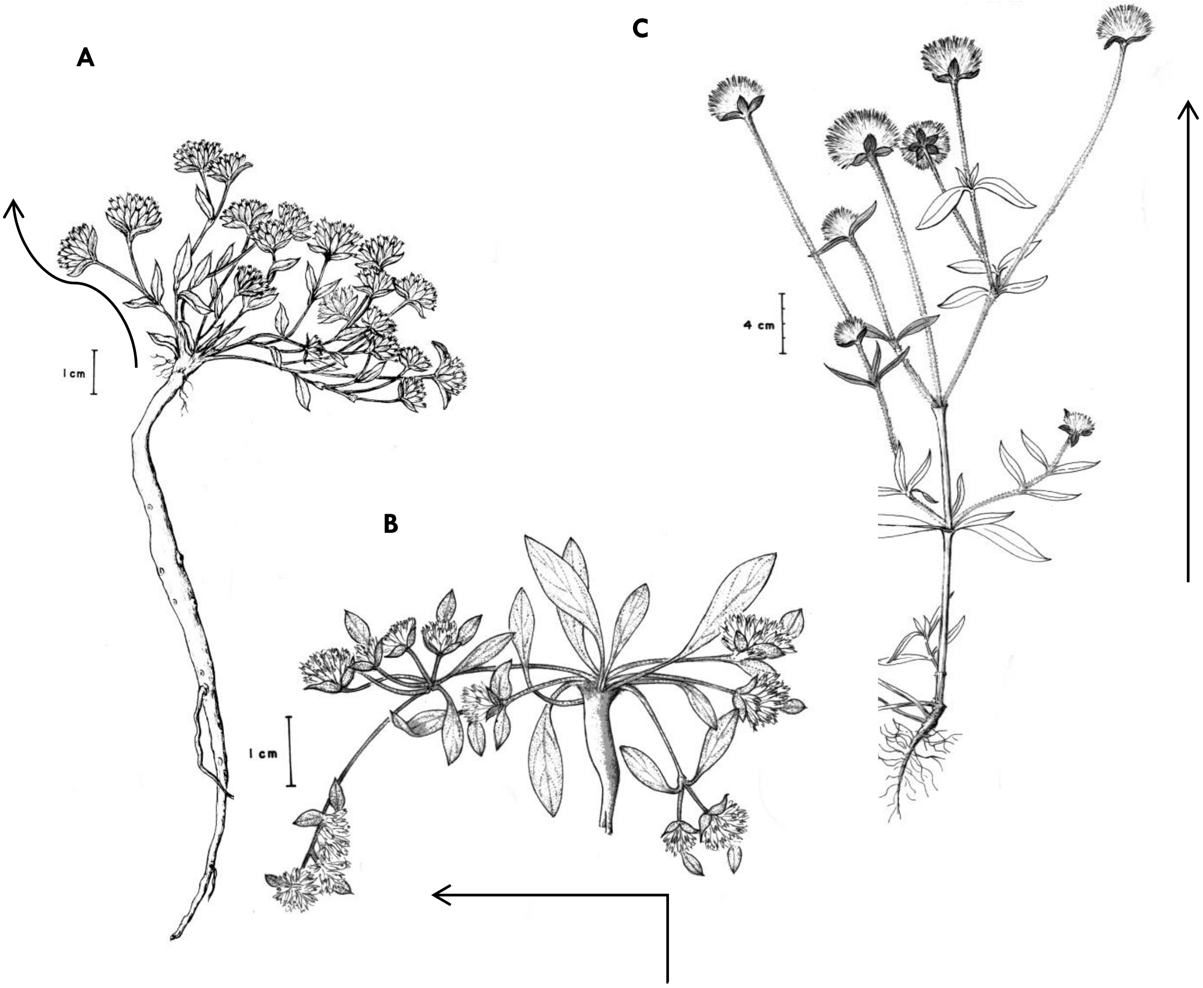


Fig. 2-4. Orientation of growth of the stems. A) Decumbent *Guilleminea densa* deciduous radical leaves. B) Prostrate, *Gossypianthus brittonii* permanent radical leaves (Cuba). C) Erect, *G. hanekeana.*

Vegetative branching system. Character 5

Gomphrena species have different branches in their stems. In some of them it is possible to differentiate a main or principal stem; secondary stems and tertiary stems is founded more common in the species as in *G trollii*, *G. ferruginea, G. perennis*, *G. phaeotrichia*. However, some species can be secondary branches as *G. stellata*, *G. cardenasii*, (Fig. 2-5C) and more than cuaternary stems as *G. umbellata*, (Fig. 2-5D) is possible recognized these three types of stems, this feature allows the plants to expand in the soil surface, with a nearly radial disposition, probably this feature is an adaptation to xeric climate in contrast, also most frequent founded ares the species with only unbranched stem as *G. lanigera, G. agrestis*. Here we codify two type most patronizes.

Only with unbranched principal stems (0), Always with secondary and tertiary stems (1)

Determinate vs. indeterminate growth of stems. Character 6

The specific term “determinate growth”, is used to characterize the main axes (stem formed by apical meristem), that is may remove or abort after some period of functioning or it may transform into a specialized structure such as flower, inflorescence, impeding this further extension capacity (Barthélémy, 2007). In many species of *Gomphrena* is possible recognize these features because the stems finished in the synflorescens such as *G. haenkeana*, *G. flaccida*, *G. meyeniana*, etc (Fig. 2-6B). In contrast, indefinite extension refers to an axis on which apical meristem indefinitely maintains its growth potential. As the indefinite functioning of an apex is always limited at least by the limited life span of the plant it belongs to (Barthélémy, 2007) *G. tomentosa*, *Guilleminea densa* have these features (Fig. 2-6A).

Without determinate growth of stems (0), determinate growth of stems (1)

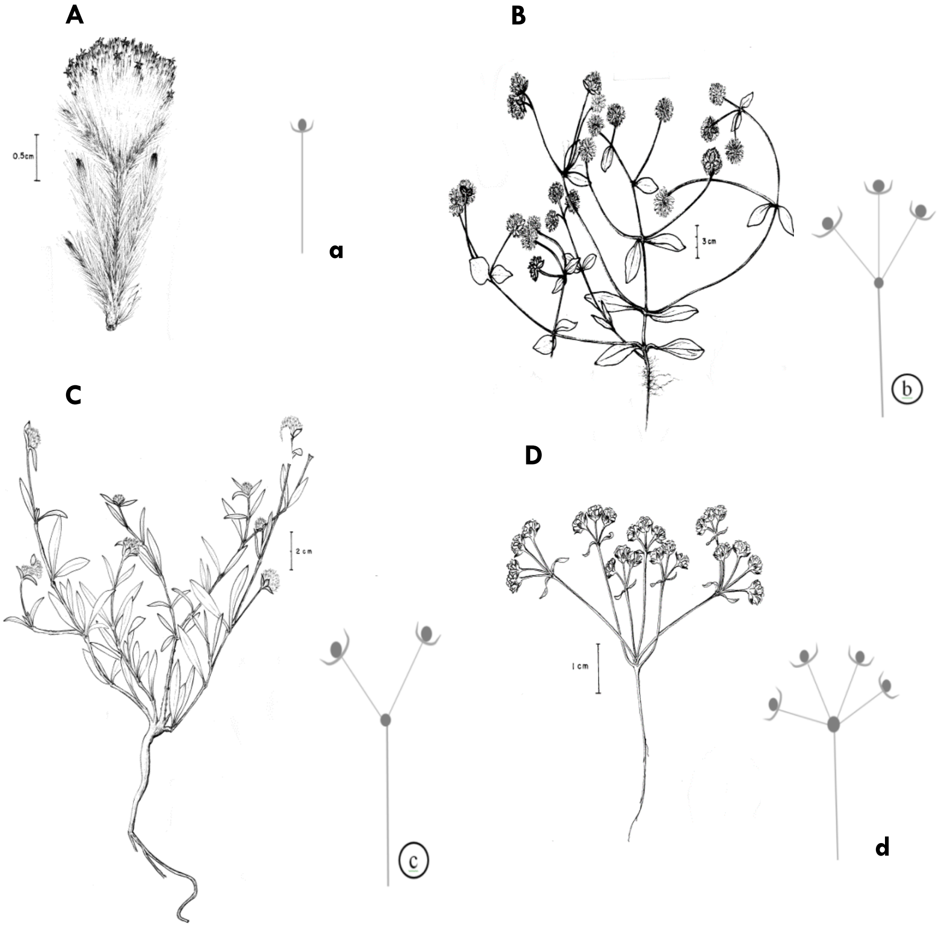


Fig. 2-5. Vegetative branching system. A) *G. lanigera,* with *umbranched stems* (a). B) *G. phaeotricha*, with tertiary branched (b). C) *G. stellate*, with secondary branched (c). D) *G. umbellata*, with terciary or cuaternary branched (d).

2.3.2. Inflorescence morphology

Shape of paracladia. Character 7

Fig. 2-6. Determinate vs. Indeterminate growth of stems. A) *G. tomentosa*, perennial herb without determinate growth, this species to continue the apical vegetative growth after the stage of flower production. B) *G. umbellata*, annual herb determinate, growth of the plant is truncated in the terminal symphorescence.

Floral developmental studies in Amaranthaceae few such studies have been carried out. Payer (1857) investigated flowers in three genera; Alternanthera, Amaranthus, and Celosia. In *Alternanthera tenella*, he described the inflorescence as a spike with bisexual flowers in the axil of a bract. Each flower has two bracteoles. Opposite the tepals, five free stamens originate simultaneously, which "immediately become connate" (Payer 1857: 320), forming a cup around the gynoecium. In Gomphrenoideae, the anthers are disporangiate. The androecial cup grows and forms five bulges alternating with the filaments. These bulges develop in to serrated ribbon-like structures. About the origin of the gynoecium, Payer (1857) wrote that initially a single carpel primordium appears opposite sepal one. The first carpel primordium be -comes quite large, then fusing with the two other carpels (opposite sepals two and three), it forms a bag-like structure, which Payer called "sac ovarien [ovarian bag]" (Payer 1857: 319–320).

On page 320, Payer (1857) described the further development of the gynoecium as follows: "the developing bag-like structure subsequently forms a single style with on top a stigma. Mean while, the distal part of the receptacle, which is more and more surrounded by the gynoecial bag like structure, becomes enveloped by two layers, transforming itself into a campylotropous ovule on a long funiculus".

Globose to subglobose in shape with flowers dessely adjacent (0), elongate to cylindrical with flowers not as densely aggregated (1)

Arrangement of paracladia (synflorescence structure). Character 8

Gomphrena and another Gomphrenoideae exhibit very complex synflorescence structures, part of which did describe by Acosta et al. (2009). 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 paracladiam (Fig. 2-6, 2-7).

States: Paracladia are often solitary and terminal on the main vegetative axes (*G. mollis*, *G. rupestris* state (0) or as well on principal lateral branches (*G. celosioides*) (**state 1**). Alternatively, solitary paracladia can appear in the axes of one of the cauline leaves, and in terminal parts of major branches of the plant there can be elongated or reduced axes often only appearing in one of the leaves' axils (e.g. *G. radiata, G. tomentosa* (**state 2**). In many species of *Gomphrena* the axes bearing paracladia are strongly condensed 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 (e.g. *G. pallida*, *G. boliviana*, *G. perennis*). It remains to be identified by ontological analysis in how far this structure is the result of a strong condensation of a thyrsoid branching system or also involves collateral duplication of buds developing into paracladia (**state 3**). A very specific synflorescence structure appears in *Guilleminea* with a regular asymmetric arrangement of a big paracladium arising from the axillary bud of a large cauline leaf and a very condensed structure with multiple branching orders and smaller paracladia arising from axillary buds of smaller cauline leaves that usually appear only one side of the stem (**state 4**). This synflorescence structure is similar to what did find in *G. radiata* and *G. tomentosa* but with a more complex branching pattern and generally much stronger reduced synflorescence axes. In Hebanthe, Froelichia and Pedersenia, the paracladia are 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 (**state 5**).

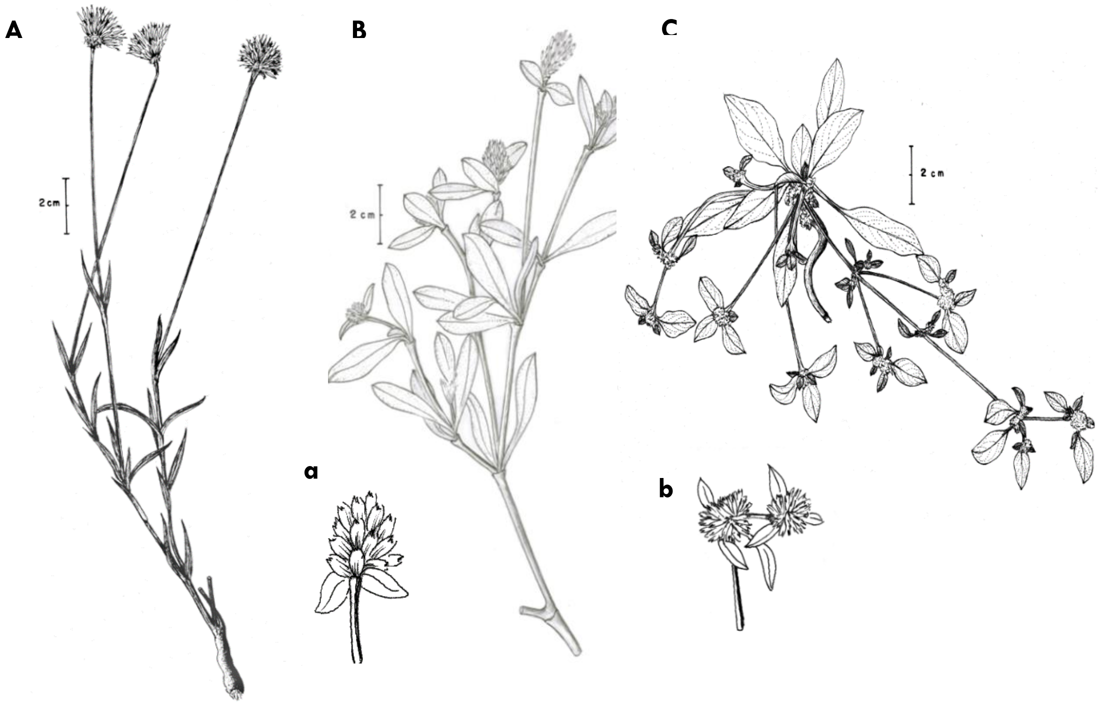
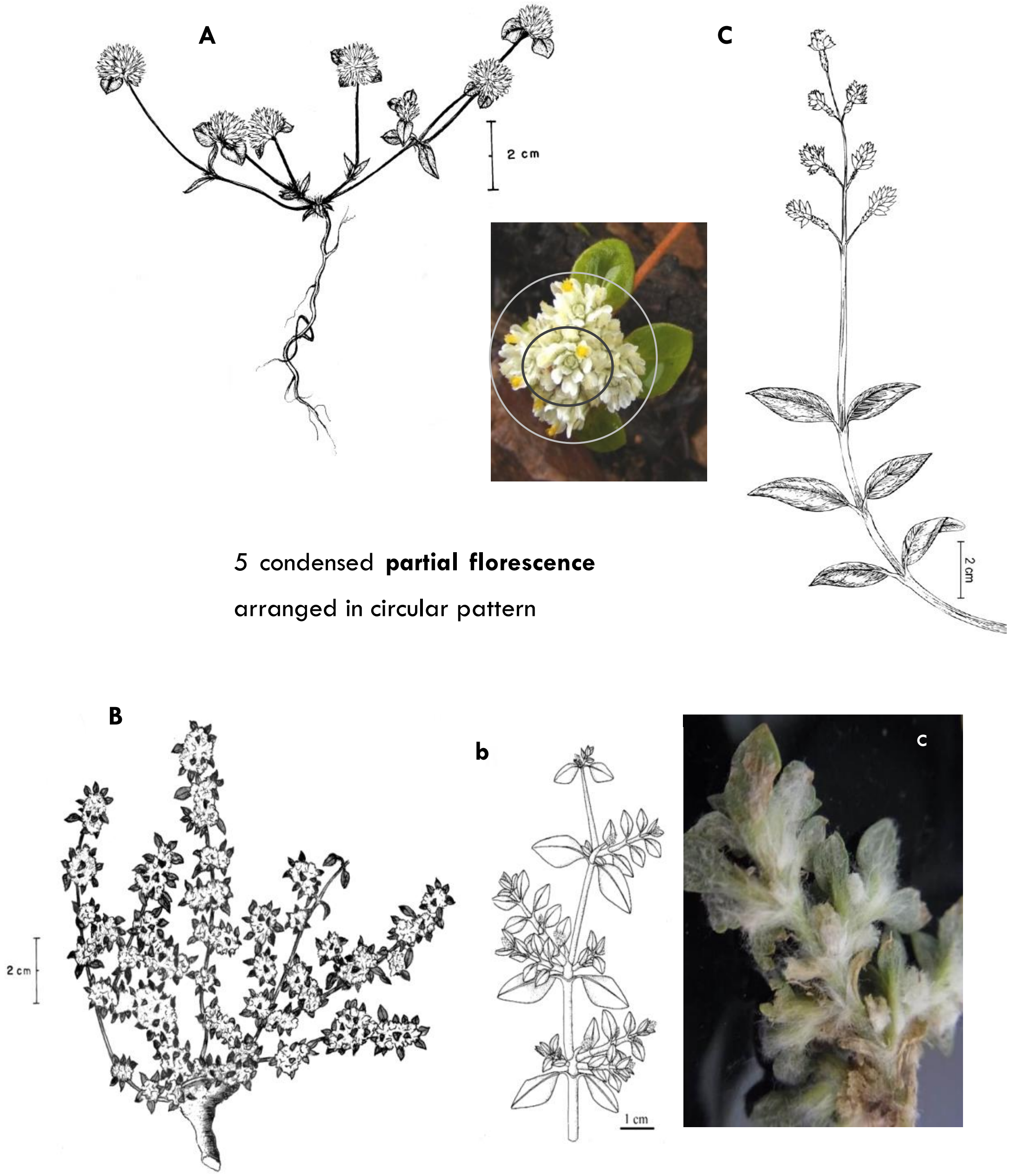


Fig. 2-7. Arrangement of paracladia. A) *G. rupestris*, paracladia solitary and terminal on the main vegetative axe. B) *G. celosioides*, paracladia solitary and terminal on principal lateral branches. a) Detail of the terminal paracladia. C) *G. tomentosa*, alternatively, solitary paracladia appear in the axes of one of the cauline leaves, and in terminal parts of major branches of the plant there can be elongated or much reduced axes often only appearing in one of the leaves' axils. b) Detail of the axillar and terminal paracladia.



5 condensed **partial florescence**
arranged in circular pattern

Fig. 2-8. Arrangement of paracladia. A) *G. pallida.* paracladia strongly condensed, compressed bearing in the axes, multiple paracladia appear in a terminal whorl-like structure with a terminal partial florescence surrounded by usually 5 (3-6) paracladia without visible axes. a) Photo of inflorescence. B) *Guilleminea densa*, regular pattern asymmetric arrangement of a big paracladium with condensed structure with multiple branching orders and smaller paracladia arising from multiplex buds nested always first of two axillary apical leaves, also two new branched are development laterally this complex branching pattern are generally much stronger reduced synflorescence axes. b) Detail the branch showing growing pattern. C) *Froelichia* sp. paracladia are arranged in a complex thyrsoid structure. c) Detail of the lower part with denser trichrome protected the structures of the trampling, always growing on road routes.

Apical leaves subtending paracladia. Character 9

In the case of synflorescences with condensed axes bearing partial florescences (here understood as paracladia with a main axis along which solitary flowers each subtended by a bract and two bracteoles are arranged), there may be specialized cauline leaves that subtend the paracladia (in closely attached position). For the leaves that are morphologically deviant in shape but also often in indumentum and texture (not only in size) from the cauline leaves we propose the term "apical leaves subtending a complex of paracladia". This term used in Gomphrena now, is of pseudantial definition propose by Weberling (1989) refer to the inflorescence which imitate a single flower (Fig. 2-12T, Fig. 2-10A). This would not include the majority of inflorescence where three flowers maintain their complete individuality. However, which present elements of a structure of higher order by means of a more or less marked division of labour in respect of features such as a display organ nectaries, or special structure only concerns some outwardly directed calyx lobes of peripherally placed (primary) flowers. Nevertheless, there is no doubt that they contribute to the attraction of pollinators by optical means, these are not therefore arbitrarily distributed, but are link with the symmetry of the inflorescence as a whole, which enhances the optical effect (Weber 1955, Leppik 1977) (Fig. 2-12T). One example as *Hacquetia epipactis* (Apiaceae) that form a structure of the pseudanthium easily to seen and mainly in this case not only the peduncles of the umbellules are reduced, but also the pedicels remains very short. However, there is no thickening of the inflorescence axis in Amaranthaceae. In the case of condensed pseudanthium in *Gomphrena*, the number of subtending apical leaves is reduced to one per paracladium (= partial florescence). Alternatively, leaves subtending partial florescenes can be completely absent, so that partial florescences appear pedunculated (Fig. 2-9).

Cauline leaves subtending partial florescences absent (= paracladia appearing pedunculated; (0), two opposite and unspecialized (1), with broadend, often stellately arranged (4-) 5 (-6) pseudantial leaves arranged in a whorl (2), with 5-10 specialized, narrow leaves that are very different from the cauline leaves [in *G. macrocephala*, but check if it can be understood as pseudanthium, also check the inflorescence structure again] (3).

Cauline leaves reduced to scales 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 normal photosynthetic cauline leaves also in texture and anatomy. With the presence of such scales, an inflorescence will appear leafless.

Leaves in synflorescence: cauline-like (0), membranous scales (1).

Fig. 2-9. Apical leaves subtending paracladia. A) *G. mollis*, without cauline leaves subtending partial florescences paracladia. a) Detail of the paracladia. B) *G. tomentosa*, two opposite and unspecialized. b) Detail the axillar flower. C) *Blutaparon portulacoide,* two opposite and unspecialized c) detail the terminal flower.

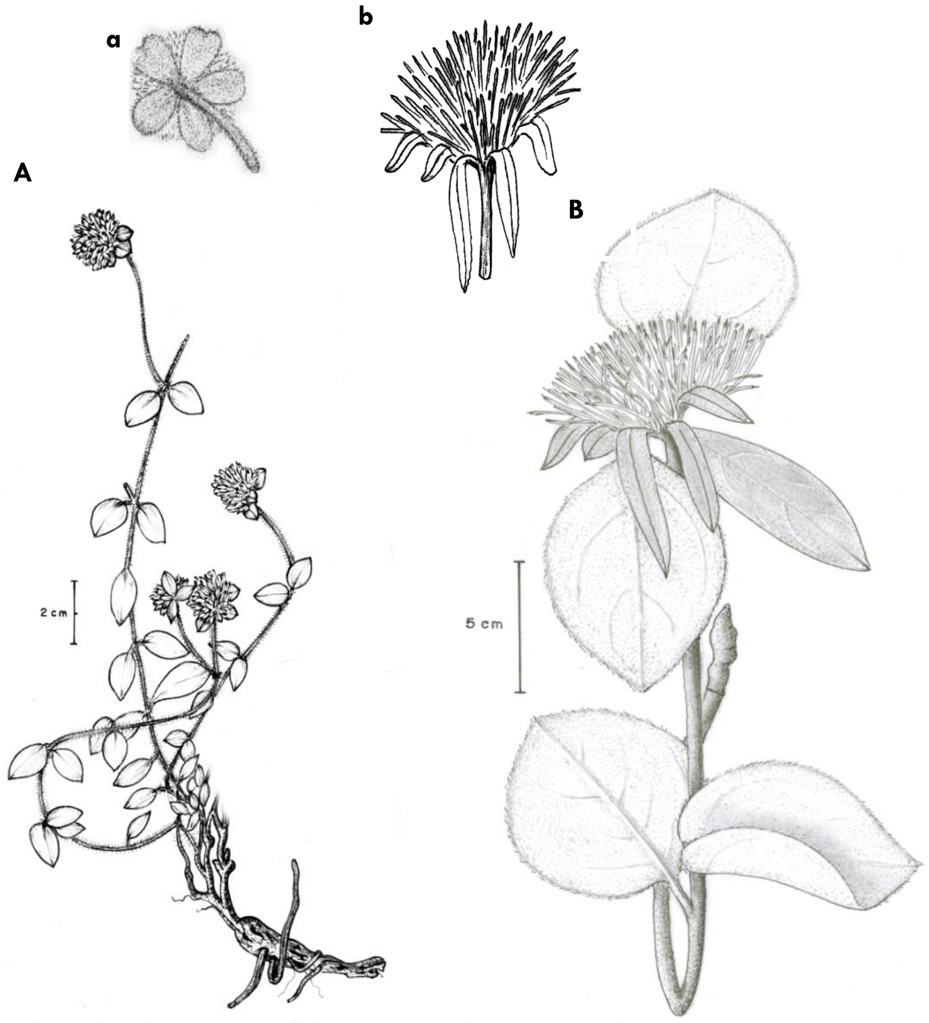


Fig. 2-10. Apical leaves subtending paracladia. A) *G. fuscipellita* with cauline leaves subtending partial florescences paracladia. a) Detail of the paracladia show five leaves symmetrically arranged. B) *G. macrocephala,* with 5-10 specialized, narrow leaves that are very different from the cauline leaves. b) Detail of the paracladia.

Size of paracladia

The synflorescences have variations in the form some are elongated or globose depending on the species, for example, *G. celosioides*, also the species of *Blutaparon portulacoides* and *B. vermicular* have elongated form composed by a paracladio, whereas, e.g. *G. meyeniana*, *G. martiana*, the form is globose and conforms five paracladios. The symphorescences can be reduced from 0.3 to 0.6 cm in diameter in the case of *G. umbellata*, or *Guilleminea densa*, *Lithophyla muscoides*, at the other end the species *G. macrocephala* that has inflorescences measuring 4.5 cm and can reach 13 Cm. G. lanigera, *G. haenkeana* and species of Australia G. flaccid and canescens reaching 1.5 - 3 (- 4 cm), most species are in a range of 1-2.5 cm.

The color of the inflorescences has a role in the attraction of insects, or other animals for pollination and seed dispersion, as well as in the protection of plants from damage caused by UV radiation, besides their potential health benefitsis, previous study pigments show that These are due to storage in the tissues of phenolic elements stored in vacuoles, called betalain. These are typical components found in some families of Caryophyllales (see above) and identify them as betalain and anthocyanin, there are two basic types of betalains, the red -purple betacyanins and the yellow-orange betaxanthins. At the moment few species of *Gomphrena* have studied, the most studies were *G. globosa* and there are works in species of ornamental potential in Australia that include *G. leontopodioides* and *G. flaccida*, and was founded first the anthocyanin not found at the moment in *Gomphrena*, most component are betacyanins (purple-red pigment) and not betaxanthins.

Many species the synflorescence is white (see Table 2), as in *G. phaeotricha*, *G. palida*, *G. ferruginea*, can also be pale yellow like case of *G. tomentosa*, *G. radiata*, and intense yellow the variety G. celosioides, In the white color highlights the color of the anthers that is intense yellow in general but some have been observed with pink tones in *G. meyeniana*, the androceo also arrives to acquire pale brown colors , Yellow, and in species like *G. haenkena* acquire an intense pink color, in *G. trollii* purple and in new species in Chataquiola Sucre synflorescenca intense yellow, *G. lanigera*, The color also occurs in the tepals for most the species. The diversity of synflorescens is showing in figure 2-10, 2-11.

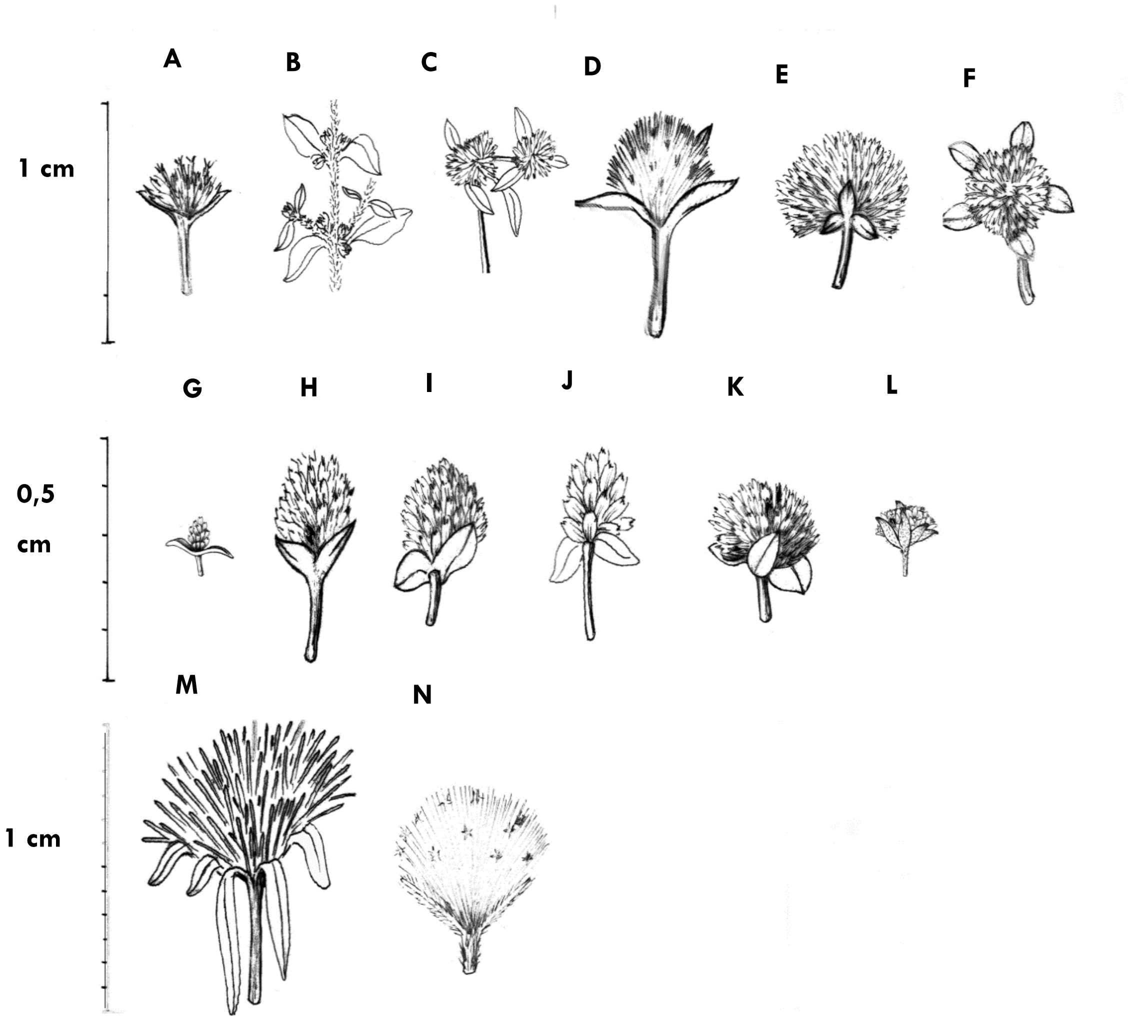


Fig. 2-11. Size of paracladia meausure of diameter in cm. A) *Gomphrena mollis* (1,6-2.2). B) *Guilleminea densa* (0.4-0.5). C) *G. tomentosa* (0,7-1) (--2). D) *G. flaccida* (0,9-2,8) (--3.8). E) *G. haenkeana* (1,9-2,3). F) *G. martiana* (1.8-2.5) G) *Lithophila muscoides* (0,4-0,7) H) *Blutaparon vermiculare* (0,8-3,3). I) *B. portulacoide* (1-1,5). J). *G. celosioides* (0,9-1,2). K) *G. agrestis* (0,75-1,2). L) *G. umbellata* (0,2-0,6). M) *G. macrocephala* (1,5-10). N) *G. lanigera* (2,1-3,8).

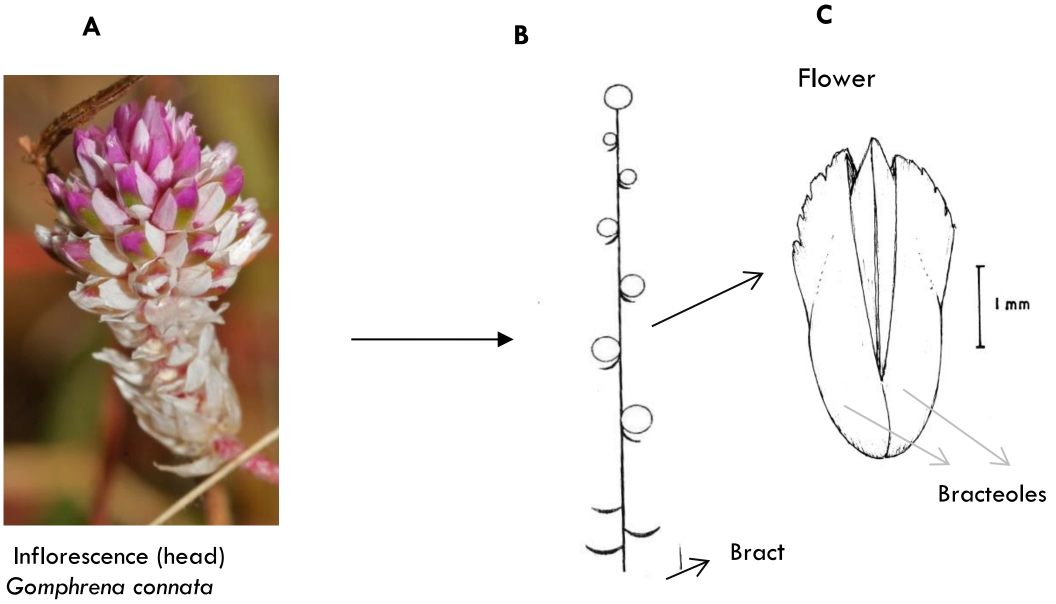
Fig. 2-12. Type pf paracladia (inflorescences). A) *G. prostrata* (Fank de Carvalho). B) *Guilleminea densa* ruderal plants from Cota Cota, La Pa. C) *G. meyeniana*, Hampaturi – La Paz. D) *G. meyeniana* El Alto. E) *Gossypianthus brittonii* Cuba (photo Castaneda). F) *G. tomentosa* Tupiza-Potosí. G) *G. umbellata* (Salariato, D.) Jujuy, Argentina. H) *Lithophyla muscoides* Archipielago Guadalupe http://www.biusante.parisdescartes.fr). I) *B. portulacoide* Bahia- Brasil. J) G. *canesces* (Barret, R.) Australia. K) G. *flaccida* (Barret, R.). Australia. L) *G. macrocephala* (Fank Ode Carvalho). Cerrado-Brasil. M) *G. celosioides*. N) *G. stellata* Rio Grande- Chuquisaca. O) G. sp. nov. Spec. 2-Chuquisaca. (Huaylla, H.). P) *G. phaeotricha* Parque Cardones, Argentina. Q) G. sp. nov. (Spec. 3) Chataquila-Chuquisaca. R) *G. haenkeana Quillacollo*-Cochabamba. S) *G. trollii* Tupiza-Potosí. T) Gomprena. sp. nov. (Spec. 7) Tupiza-Potosí.

2.3.3. Photosynthesis

Photosynthesis C3 and C4 pathway. Character 11

C3 plants are those which fix and reduce inorganic CO2 into organic compounds using only the C3 pathway in photosynthesis. Large air spaces bordered by loosely arranged spongy mesophyll cells; mesophyll cells but not bundle sheath cells (BSC) contain chloroplasts (Simpson, 2010). Gomphrena mollis and G. rupestris. C4 plants employ both C3 and C4 cycles spatially (C4 in the mesophyll cell then C3 in the bundle sheath cell). Generally thinner leaves, closer arrangement of vascular bundles, smaller air spaces than C3; veins surrounded by thick-walled BSC further sorrounded by thin-walled mesophyll cells (wreath-like arrangement of BSC is called Kranz anatomy); mesophyll cells and BSC contain chloroplasts, those of the BSC much larger (Simpson, 2010). Most the Gomphrena clade are included Guilleminea densa and G. prostrate.

Plants C3 photosynthesis pathway (0), Plants C4 photosynthesis pathway (1)



Inflorescence (head)
Gomphrena connata

Scheme of paracladium (= partial florescence),
showing the arranged of bract and solitary flowers

Fig. 2-13. Paracladio Arranged parts. Scheme of the parts and arranged of paracladio. A) Inflorescence. B) Partial florescens. C) Flower cover with two bractoles. Photo *G. connate* Barret.

2.3.4. Bract and Bracteoles

The inflorescences in Amaranthaceae either consist of cymes arranged in more or less complex thyrsoid structures or of solitary flowers (Schinz 1891, Townsend 1993, Acosta 2009) which are interpreted as reduced cymes (Acosta 2009). The subfamiliy Gomphrenoideae has only solitary flowers (Eliasson 1988). Solitary flowers are arranged along an axis in paracladia that could be short or long, depending on the species; i.e. *G. martiana* and *G. meyeniana* have a paracladial axis, while for example in *G. celosioides* the paracladial axis long and erect. The number of flowers of each paracladium varies depending on the species. Each solitary flower is born of the bud situated in the axil of fertile "bract" (Payer 1857, Acosta 2009). On the resulting branch, the flower pedicel, two opposite “bracteoles” grow.

The bracts are ovolanceolate, ovate, elliptic-ovolanceolate, elliptic-oblong, rounded, or even rounded-spatulate (Fig 2.14). The apex is commonly acute (e.g. in *G. perennis*), acuminate as in *G. haenkeana* or *G. lanigera*, to ovate (e.g. in *G. potosiana*, *G. oligocephala*). There most deviant are the bracts in *Gomphrena*. sp. nov. (Spec. 2) from Chataquilla [Wood, Huaylla & Gutierrez, 22662 (LPB, USZ, B, K), see chapter 4]., were have apical part prominent and broadly described as "semifornicada" This morphology is currently not found in other species of *Gomphrena*. The margins are either entire, superficially or deeply dentate.

Possible to distinguished differents textures, according to the grade of transparency, which can be membranous to hyaline or translucent, or chartaceous. The predominant colors in most the species are white, pale-yellow, or light-brown, exceptionally some species have dark brown color. This is the case of *G. bicolor* that has light-brown bracts at the base becoming dark-brown near the apex.
Some species have trichomes on the bracts. They can be distributed in different density and located in different parts of the bract. For example, in *G. tomentosa* they cover the upper dorsal part, in the *Gomphrena*. sp. nov. (stolonifera) [Borsch, T & T. Ortuño, 3610 (LPB, B)] in the margin (see Chapter 4), they are on the margin. The trichomes in *G. bicolor* are loosely scattered in the external dorsal part and the trichomes are similar as on the cauline leaves and on stems.

The two bracteoles enclose the flower, and usually are bigger than the bract. But they are similar in texture and colour. The shape of the bracteoles varies from ovolanceolate to broadly ovate (Fig. 2-13). The apex is generally acute, but also acuminate or rounded; and the margin can be entire, undulate or dentate. The bracteoles are symmetrical with a strong midvein and laterally more or less compressed. The Brazilian species *G. mollis* and *G. rupestris* are deviate by an asymmetric form with one lateral part being smaller than the other.

The bracteoles are arranged with an angle of 90 degrees with respect to the bract. Externally in the upper and dorsal position, most of the American species have a winged and dentate crest that runs along the middle nerve. The form and width of the crest are widely variable (Fig. 2-14) the crest can be thin or broad, while in some species the crest is absent as in *G. martiana* and *G. trollii*. The white color is predominant in the bracteoles. Few species have pale-yellow, light yellow (e.g. *G. tomentosa*, *G. radiata)*; or light brown (e.g. *G. agrestis*, *G. lanigera*, G. perennis) bracteoles. A special two cases are the dark brown bracteoles in *Gomphrena*. sp. nov. (Spec. 3), and furthermore, the bracteoles red to magenta in *G. canescens (*Australian).

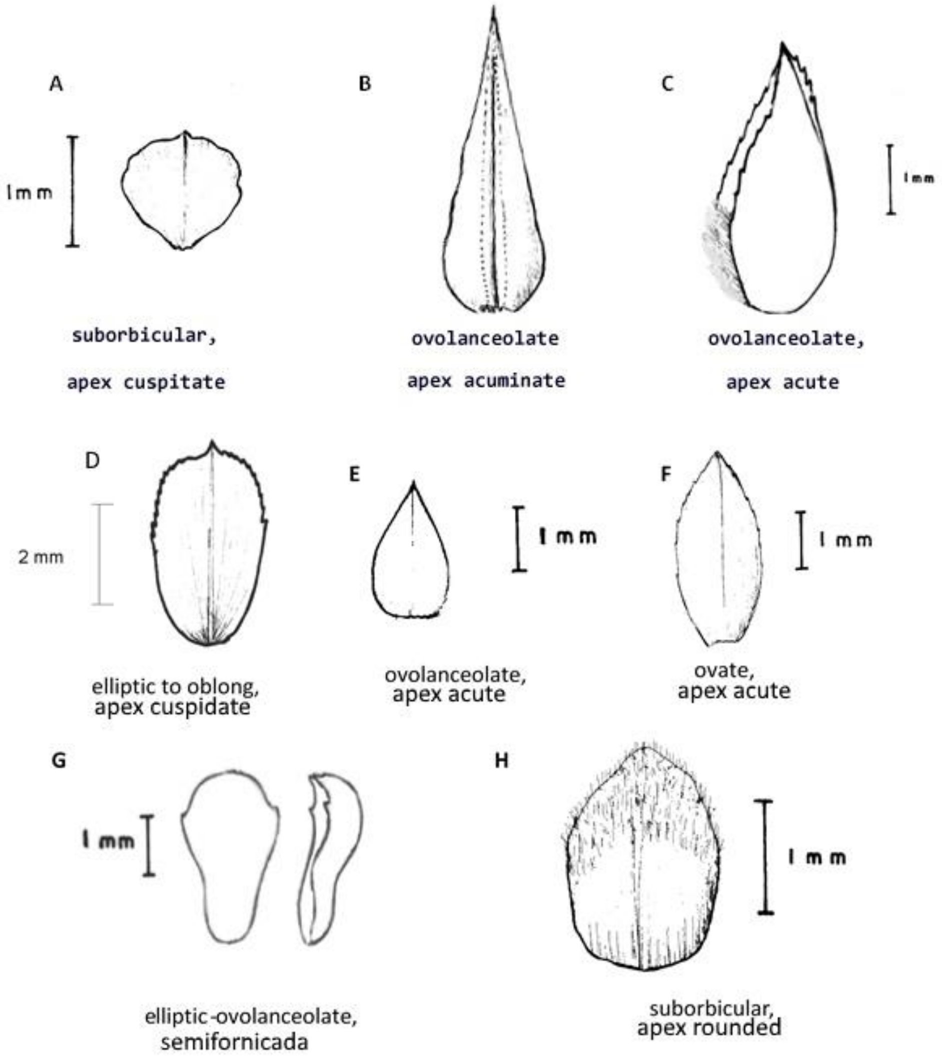


Fig. 2-14. Bract form. A) Suborbicular, apex cuspitate, *G. radiata*. B) Ovolanceolate, apex acuminate, *G. lanigera*. C) Ovolanceolate, apex acute, *Gomphrena* sp. nov. Spec. 7. D) Elliptic to oblong, apex cuspidate, *G. mizqueensis*. E) Ovolanceolate, apex acute, *G. ferruginea*. F) Ovate, apexacute, *G. pallida*. G) Elliptic-ovolanceolate, apex semifornicada, *Gomphrena* sp. nov. Spec 2. H) Broadly ovate, apex rounded, *G. tomentosa*.

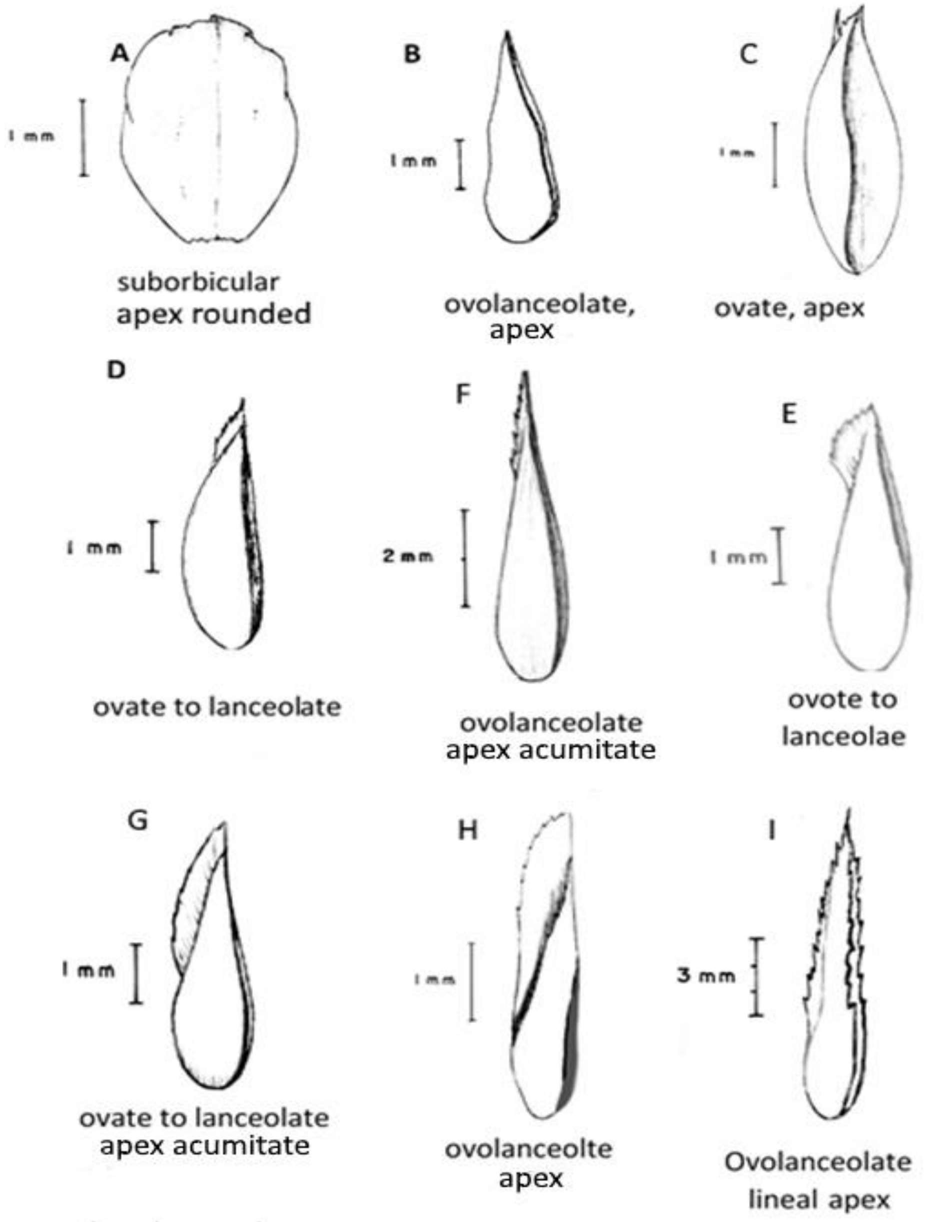
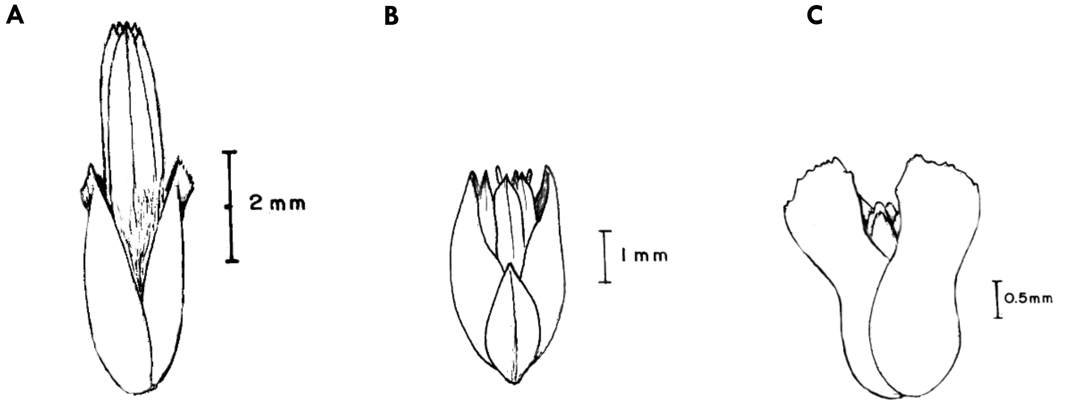


Fig. 2-15. Bracteoles. A) Broadly ovate, apex rounded, no crest, *G. umbellata*. B) Ovolanceolate apex acuminate, no crest, *G. martiana*. C) Ovate, apex acute dorsal crest 1:6, *G. potosiana*. D) *Ovate to lanceolate* apex acute, dorsal crest *1:5, G. bicolor*. E) Ovolanceolate to linear apex acuminate dorsal linear crest 1:3, *G. haenkeana*. F) ovate to lanceolate apex acuminate dorsal winged crest 1:3, *G. pallida*. G) Apex acuminate dorsal winged crest 1:2, *G. fuscipellita*. H) Ovolanceolate apex acuminate dorsal crest 2:3, *G. ferruginea*. I) Ovolanceolate lineal apex acuminate dorsal linear crest 3:4, *G. lanigera*. Most species have ovolanceolate bracteoles (not specifically mentioned); the proportion of total bracteole length on which the crest extends is indicated.

Figure 2-15 shows the spectrum of this morphological variation, and the terms charactersthat will be used for the descriptions of species in Chapter 4. A further character is the relation of the sizes of bracteoles with respect to the tepals (Fig. 2-15), which has also been used by previous authors (Holzhammer 1955, 1956, Siqueira 1992, Palmer 1998). In the flower, the bracteoles can be shorter, equal or longer than the tepals. However, this size-relation is influenced by the position of the bracteoles on the flower pedicel and therefore, and therefore it should be assessed as a character independent of the length measurement of tepals and bracteo.



Tepals > Bracteoles

Tepals > o = Bracteoles

Bracteoles > Tepals

Fig. 2-16. Relations between bracteoles and tepals. A) *G. perennis*, bracteolas shorter than tepals. B) *G. martiana*, bracteoles same side of tepals. C) *Gomphrena* sp. nov. (Spec. 2) bractoeles bigeer than the tepals.

Measurement floral character respect to the flower, bracteoles and bracts

In this study the determination of the specimens collected, was made used literature of previous studies of contemporaneous authors as Pedersen (1967,1976, 1997,1990), Hunziker et al. (1977), Elliasson (1988), Siqueira (1992), Henrickson (1987), Palmer (1998), Ortuño & Borsch (2005, 2006), Senna (2010). For confirm the differences, and made the description especially in the case of specimens from Bolivia, was measurement all the specimens used in the next chapters, taken at detail note, about some character as the proportions of the crest (Fig. 2-16) in the bracteoles, and the bract, the presence of the trichomes, type of the margin, texture, color. All the data are including in annex 2.

MEASUREMENTS “FLORAL CHARACTERS “

f1 = size large of the solitary flower.

g1= size of the width of the solitary flower.

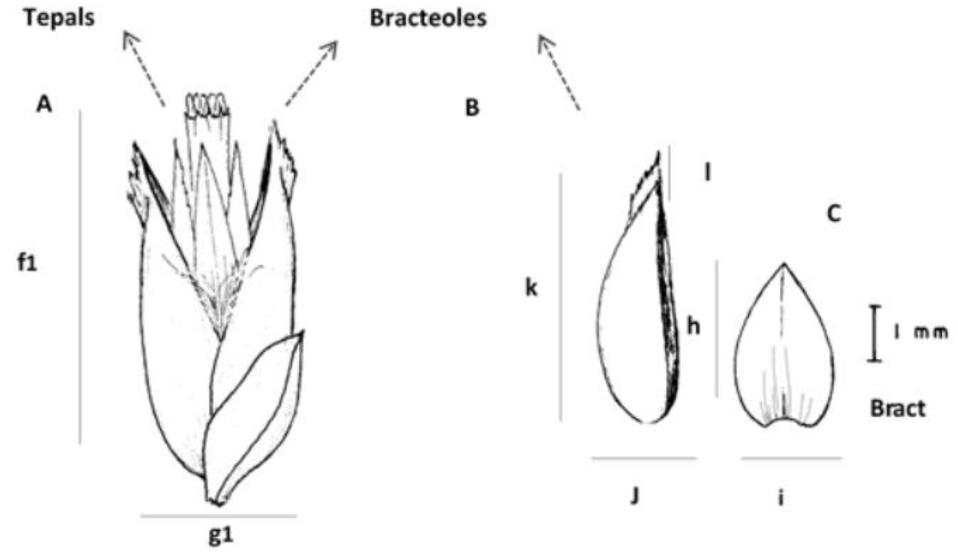
h = size of the large of the bract.

i = size of the width of the bract.

J = size of the large of the bracteoles

k = size of the width large of the bracteoles

l = proportion and the positions of crest the bracteoles, if the specimen have.



Solitary flowers

Bracteol and bract.

Fig. 2-17. Measurement of Flowers, bracts and bracteoles.

Perianth morphology

The perianth parts in Amaranthaceae have been given various names by previous authors, i.e. perianth segments, petals, sepals and tepals. ‘Tepals’ has been used in the description of species of the Australian genera *Ptilotus* R.Br. (Benl 1971), *Omegandra* Leach & Townsend (Leach et al. 1993) and *Hemichroa* R.Br. (Chinnock & Badman 1986), and is used here. The perianth (Fig. 2-16) consists of five tepals of equal length or the inner two tepals are shorter or longer and narrower (unequal). In most of the case the middle nerve thickens towards the base of the inner tepals and becomes concave around the fruit. Each tepals comprises a distinct thickened midnerve of varying length and width surrounded by a membranous coloured or translucent border; the membranous border is also of varying length and width. The margin tepals are entire, or they dentate, i.e. *G. lanigera* where it is lacinulate-serrulate. The margin tepals are referred to collectively here as the tepal margin. The midnerve either terminates before the tepal apex, i.e. *in G. diffusa*, or it terminates at the tepals apex in the form of a narrow vein e.g. in *G. canescens*. This latter state seems to be the case for the large-spiked groups of *G. canescens*, *G. flaccida*, and also the two introduced species.

Morphological differences between inner and outer tepals. (Character 12)

Five individual sepal primordia appear in quincuncial order, followed by the appearance of five individual stamen primordia opposite them. At semi-maturity, the stamens are raised by the formation of a tube below them, with at its inside surface a glandular zone. Alternating with the stamens, appendages develop from individual primordia on the rim of the androecial tube. In bisexual/female flowers, from a primary gynoecium primordium, secondarily, an annular gynoecium wall primordium is formed, surrounding a central zone from which a single ovule develops.

The morphology of the inner two tepals can differ and has been regarded as a diagnostic character of *Blutaparon* and *Litophila* (Townsend 1993). Recent work in Caryophyllales suggests that these organs are in fact sepals as petals have been lost during evolution (Vrijdaghs et al. 2014). However, since the evolution of the perianth is not an objective here, we provisionally continue to use the term “tepals” as in most literature on Amaranthaceae.

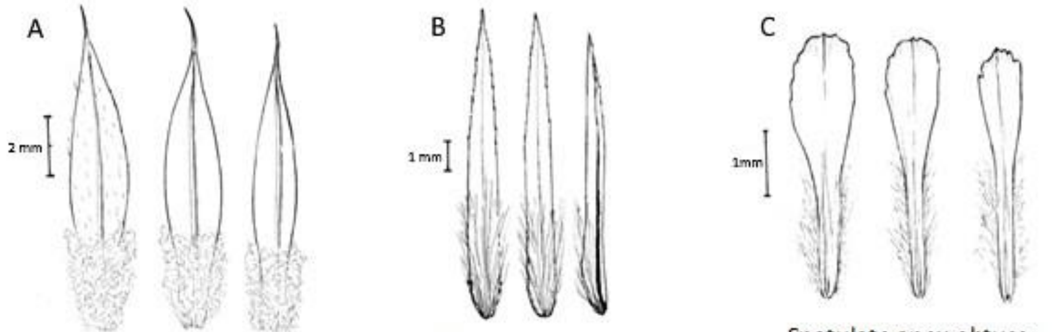
All five tepals equal in shape and texture (0), Inner three tepals smaller than the outer two, strongly compressed and carinate in fruit (1) Inner three tepals smaller than the outer two (2)

Tepal shape

The tepals shapes are ovolanceolate, lanceolate, linear-lanceolate, oblong-lanceolate, spatulate- lanceolate and spatulate (Fig 2.17), the lanceolate narrowly at middle, are characteristic in species as *G. pallida*, *G. phaeotricha* with obtuse apex. The apex are commonly acute (e.g. in *G. bicolor*), acuminate as in *G. lanigera*, abruptly acute (e.g. in *G. potosiana*, *G. oligocephala*), and rounded as *G. umbellate*. The margins are either entire, superficially or deeply dentate in the margin and the apex, or only in the apex.

Tepal apex and margin

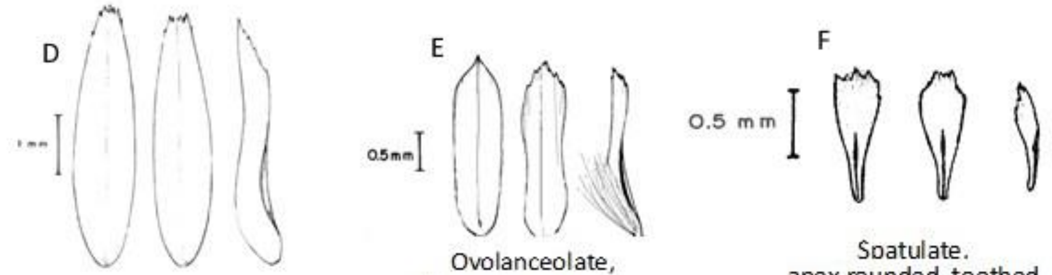
Tepalos in *Gomphrena* are an important character to determine the group of species; these show great variability in disposition and size between external, intermediate and internal tepals, these differences are shown to be stable, as is the indumento. In a study in *G. tomentosa* (Argentina) Hunziker (1977), observe differences in the cells of the epidermal tissue of tepals, finding that their margin form of the cells can be separate some species, no not exist other studies. The observations in electronic microscope (SEM) and optical microscope of the group of *Gomphrena* studied, show that in the majority of the tepals, they have similar cell shape and they are arranged aligned in parallel (Fig. 2-19A,B,C,DF.H), with few or more common few overlapping or superimposed cells, in several rows, forming a uniform lamina. The cells are elongated, fibrous, the extremes are irregular, more acuminate, rotund, or obtuse fitting perfectly with each other, in the margins of the tepals (see above), the cells can acquire a toothed form or entire, vary the arrangement of the fibers, the extreme difference is when having trichomes in the border, they seem to be a continuation of the fibers, because is not possible distinguish the basal cells this occur only in few species. The tissue is always membranous, and can vary in the maturity especially in the basal and in the middle part, and close the main nerve, the texture becomes more coriaceous. The thickness of the membranous tissue vary depending of the specie, usually vary to the fine membranous, with the most extreme example *G. umbellate*, *G. phaeotrichia*, or membranous carinate, e.g. in *G. haenkeana*, *G. lanigera*. The species allied to *Gomphrena* such as *Guilleminea*, *Blutaparon*, *Gossypianhus*, and *Lithophilla*, are organized in similar surface than in Gomphrena. The different type the tissue was founded in the species as *G. mollis*, *G. rupestris*, and in the other genus as *Froelichia*, *Hebanthe*, *Pfaffia*, were the tissue are organized in more than one surface lamina, especially close the nerves and present rounded irregular cells (Fig 2-19E and Fig. 2-19G) giving the spongy appearance. Usually *Gomphrena* s. str. species have one prominent irregular size of tepals, the inner tepals more cimbiform, middle nerve, and the tepals are basally connate.



Oblong-lanceolate, apex narrowly acuminate, margin

Linear-lanceolate, apex acuminate, apex and margin toothead

Spatulate apex obtuse, apex toothed



Ovolanceolate, abruptly acute, apex toothed

Ovolanceolate, abruptly acute, apex toothed

Spatulate. apex rounded, toothed

Lanceolate narrowly at middle, apex acute, toothed

Lanceolate apex apex acuminate

Fig. 2-18. Tepals form and apex. A) Oblong-lanceolate, apex narrowly acuminate, margin entire, *G. rupestres*. B) Linear-lanceolate, apex acuminate, apex & margin toothed, *G. lanigera*. C) Spatulate- apex obtuse, apex toothed, *G. tomentosa*. D) Ovolanceolate, abruptly acute, apex toothed, *G. potosiana*. E) Ovolanceolate, abruptly acute, apex toothed G. sp. nov. (spec2). F) Spatulate, apex rounded, toothed, *G. umbellate*. G) Lanceolate narrowly at middle, apex acute, toothed, *G. pallida*. H) Lanceolate apex acuminate, *G. agrestis*.

Tepal color

The predominant colors in most the species are white some acquiring the green or yellow color close the middle nerve in the maturity, some species vary the color of white to light-yellow, to light-brown, as *G. tomentosa*, or light brown to dark yellow as *G. lanigera*, and sp. now. (spec 3), these last species have yellow-lights brown in the upper half part, and dark brown in the base, the yellow color are also observed in *G. celosioides*. The other common range color is purple, pink, magenta to red as founded *G. macrocephala*, *G. trollii*, *G. haenkeana*, *G. globosa*, *G. canescens*, *G. flaccida* (two last from Australia), the color are related to the presence of betalaine and flavonoids (see above), with specific chemical component, the function also at the moment is ambiguous, one of the probably is the proteccion with a radiations, but probably is related to the pollinations, but require most studies in the genus and in the family at the moment missing more research (see below).

Tepal indumentum

The trichomes on the tepals are frequently founded in the tepals, most of the case are specific type, (see below trichomes). The distribution varies also depending of the type the tepals, refers if the tepals are external, intermediate o inner. It possible founded, that: all the tepals have dorsal trichomes, all the tepals in the species are glabrous; the external glabrous and the rest with trichomes, or only in the inner tepals with trichomes. Apparently, this character is specific (and some case intraspecific limited varieties) and stable in the species, but this is character usually are in discussions because is usually the presence of trichomes are cataloged is a homoplastic character, but practically in the revision of species, it possible to see the patterns are repetitive, but needed meticulous in observing. Currently this character was used in *Gomphrena* specially by Pedersen (1976), he also distinguishes varieties, and example are *G. pallida,* have trichomes in the margin, to difference *G. phaeotricha* are glabrous or some related species have trichomes only in the dorsal part, but also used additional character as the size tepals.

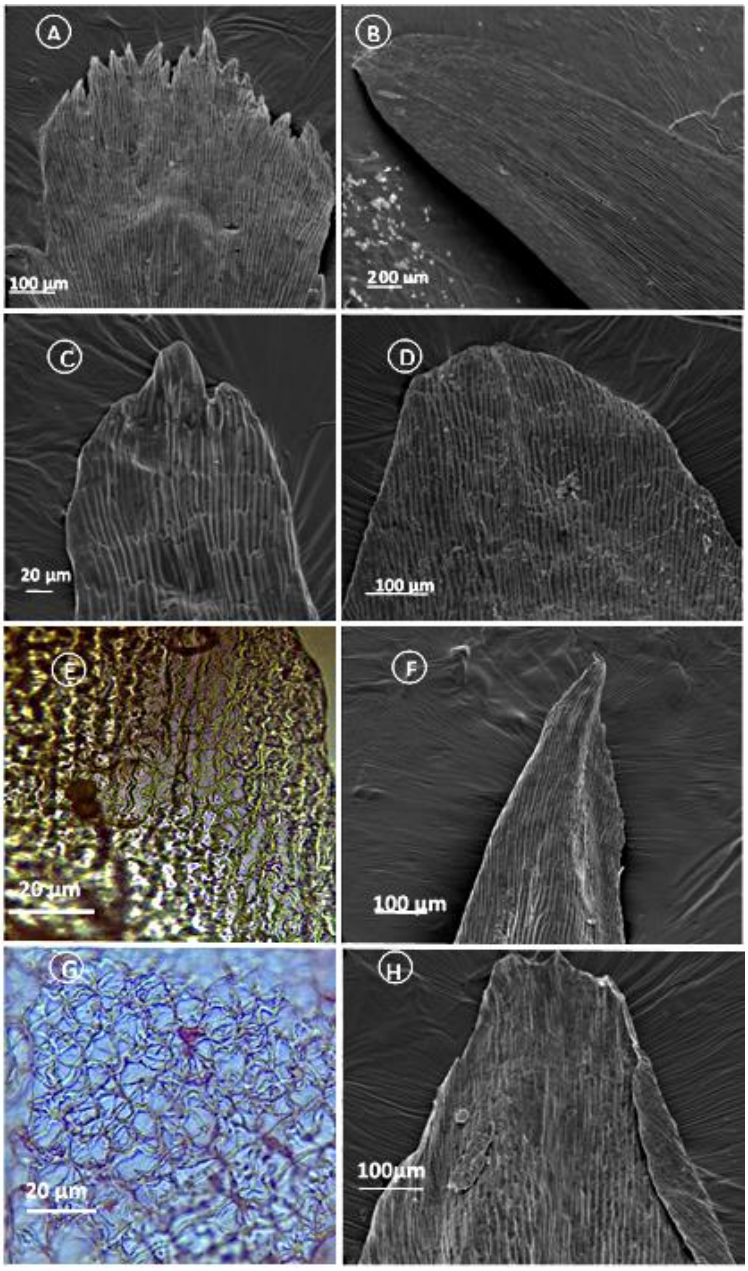
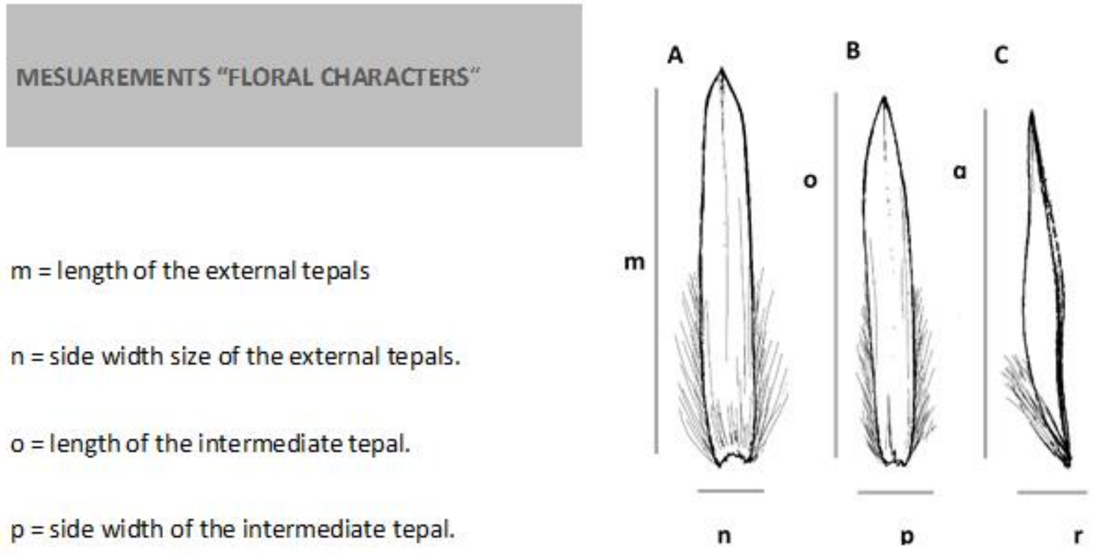


Fig. 2-19. Tepal apex and dermal tissue: A) Toothed in the apex, dispositions of the cells in one surface lamina elongate fibrous cells, *G. mizqueensis* [voucher: Borsch & Ortuño, 3584 (B, LPB)]. B) Entire apex, acute, elongate fibrous cells, *G. flaccida* [Lazarides, M. 8882 (B, NSW)]. C) Few dentate apex, elongate fibrous cells, G. sp. nov. (spec2) [Wood, et al. 23269 (LPB, B, K)]. D) Rounded apex, elongate fibrous cells, *Blutaparon vermiculare* [Borsch, 3444 (B)]. E) More than one surface lamina, rounded irregular cells, *G. mollis* [Harley 27179 (B)] F) Acuminate apex elongate fibrous cells, *G. cardenasii* [Wood, et al. 18813 (LPB, B, K)]. G) More than one surface lamina, rounded irregular cells, *G. rupestris*. [Harley, 26990 (B)]. H) Obtuse apex, elongate fibrous cells, *Lithophila muscoides* [Proctor, G 33175 (B)].

Measurement floral character respect to the tepals.

In the same way than the bract, and bracteoles, for the tepals was measurement all the specimens used in the next chapters, taken at detail size, we take note, about type of the margin, presence and positions toothed part, the position and presence of trichomes, texture, color. All the data are in table 2-4.



MESUAREMENTS "FLORAL CHARACTERS"

m = length of the external tepals

n = side width size of the external tepals.

o = length of the intermediate tepal.

p = side width of the intermediate tepal.

Fig. 2-20. Measurement of the tepals: A) external tepas, always are two. B) Intermediate always one, C) inner tepals always two.

Perigynous versus flowerS. Character 13

In the genus *Gomphrena* sensu lato and allied genera flowers are hypogenous with tepals and androeceum tube attached to the axis below the ovary. This feature is different in the species of *Guilleminea* where the androeceum is adnate to the perianth and the flowers are perigynous (Fig. 2-21A) (Mears 1967; Eliasson 1988; Henrickson 1987; Townsend 1993).
Perigynous (0), Hypogynous (1)

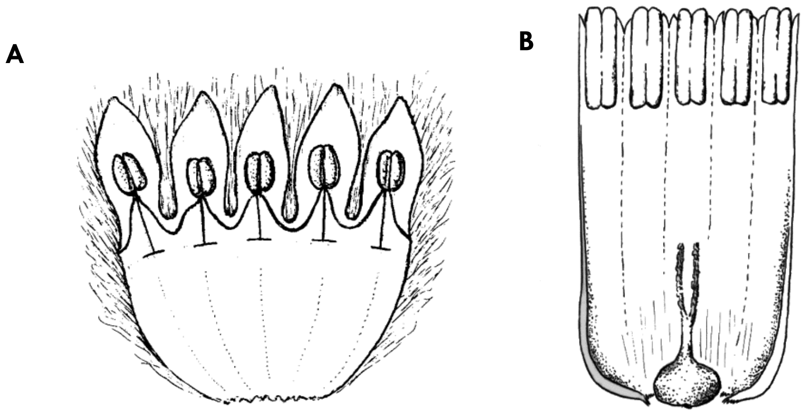


Fig. 2-21. Perigynous flowers. A) Design of perigonious perianth of *Guilleminea densa*, showing the insertion of the filament in the half upper part of tepals. B) *G. mizqueensis*, specie hypogenous, showing the inserccion and position of the gynoecium.

2.3.5. Androecium

Gomphrena genus usually has five functional staments, with exception of *Lithophilla* that has two stamens. However, *Lithophila* has in it a filament margin cup three tooth, which probably correspond to the rudimental statement (Eliasson 1988). The filaments are united into a cup–like tube or elongate tube, with a small free portion (Eliasson 1988, Vridaghs et al. 2014). The free portion of the androceum tube can be a simple extenssion of the filament, which is generally linear with an acute or rounded ápex. It can also present what we will call filament appendages, which are two prolongations in both sides of the union of the anther with the filament, and can be united at the base in a fork way.

In our opinion, gomphrenoid androecial tubes and their appendages result from a reorientation of parts of the ancestral meristematic potential in the floral apex into androecial tubes, coupled with new functions such as attraction of pollinators and/or contributing to the pollination process. Support for our hypothesis is provided by the following observations: the inner base of the cup formed by the androecial tube is glandular, and at least in *Iresine, Hebanthoides* and *Alternanthera microcephala*, the androecial tube appendages are conspicuous and brightly coloured. Regarding the nature of the appendages, our anatomical data do not support that appendages are staminodes.

The figure 2-22 showing the parts and measurements of the androecium, the measured was performed by the dissection of flowers and employing the stereomicroscope and millimeter ruler.

Length of androecial tube. Character 14

Due to gradual variation we distinguish size classes. Measurements are from the connection to the floral axis (proximal) to the distal tip of the filament where it is connected to the anther.

Length of the tube: 0.6-4.2mm (0), 4.3-5.9 mm (1), 6-7 mm (2), 8.1-10.2 mm (3),>31 mm (4)

Fusion of androecial tube. Character 15

This character exhibits gradual variation and is measured from the deepest point between two stamens or between the stamen and the adjacent androecial tube appendage. The free part of the filament should thus also be defined in proportional relations of the total size of the androeceum and the free part.

Degree of free part: 0.6-6 % (0), 7- 30 (1), 31-50 (2), 51-60 (3), 61-75 (4), >75 (5).

Shape of androecial tube. Character 16

Four different states can be distinguished: 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). (Fig. 2-23).

Presence of androecial tube appendages. Character 17

The androecial tube appendages were called “pseudostaminodia” and transitions to stamen appendages have been described (Townsend 1993). Considering that either such pseudostaminodia or stamen appendages on both sides of the anther were found, both were considered to represent modifications of one character (Townsend 1993, Eliasson 1988).

Recent developmental and micromorphological studies indicate that the androecial tube appendages are not homologous with tissues of different quality (glandular) with a putative secretory function in pollination biology (Vrijdaghs et al. 2014). However, so far only samples from the genera Alternanthera, Iresine and Tidestromia were examined. We define the androecial tube appendages as an own character.

Presence of androecial tube appendages states: absent (0), present (1).

MESUAREMENTS “FLORAL CHARACTERS“

s and o = length of the tube the androecium (Character 14).
t = length of the fused tube the androecium. (Character 15).
t 1 = the size the end of the “fused tube” of the androecium.
u and r = the size of the free part of the androecium (five part).
v = the size of the underside of the filaments appendix.
w = the size of the filaments appendix (Character 21)..
w1 and q = size of the large of the anther.

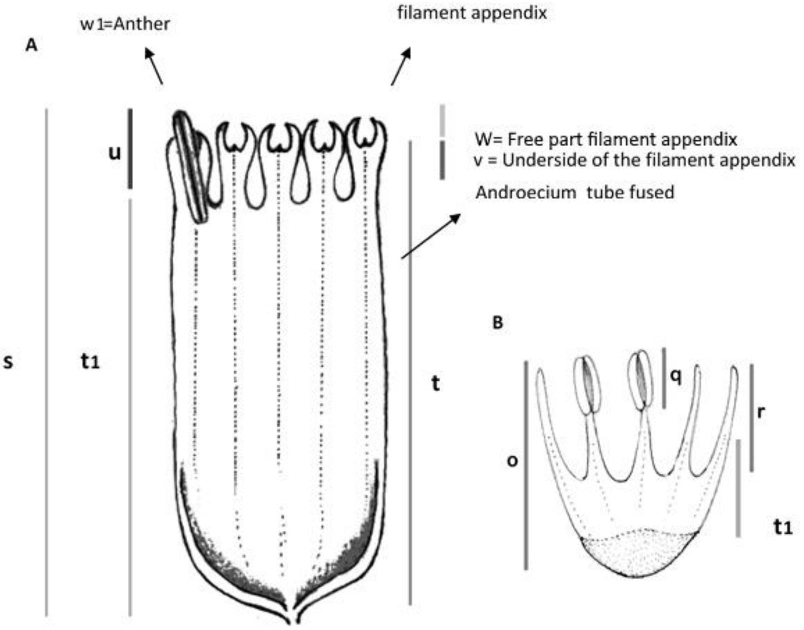


Fig. 2-22. Design showing the structures and morphological measured parts of the androecium A) *G. agrestis*, with filament appendix divided. B) *Blutaparon vermiculare* with gradually narrowing. filament.

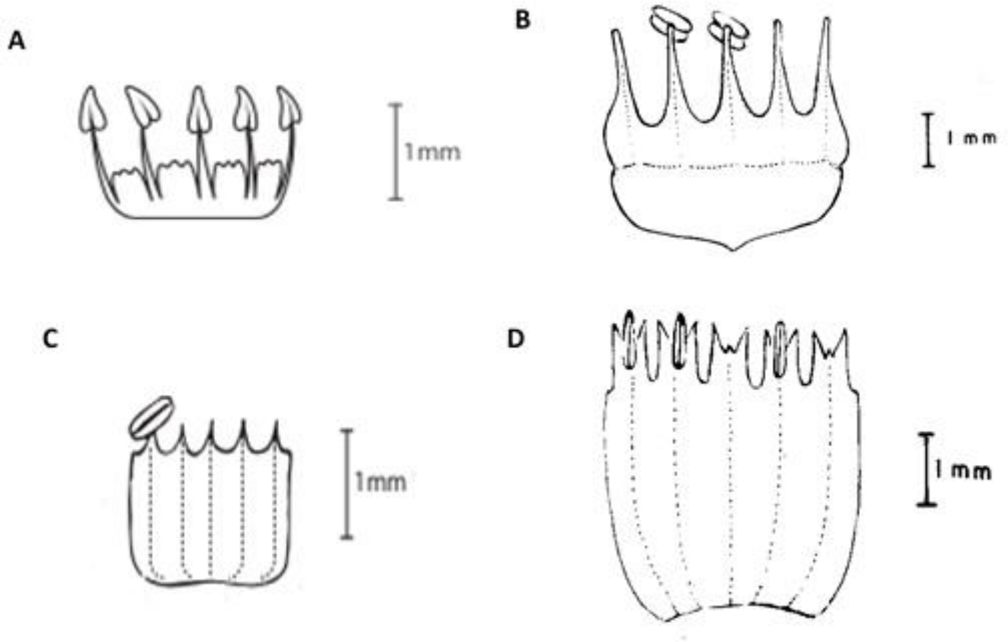


Fig. 2-23. Shape of androecial tube. A) *Pedersenia volubilis*, broadly cup-shaped with distinctly spaced linear filaments. B) *Blutaparon portulacoides*, more or less broadly cup-shaped with V-shaped connection between gradually narrowing filament. C) *G. tomentosa*, more or less broadly cup-shaped with U-shaped connection between more or less abruptly narrowing filaments. D) *G. celosioides*, filaments broadly linear with narrowly U-shaped connection between filaments.

Shape of androecial tube appendage. Character 18

States: Broadly truncate with papillae (in *Pedersenia*) (0), narrowly oblong and obtuse at apex" (in *Froelichia*) (1), linear with cleft apex (2).

Presence of filament appendages. Character 19

States: absent (0), present (1)

Length of filament appendages. Character 20

Due to gradual variation we distinguish size classes Length of tube: 0.1-0.2 mm (0), 0.3-0.5 mm (1), 0.6-1.0 (2), 1.1- 1.5 (3)

Shape of filament appendages. Character 21

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

Note It is necessary to add in the characterization of androecium two remark, in the analysis and description with an additional sampling of species, was possible observe two specific characters not clarify an earlier, and are important for the understanding the next chapters.

One is about the species *Gomphrena* from Australia as *G. canescens* androecium type, that presents unusual appendices (see above), located between the filament where is attached in the anthers, (Alternant), these appendices born on the border of the tube fused, this character is not observed in the American samples, this characteristic has been observed also in *G. involucrate, G. connata*, and *G. conferta*, unlike of *G. flaccida* and *G. humilis* that do not present, in the figure 2-25 A,B we show *G. canescens* and conferta androceum where you can distinguish them easily this typ of appendices. It is difficult to know what happens in the rest of the species of Australia, unfortunately, the study of Palmer (1998) do not have images and description to respect, also is difficult to know exactly the terminology to use in this, will be necessary improve ontogenetic studies in the genus including larger sampling of species.

The other observation is concerning the insertion of the anther in the tube of the androecium, the new species described for Bolivia, like *G. mizqueensis*, others not yet as *Gomphrena* sp. nov. (Spec. 2) [vouchers: Wood, et al. 22662, 22269 (LPB,B.K)] *G. phaeotricha* the anther are inserting between one "entire filament" and not between filaments appendix or two filament appendices. That is more common into the species of *Gomphrena* (Fig 2-25 D, C), but in this case it is difficult to find the correct terminology to describe this character.

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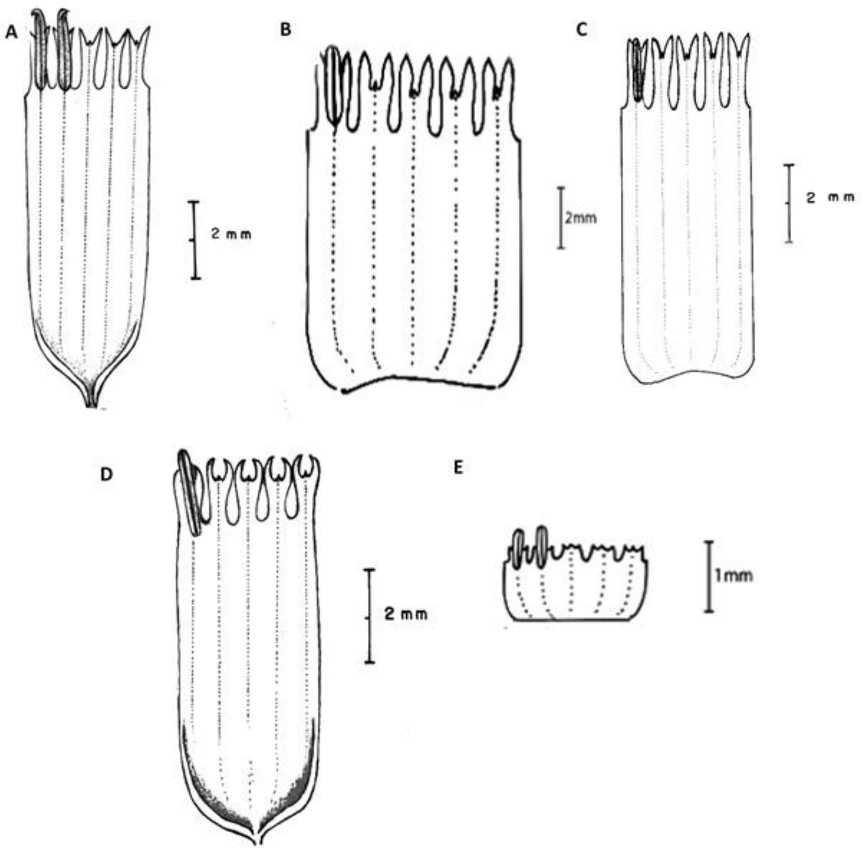


Fig. 2-24. Androecium shows the filament appendices and the shape apex. A) *G. mollis*, lanceolate-acuminate apex. B) and C) *G. haenkeana*, *G. rupestris*, lanceolate with rounded apex. D) *G. agrestis*, falcate apex. E) *G. prostrata*, narrowly acute apex.

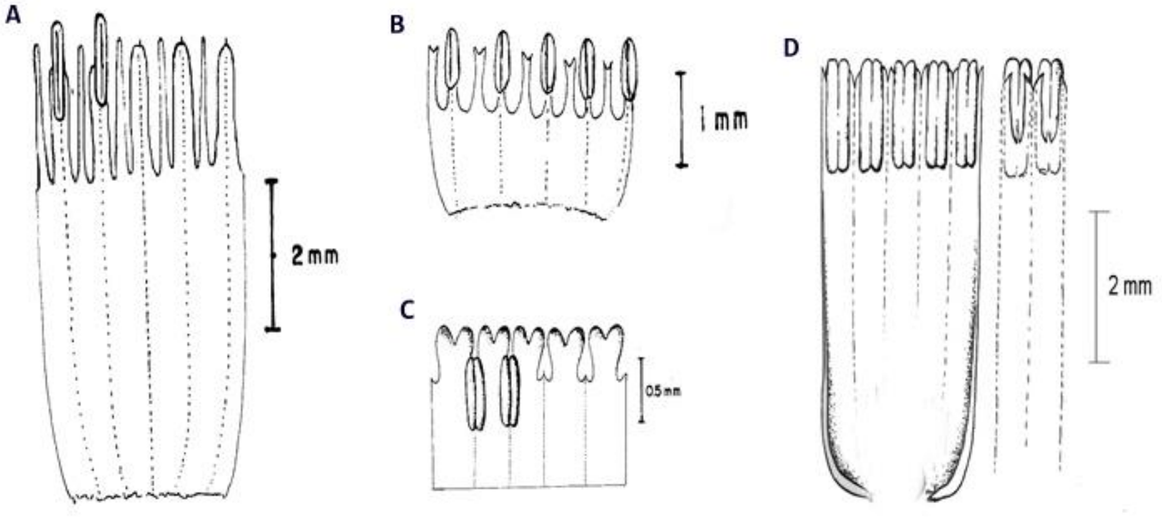


Fig. 2-25. Androecium show filament with appendices (free part of the androceum). A) *G. canescens*. B) *G. conferta*. The anthers are inserts between one "entire filament appendix". C) *Gomphrena* sp. nov. (Spec. 2) [vouchers, Wood, et al. 22662, 22269 (LPB, B, K)] and D) *G. mizqueensis*.

2.3.6. Gynoecium

The gynoecium consists of an ovary and a short style with two long stigma branches of which the inner surface is covered with papillate cells (Fig. 2-28A & B). In all species studied in Amaranthaceae sensu lato, the gynoecium wall develops from a ring primordium, surrounding a central zone in which a single campylotropous ovule develops. We hypothesize that the evolution development of an annular gynoecium wall primordium liberated the gynoecium development of the constraints of a capillary organization. As a consequence, the gynoecium wall and the ovule develop independently. In the Gomphrenoid species studied, the unequally formed annular gynoecium wall primordium may still reflect the carpellary origin of the ring primordium. In order to determine whether the development of the gynoecium wall is decoupled from the development of the ovule(s), an anatomical/developmental study of gynoecio in Amaranthaceae sensu lato is envisaged. The parts and measurements of the gynoecium are showing in the figure 2-26, the mearured was performed by the dissection of flowers and employing the stereomicroscope and millimeter ruler.

MESUAREMENTS “FLORAL CHARACTERS”

x = size of the all the gynoecium.

z = size of the large ovarium of the gynoecium.

y = size of the large style of the gynoecium.

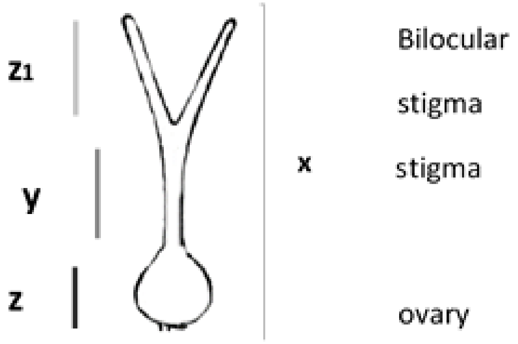


Fig. 2-26. Parts and measurements of the gynoecium.

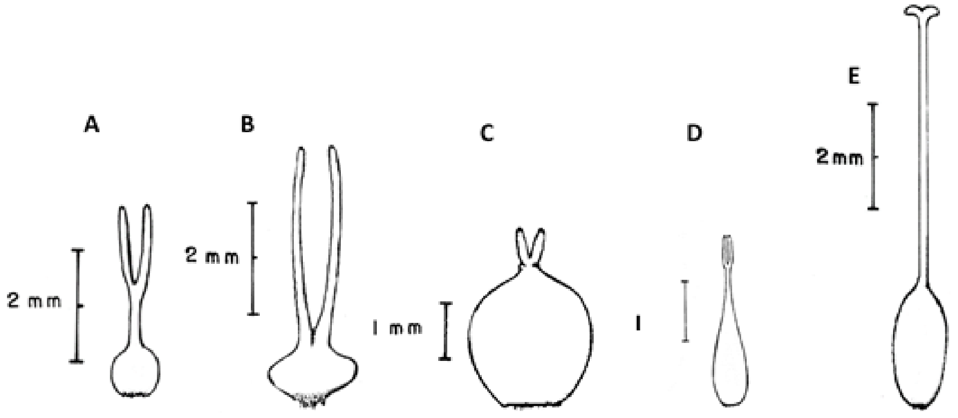


Fig. 2-27. Type of gynoecium. A) *G. oligocepha.* B) *G. macrocephala.* C) *Blutaparon vermiculare.*

In the gynoecium the ovary is superior; the shapes vary the sub globose to oval elongate. The smaller was observed in *Gossypianthus brittonii* with 0. 4 mm long; most the American species are cataloged in the range between of 0, 4-1 mm long as *G. cardenassii*, *G. potosiana*, *G. oligocephala* (Fig. 2-27A), few species was in the range 1.5 -2 mm long as *G. lanigera*, *G. macrocephala*, *G. tomentosa*, and *G. canescens*, the biggest and broad are Blutaparon vermiculare and B. portulacoide within 2-2.4 mm long.

The style is simple, most the species from America present a short size, the smaller was found in *Gossypianthus brittonii*, where do not possible to measure. Majority the species have one range of long between 0.1-0.4 mm long and the species largest was *G. agrestis* with 1.5 mm long; the Australian species vary from 0.1- 10 mm long (Palmer 1998), the two species measured here they reach 3 and 7.5 mm long in *G. canescens* and *G. flaccida* respectively.

The stigma is bilocular, with two branches, the size varies in *Gomphrena* and genus allied, in the extremely low range between in 0.2-0,5 mm long with species as *Guilleminea densa*, G. umbellata, *G. celosioides*. The majority of the species are within in the range 0.5-1.5 mm long, and the exceptional between 1.5 -2 mm long. The fruit is small utricle, usually brown, compressed-obovate or broadly obovate and smooth.

2.3.7. Micromorphology of pollen. Character 22

The morphology of pollen grains is an important source of information for plant systematics. In certain cases, palynological data have been crucial for taxonomic conclusions (Townsend 1977, 1988, Nowiche 1979, Borsch 1998a), and exposed that pollen has notable diversity in the different groups belong to the order Centrospermae (Nowiche 1979, Eliasson 1988, Müller and Borsch 2005, Sánchez del Pino et al. 2016). The previous studies distinguish; the pollen grains are significantly different in the subfamilies of Amaranthus and Gomphrena-type (Nowiche 1979, Erdtman G.1952, Townsend 1993, Borsch 1998). A correspondence is found in the last studies employed molecular data and those based on palyno-morphological data (Müller and Borsch, 2005, Sánchez del Pino 2016).

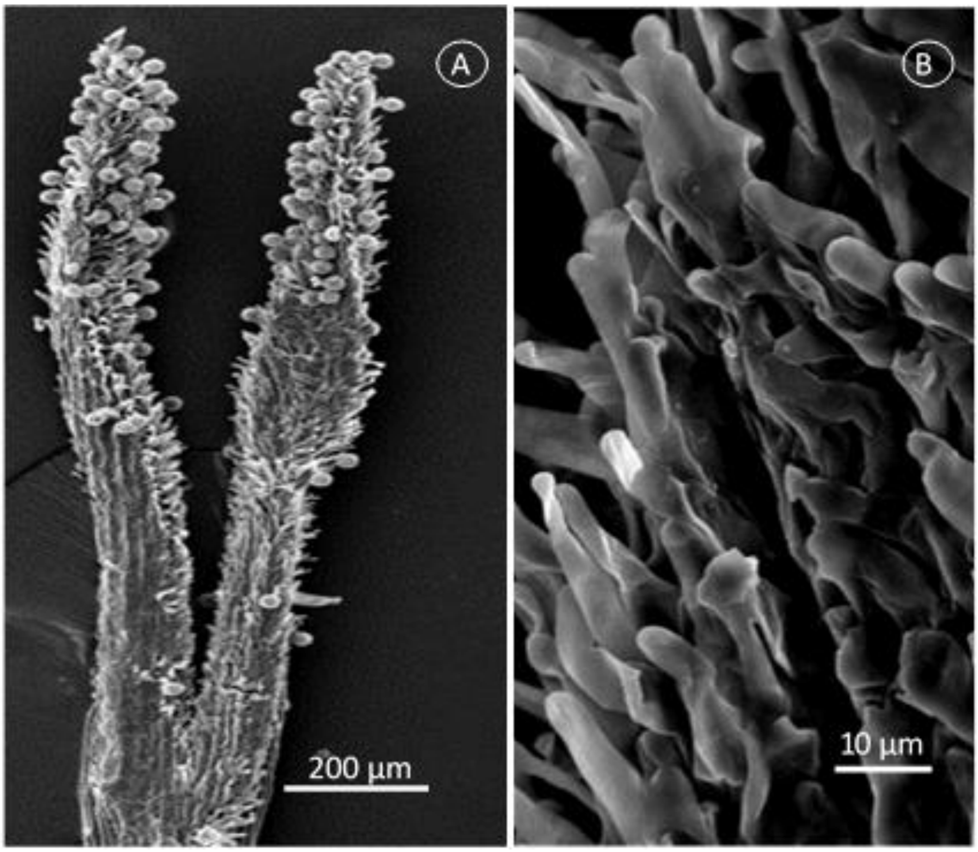


Fig. 2-28: Gynoecium detail. A) Two branches of the gynoecium. B) Detail of the papils.

Borsch & Barthlott (1998b) define the Pollen grains of *Gomphrena* type is a flat or slidhtly vaulted, simple columella, complete tectum and spines evenly distributed. Borsch (1998a) identify the difference between *Gomphrena* types and other genus pollen of the family, finding the most different respect to *Gomphrena* are *Pfaffia* and *Hebanthe* are the transitions, between *Gomphrena*-type and *Pfaffia*-type. While *Gomphrena* and *Lithophila* showing more proximal type of pollen. In his explanation for determining type of pollen between the taxa is necessary used a syndrome of characters, if was only one character it must be very distinctive, and considered, these differences variations occurs independently, with the presence of certain combinations of quantitative character as the number of apertures, sizes, and a number of microespines and number punctate union and to some extent pore size and corresponding variations in the number of extexinous bodies on the aperture membrane. For the reconstruction character here is defined the tectum characters. In add we showing the part and the example table, and figure for described some of the pollen including in the study and for reference bibliographic other to see the difference with another genus.

States: Tectum complete (0), Tectum with large foveolae on the vertical sides of mesoporia (1), tectum reduced to a distal band in the mesoporia (2)

Table 2-1. An example of character and measured the species with pollen metareticulate to identify important different of *Gomphena* type and other close genera, including *Gomprena mandonii* currently in the polyphyletic clade on *Gomphrena* s. str. (see behind and figure 2-29, 2-30).

Character	Total large Size (um)	N° pore	tectum **Character 23**	N°columellae
Xerosiphon aphyllus	16,84	30	**2**	6
Hebanthe grandiflora	15	32	**0**	~ 30
Gomphrena mandonii	14,5	22	**0**	>15
Gomphrena bicolor	25	30	**2**	20
G. sp. nov. (stolonifera)	26,4	40	**2**	~20
Gomphrena potosiana	19,71	36	**2**	20
Gomphrena oligocephala	18,91	36	**2**	20
Gomphrena perennis	21,1	38	**2**	~20

Character	mesosporia	extexinous bodies	microespines	Shape metareticule
Xerosiphon aphyllus	flat	agruped	present	Pen. & hex.
Hebanthe grandiflora	Semi-vaulted	concentric	present	Hex.
Gomphrena mandonii	vaulted	concentric	present	Pen. & hex.
Gomphrena bicolor	flat	concentric	absent	Pen. & hex.
G. sp. nov. (stolonifera)	flat	concentric	absent	Pen. & hex.
Gomphrena potosiana	flat	concentric	absent	Pen. & hex.
Gomphrena oligocephala	flat	concentric	absent	Pen. & hex.
Gomphrena perennis	flat	concentric	absent	Pen. & hex.

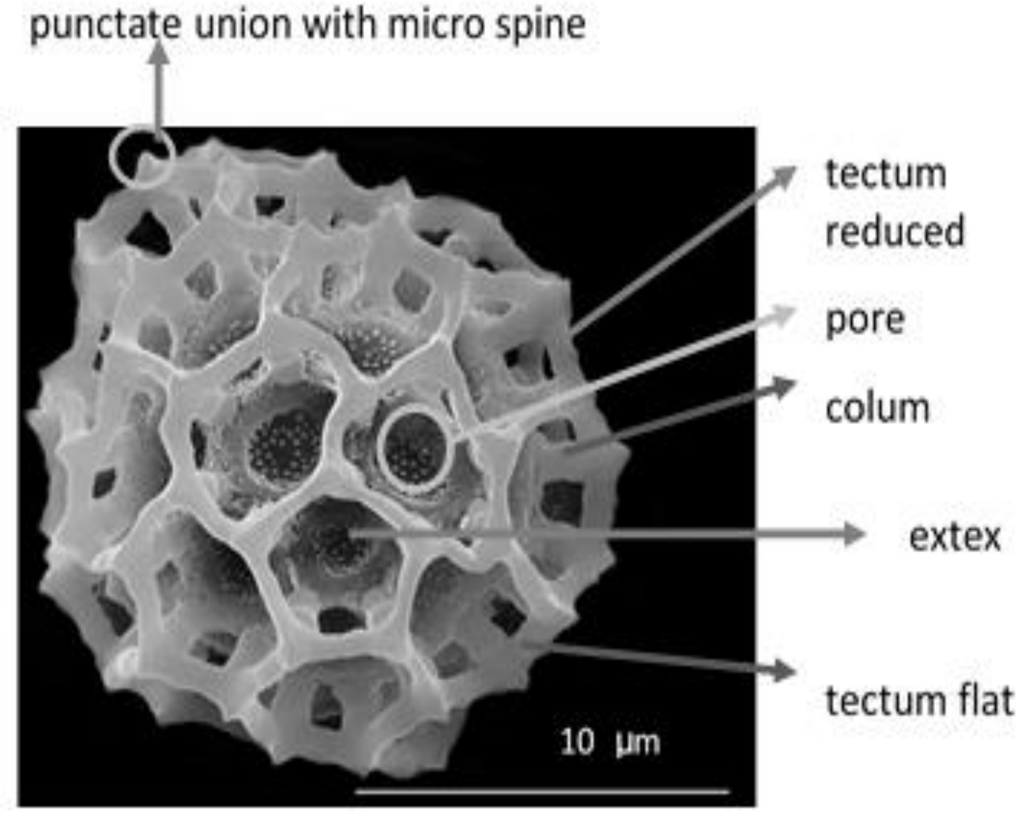


Fig. 2- 29. *G. radiata* specimens to show the parts of the metareticulate pollen of *Gomphrena*- [Voucher: Borsch et al. 3740 (LPB, B_AC442)]. Photo Sarah Kunz.

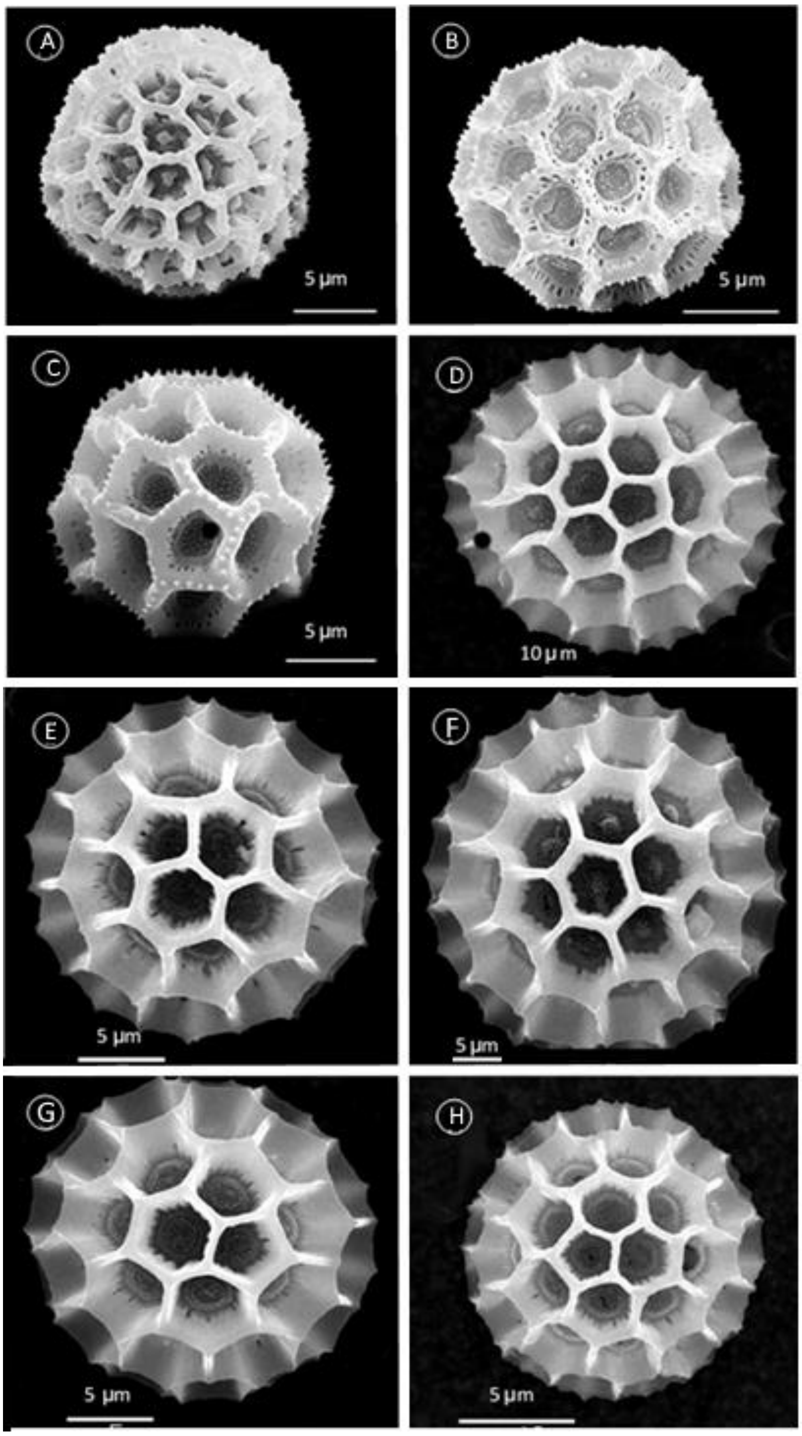


Fig. 2-30. Melareticulate pollen. Spinous tectum: A) *Xerosiphon aphyllus,* voucher Splett 701 (B). B) *Hebanthe occidentalis*, Borsch & Pedersen, & Borsch, 3515 (B, LPB). C) *Gomphrena mandonii,* Beck, 18720 (B, LPB). Photos Müller & Borsch (2005). Entire, flat tectum: D) *G. bicolor*, Borsch & Ortuño, 3581 (B, LPB). E) sp. nov- (*G. stolonifera*), Borsch & Ortuño, 3610 (B, LPB). F) *G. potosiana* Borsch & Ortuño, 3716 (B, LPB). G) *G. oligocephala* Borsch & Ortuño, 3760 (B, LPB). Ondulate ornamentation tectum: H) *G. perennis*, Borsch & Ortuño, 3664 (B, LPB). Photos Ortuño, T. scale all 5 µm exept D) 10 5 µm.

2.3.8. Trichome micromorphology

The trichomes, studies in Amaranthaceae, have played an important part in the taxonomy of the family, because many authors include this characteristic in the studies to arrive to understand better the systematic and taxonomy of this groups, and this characters can help to recognize better the species a genus, species, and varieties levels (Handro 1967, Pedersen 1976, Ortuño & Borsch 2005, Senna 2015). Actually few studies related to trichomes are focus in *Gomphrena*, two works studies are performed in Brazilians species of the Cerrado, both focus on foliar anatomy, the firsts realized by Handro (1967), Fank-DeCarvaho et al. (2010), were are described, the parts, type and ornamentation of the trichomes.

Other important work in Amaranthaceae – Chenopodiaceae was implemented by Carolin (1983), this work includes a wide data set, of different species genus of both families, where recognize 10 types trichomes, the subfamily Gomphrenoideae represented by different genus and species of *Gomphrena* from Brazil and Australia. The terminology and definition in this study follow (and in same case this are modify) to propose by Carolin (1983), and also are similar to described by Fank- -Carvaho et al. (2010). Our review the trichomes covering the species the data set using in the molecular analysis, and in the species for describe the Bolivian species. For best explaining this character we defined first the type or trichomes in the vegetative part (stems, cauline leaves and apical leaves subtended the paracladio), separated of the trichomes in the tepals corresponded to the floral part.

Generally, the *Gomphrena* trichomes, here observed have a uniseriate trichomes, formed in a single row of cells, development into the one epidemic cells. Three parts are distinguishing: the *basal cells*, correspond to the lower one or two cells; the *uppers cells,* vary in numbers cells (ca. 2-8 cells); and the *interlocking junctions* (or articulation), usually are seeable as nodes or scar, in this point the cells, are interlaced by a linear projection of the extreme border cells overlapping the neighboring cells (Fank-De- Carvalho et al. 2010).

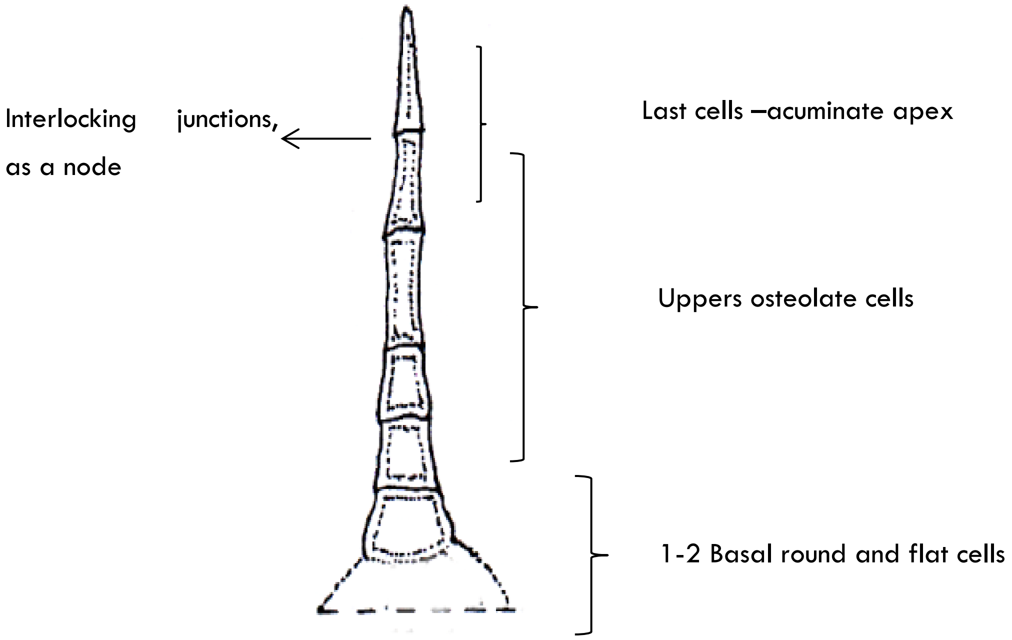


Fig. 2-31. Scheme showing the multicelular uniseriate trichomes in Gomphrena

Three different type of cells according the consistence is possible encounter 1) the firm cells, where the cuticle walls rigid, defined as osteolate cells Payne (1978) with a shape as a thigh bone, with the central part cylindrical, and the terminal extremes somewhat swollen (Fig. 2-32A) 2) the collapsed cells, with the cuticle walls thin, losing the typical form osteolate, with degraded walls (Fig. 2-32B). 3) flexible cells conserve the ostelate form, but they are sinuous, and usually they are in the last part of the trichomes (Fig. 2-32C). At is observed in this work, some species not below to the *Gomphrena* s. str. have other types of trichomes such as *G. mollis*, this specie having a dentritic trichomes (Fig. 2-32D), with irregular branches born in each nodes, in which new branches arise from different points along the main axis, *G. mandonii*, the trichomes are candelabra, (Fig. 2-32F) with monopodial branched with branched whorled, and *G. rupestris*, this species have also uniseriate trichomes but, the bade in the base of the biggest claw (Fig. 2-33C) that was not founded in *Gomphrena* s. str.

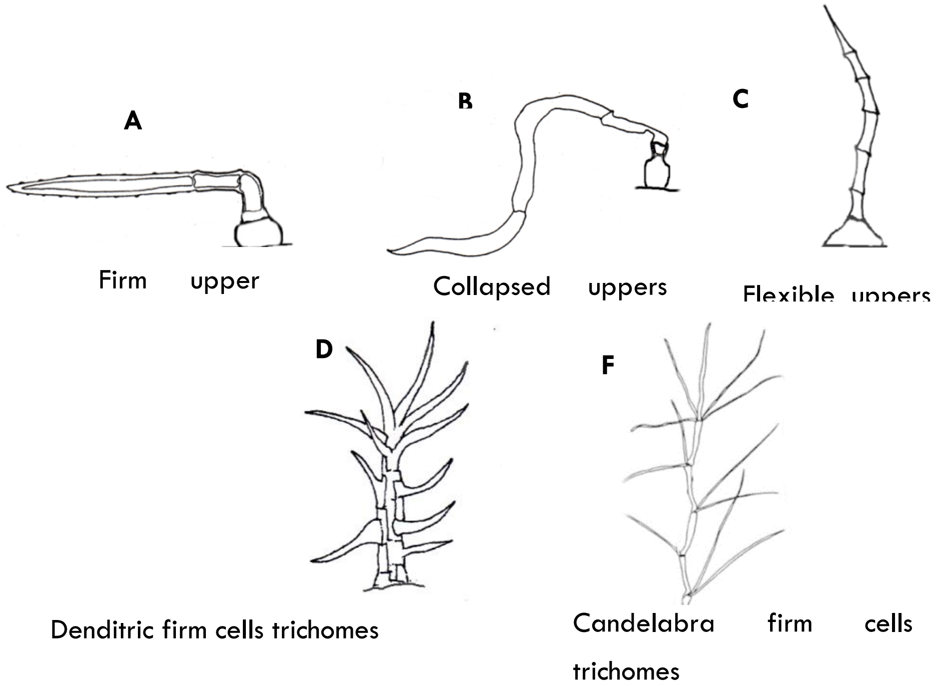


Fig. 2-32. Scheme shows the different types of trichomes based on the type of cell. A) Trichomes with a firm, rigid, straight cells. B) Trichomes with collapsed cells. C) Trichomes whit the last terminal sinuous cells. D) Dendritic, with firm, in each node arise cells more branched usually with ramifications. F) Candelabra, firm trichomes, in the main nodes, arise monopodial branches, arranged symmetrically.

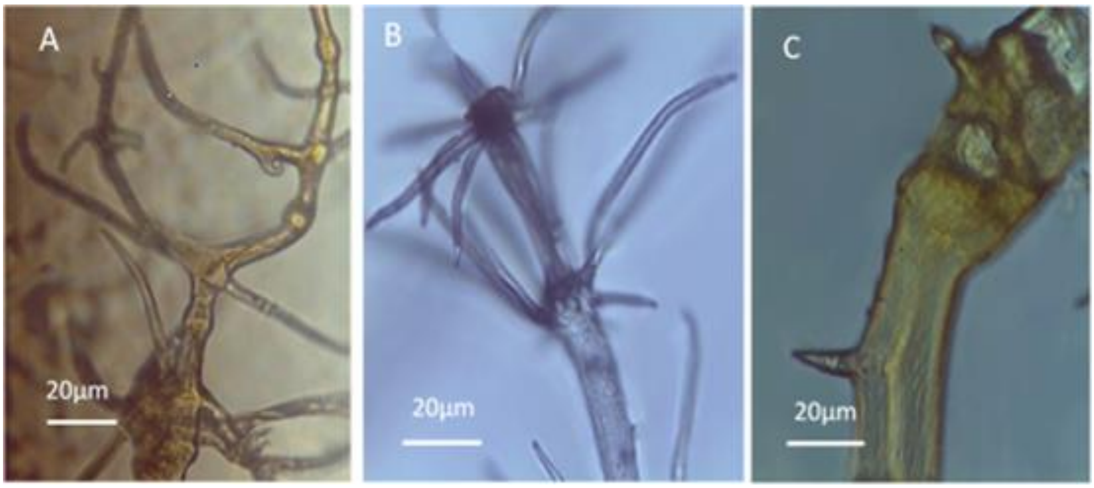


Fig. 2-33. Different types of trichomes. A) *G. mollis*, dendritic trichomes [voucher, Harley, 26695 (B, MO)]. B) *G. mandonii,* candelabra trichomes [Beck, 11113 (LPB)]. C) *G. rupestris*, uniseriate trichomes, with claw in the basal cells [Harley, 26990 (B. MO)].

Vegetative trichomes: stems, caulinar leaves apical leaves subtending the paracladio.

Basal cells of the trichomes in most the especies in *Gomphrena* are composed by a) 1-2 firm cells, broadly rounded shaped, flat e.g. *G. fuscipellita*, *G. phaeotrichia* (Fig. 2-34A), b) few species the first and seconds cells are elongate at cylindrical, straight cells e.g. *G. martiana* (Fig. 2-34B) c). only in *G. tomentosa*, *G. radiata* and *Gossypiantus brittonii* the fisrt and second cells are collapsed Fig. 2-34C).

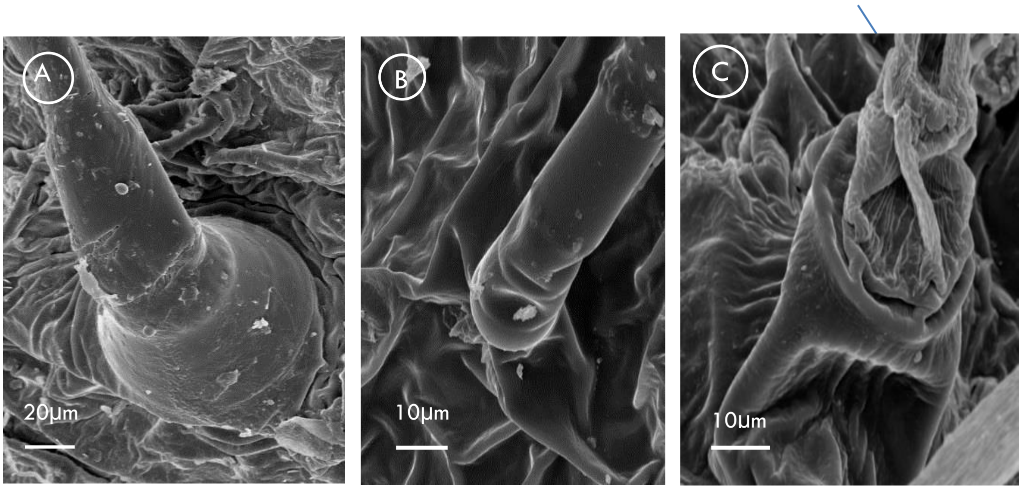


Fig. 2-34. Type the basal cells. A) 1-2 firm cells, broadly rounded shaped, *Gomphrena fuscipellita*, [voucher Huaylla, 3653 (LPB)]. B). Few species the seconds cells are elongate at cylindrical, straight cells, *G. martiana* [Borsch & Ortuño, 3737 (B, LPB)]. C) The cells are collapsed, *G. tomentosa,* [Ortuño, 1235 (B, LPB)].

Uppers cells of the trichomes, based on the type of cells are groping in uniseriate trichomes: a) with the first uppers cells, firm cells and the end upper collapsed to flexible e.g. *G. martiana*, *Guilleminea densa*, *G. meyeniana* (Fig. 2-35A), b) all the cells with firm straight, rigid cells, e.g. *G. trollii*, *G. haenkeana*, *G. macrocephala* (Fig. 2-35), c) all the cells the first firm and the lasted flexible; e.g. *G. pallida*, *G. potosiana*, G. oligocephala (Fig. 2-35C), d)-all the cells collapsed twist (tortuose) e.g. *G. tomentosa,* (Fig. 2-35D). In the stems and leaves of *G. mollis* the trichomes are dentritic (Fig.2-33A), and in *G. mandonii* are candelabra (Fig. 2-33B). Also the stems and leves can be e) glabrous e.g. *G. umbellate*, *G. radiata*, *Blutaparon vermiculare*. Other type the trichomes have *G. mollis* and *G. mandonii*, with dendritic and candelabre trichomes respectively.

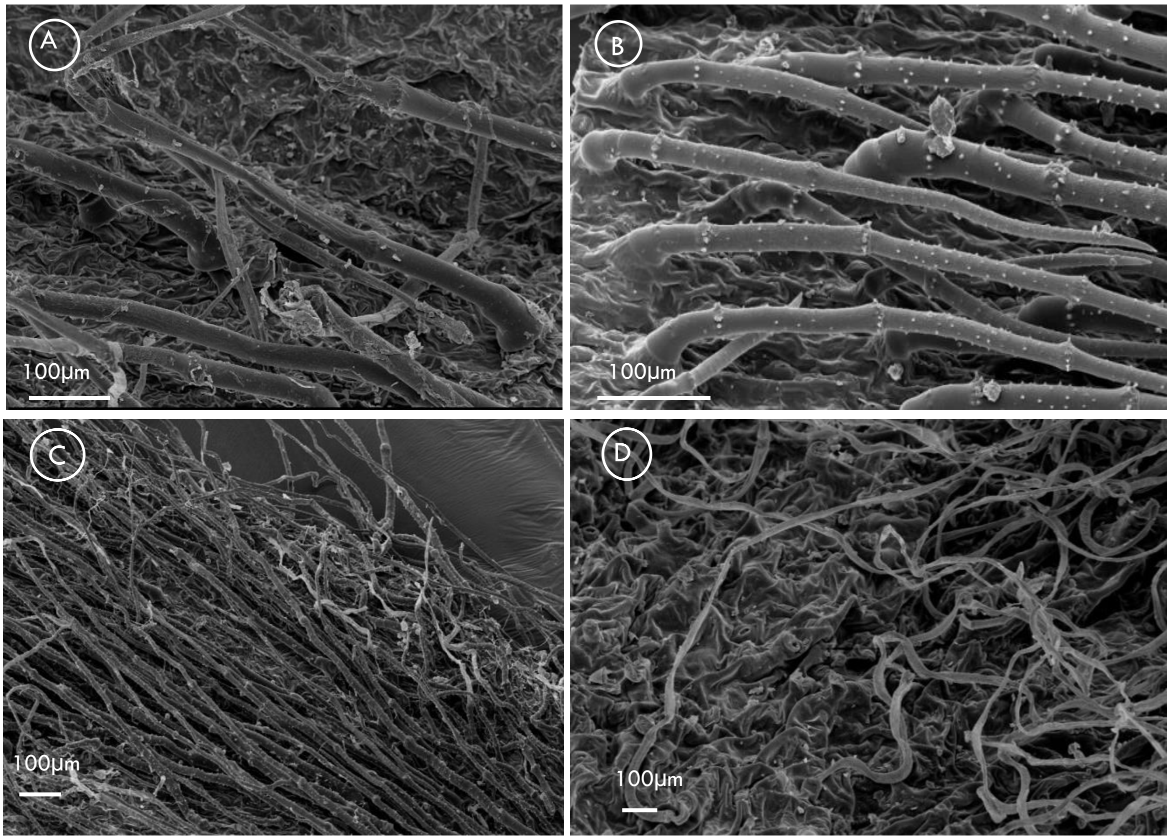


Fig. 2-35. Type of arranged the uppers cells. A) Firm cells and the end upper collapsed to flexible *Gomphrena meyeniana* [voucher: Borsch & Ortuño, 3955 (B, LPB)]. B) All the cells with firm straight, rigid cells, *G. trollii*, Ortuño, 1255 (B, LPB). C) The first cells firm and the lasted flexible, *G. pallida*, [Borsch & Ortuño, 3587 (B.LPB)]. D) All the cells collapsed twist, *G. tomentosa,* [Ortuño, 1235 (B, LPB)].

The variations in the Interlocking junctions are: a) conspicuous as broad node with linear scar, composed by linear projections interlaced and arranged in 0° angle degrees, overlapping, in to proximal two firm cells, most the species are in this group as *G. oligocephala*, *G. fuscipellita*, *G. meyeniana* (Fig. 2-36A), b) conspicuous, composed with elongate granulose projections interlaced and arranged in 45-90° angle degrees, overlapping in to proximal two firm cells, as *G. haenkeana*, *G. trollii*, *G. ferriginea*, *G. perennis* (Fig. 2-36B). Not conspicuous simple scar unit two proximal collapsed cells as *G. tomentosa*, *Gossypianthus brittonii* (Fig.2-36C). Other variations are finding in the ornamentation in the border of the interlocking junctions in the first cells, showing: granulose row in the first cells as in *G. trollii*, *G. haenkeana*, *G. ferruginea*, *G. cardenasii* and *G. macrocephala* (Fig.2-36D and E) similar arranged *G. perennis* but with spines proyeccion divided in two as “T”; and only *G. rupestris* present one big claw (Fig. 2-36F).

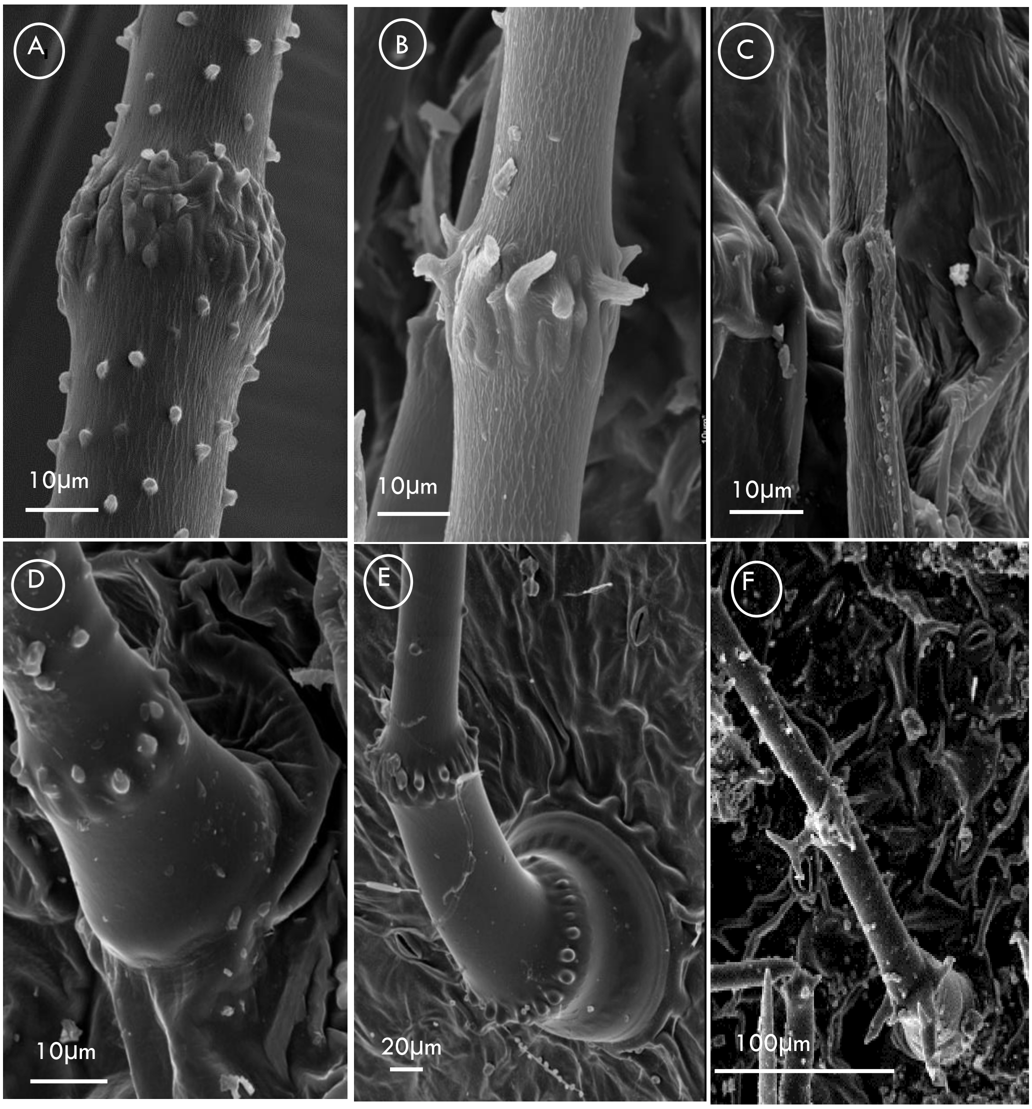


Fig. 2-36. Type of the Interlocking junctions. A) Conspicuous as broad node with linear scar, composed by linear projections interlaced and arranged in 0° angle degrees, overlapping, in to proximal two firm cells, *G. celosioides*, [voucher: Meneses, 160837 (LPB)]. B) Elongate granulose projections interlaced and arranged in 45-90° angle degrees, overlapping in to proximal two firm cells *G. trollii*, [voucher, Ortuño, 1255 (B, LPB]). C) Simple scar unit two proximal collapsed cells *G. tomentosa*, [Ortuño, 1235 (B, LPB)]. D) Granulose ornamentation row in the first cells *G. ferruginea*, [Borsch & Ortuño, 3751(B, LPB)]. E) Granulose ornamentation row in the first cells *G. macrocephala* [[Zardinii, 60543 (B, MO). F) Spines proyeccion divided in two as "T" in the first cells, *G. perennis* [Borsch & Ortuño, 3626 (B, LPB)].

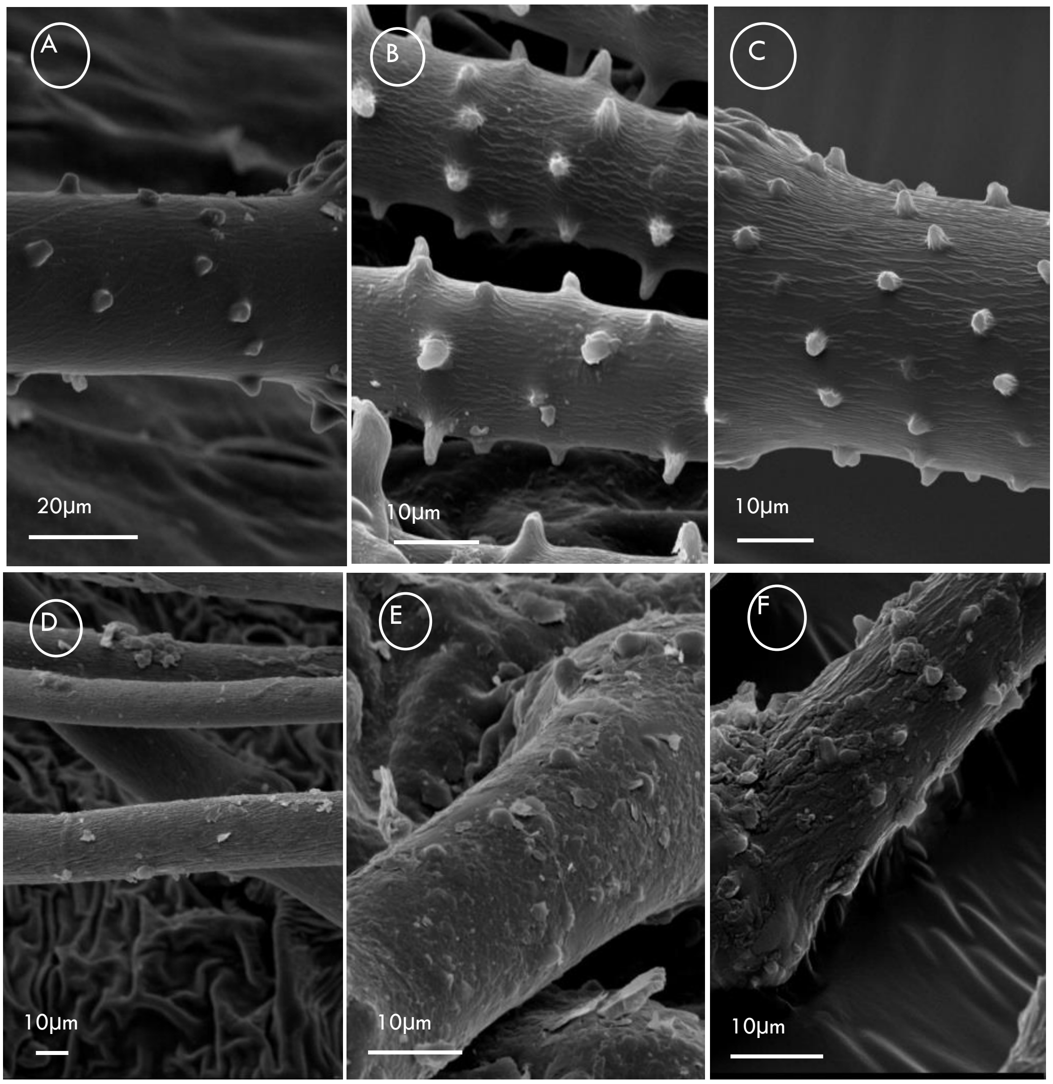


Fig. 2-37. Type of the ornamentation. A) With projection lumen as granulate *G. macrocephala*, [Zardini, 60546 (B, MO)]. B) Projections lumen as spinous *G. trollii*, [Ortuño, 1255 (B, LPB)]. C) Spinous to granulate, *G. celosioides* [Meneses, 160837 (LPB)]. D) Cuticle cover with cristal of epicuticular wax, salicose *G. meyeniana*, [Borsch & Ortuño, 3955 (B, LPB)]. E) Cuticle granulate to salicose *G. haenkeana* [Borsch & Ortuño, 3963 (B, LPB)]. F) Cuticle spinous to salicose, G. oligocephala [Bosch & Ortuño, 3641 (B, LPB)].

This also varies in the ornamentation in the cuticle, and the cuticle may also presents epicuticular wax that is in essence a hydrophobic wax with varity of substituted functional groups (depend of the species), usually cover the surface of different part of e.g. leaves, fruit, to help to decrece surface wetting and moisture loss, also the reflection of ultraviolet light cleaning the surface, they are visible as “white-salt cristals”, for this reason here are denominated this characteristic as “salicose”. In the species was possible distinguish ornamentation cuticle cells a) with projection lumen as granulate as in *G. macrocephala* and *G. phaeotricha* (Fig. 2-37A), b) projections lumen as spinous as *G. trollii* (Fig.2-37B), *G. fuscipellita*, *G. potosiana*, c) cuticle cover with cristal of epicuticular wax, salicose as in *G. meyeniana*, *G. boliviana*, *G. tomentosa* (Fig.2-37D), d) cuticle granulate to salicose as *G. haenkeana, G. bicolor* (Fig. 2-37E), e) cuticle spinous to salicose, *G. oligocephala*, *G. perennis*, *G. ferruginea* (Fig. 2-37F), f) cuticle granulate to spinous as in *G. cardenasii*, *G. lanigera*, *G. agrestis*, *G. celosioides*.

The texture in the cuticle epidermis, present variability in the trichomes are recognized, a) flat cuticle, as in most the basal trichomes (Fig. 2-36E) Most the cells have striated cuticle vary in deep, more conspicuous as in *G. tomentosa* (Fig. 2-36C). c) And only in *G. meyeniana*, are helicoid or spiral arranged "stretch marks". The colour of the trichomes usually are white to light yellow, some species as *G. martina*, *G. meyeniana* are hyaline or translucent, also was finding the light brown colour e.g. *G. agrestis*, *G. mollis*; white to dark brown in the upper part near the inflorecens. *G. macrocephala*, white to yellow to ligth brown, brown or dark brown to black in *G. fuscpellita*, *Gomphrena* sp. nov. (Chataquila Spec. 2).

In apical leaves subtending the paracladia of some species are discernible to simple view differences between the abaxial and the adaxial surface, in the density, indumentum type and trichomes size and shape, this differences occurs in small group of species that have adaxial surface with more short trichomes type, with 3 to 4 firm and thin cells as *G. perennis* and *G. ferruginea* (Fig. 2-38A), and others with only 3 cells in the species *G. oligocephala*, *G. pallida*, *G. stolonifera*, *G. mizqueensis* (Fig. 2-38B) including the basal cells, these are spinous ornamentations and light to brown color. The most peculiar species are *Gomphrena* sp. nov. (Spec. 7) and *Gomphrena* nov. comb. (flexusa), these have trichomes with two broadly, wide, and elliptic (oval) cells, both differ in the type of interlocking junctions and colors, G. sp. nov. (Spec. 7) a narrowed union and dark yellow color (Fig. 2-38D), while *Gomphrena nov. comb.* (flexuosa) are broad unions and light brown color (Fig. 2-38C). In all these species the Abaxial surface of the leaf and the margin are similar than the stem and cauline leaves, vary in the color more darkness, and more hirsute in the margin.

Floral trichomes in the part tepals

The trichomes in the flowers are located, punctually distributed depending on the species, and of the floral part: Bract, bracteoles, tepals, and basal axe paracladial. Here for we focus in the type and distribution the trichomes in tepals because they present dense and shifting trichomes, and is the important character for determining some species.

The tepals thichomes are ubicated in a) the dorsal part and in the margin, b) only in the dorsal part, or c) only in the margin. They are usually very longer, compressed in a case when are wooly. Always the trichomes are multicellular uniseriate, but is possible distinguish three types, the most common are: a) trichomes with firm or collapsed (e.g. *G. tomentosa*), 1-2 basal, cells, and the first uppers cells some also rigid, follow next by collapsed cells, with interlocking junctions visible as a node or simple union, they are sinuous and strong undulate, *G. mizqueensis*

(Fig. 2-39A), *G. ferruginea* (Fig. 2-39B), *Gossypianthus* (Fig. 2-39Ed), b) trichomes where the cuticle of the epidermis

looks more broadly, given structure more firm to the cells, but most of them are collapsed cells or twist,

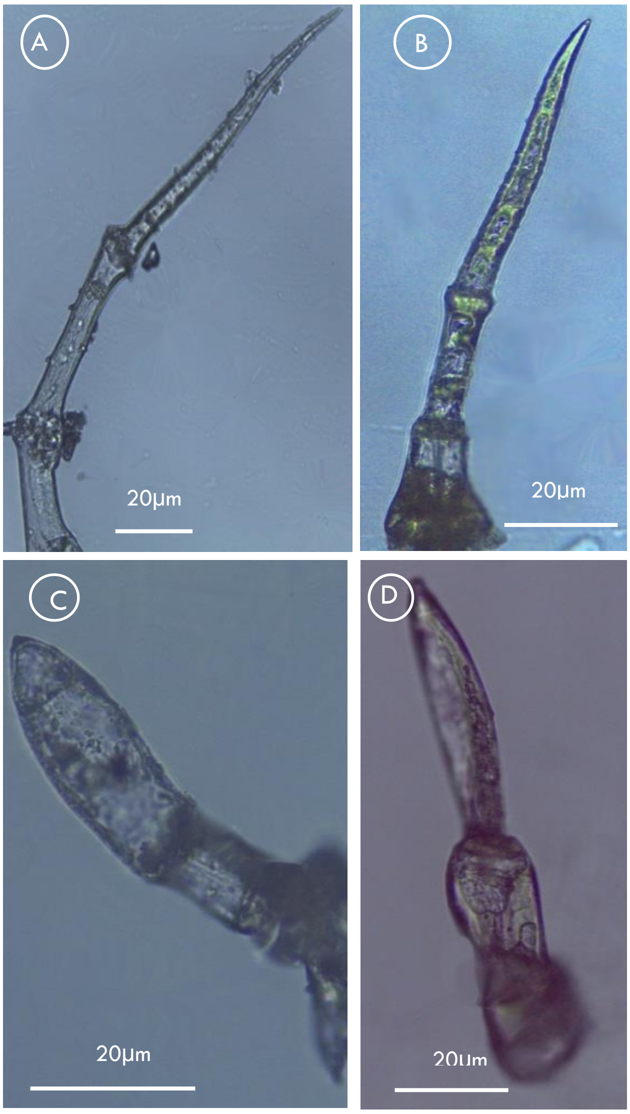


Fig. 2-38. Type of the trichomes in the apical leaves subtending the paracladio. A) *G. perennis*, [Borsch & Ortuño, 3529 (B, LPB)]. B) *G. pallida* [Borsch & Ortuño, 3755 (B, LPB)]. C) *Gomphrena* nov. comb. (flexuosa) [Borsch & Ortuño, 3753 (B, LPB)]. D). *Gomphrena* sp. nov. (spec7), [Ortuño, 1677 (B, LPB)].

they are arranged as a brush in the bases dorsal part and margin the tepals, the interlocking junctions are simple node, e.g. *G. lanigera* (Fig. 2-39Fh), *G. cardenassii* (Fig. 2-39C), c) the thirty type of the trichomes have rigid or sinuous firm cells, usually are in the margin of certain species as *G. pallida* (Fig. 2-38D.), *G. oligocephala*, *Gomphrena* sp. nov (Spec. 3) giving the appearance the continue the fiber of the tissue of the tepals, also some in some species as *G. macrocephala* is possible to see this type the trichomes in the dorsal part but very fews. Not all the trichomes are growing in the margin have this type of trichomes, also is usual they are “lanate trichomes” as e.g. *G. haenkeana* (Fig. 2-38G).

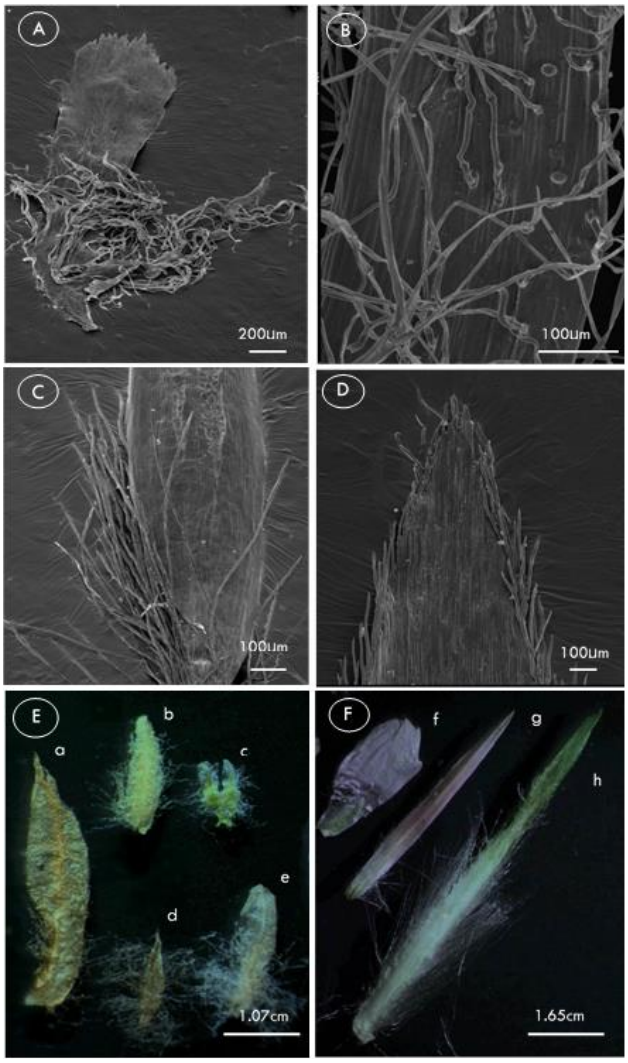


Fig. 2-39: Type of the trichomes in the tepals. A) *G. mizqueensis*, [voucher Borsch & Ortuño, 3584 (B, LPB)]. B) *G. ferruginea* [Borsch & Ortuño, 3751 (B, LPB)]. C) *G. cardenassii* [Wood, 18812 (K, LPB)]. D) *G. pallida* [Borsch & Ortuño, 3587 (B, LPB)]. E) External tepals showing lanate trichomes: a) *G. rupestris*, b) *G. prostrata*, c) *Guilleminea densa*, d) *Gossypianthus brittonii*, e) *G. tomentosa*. F) External tepals: f) *G. meyeniana*, with tepals glabrous, g) *G. haenkeana*, lanate trichomes, h) *G. lanigera*, with firm and rigid, hirsute trichomes. Photos taken in stereo-microscope.

In the figure 2-39 F and E, we showing a group the external tepals, including *G. rupestris*, *G. prostrata*, *Gossypianthus britonii*, and *Guilleminea densa*, in this we have idea more general about the variations in form, color, and specially the different the arranged the trichomes in the dorsal part. The figure E, most the species are lanate trichomes, and clearly *G. rupestris*, (Fig. 2-39Ea) and *G. prostrata*, are dense cover with trichomes lanate very undulate in all the dorsal part, this type of arranged the trichomes is not observed in the other species the *Gomphrena* s. str.

Indumentum in vegetative and floral part

The type the indumentum observed in *Gomphrena* in the stems, caulinar leaves, basal leaves apical subtented leaves paracladio presents variations in density, type of and arranged of trichomes, based on in this pattern and in the concept of Payne (1978) here we using the follow definitions:

Tomentose, densely woolly with soft, matted tangles, wool-like trichomes (Payne 1978).The trichomes uniseriate with the uppers cells collapsed, usually undulating and covered highly surface. *G. tomentosa* (Fig. 2-40A) have this type the indumentum in all the plant, also *G. umbellata*, *Gossypianthus brittonii* and *G. radiata* few in the nodea in basal leaves.

Lanate, covered with fine, long hairs, having a woolly surface, lanose (Payne 1978). The trichomes multicellular, uniseriate, with firm basal cells and first the upper cells, the lasted are collapse or crooked, covered highly surface. *G. meyeniana* (Fig. 2-40B), have indumento lanate to appresed, and also this type the indumento is the most characteristic finding in the floral indumento specialy in the tepals, and axe paracladial.

Villous, covered with long fine straight hair. The trichomes multicellular, uniseriate, with the first uppers cells firm, the lasted cells are flexible. Some times sparse, medium denser or cover highly surface. This indumento is very similar to strigoso but for some author usually are relation of short trichomes, for this reason we used better villous, the indumeto villous to appresed are founded e.g. in
G. pallida, *G. celosioides*, *G.potosiana* (Fig. 2-40E), and one inusual indumento has the caulaine leaves of sp. nov. (Spec. 7) with villous and flat trichomes conform per collapsed cells (Fig. 2-40F).

Appressed, lying flat against, pressed closely the surface leave. The trichomes multicellular, uniseriate, with the basal and uppers straight and firm cells. Cover medium to highly surface overlapping, usually high or medium denser in the surfaces. This type the indumentum is the most common founded in the genus, especially in the leaves some examples are *G. rupestris*, *G. canescens*, *G. cardenassii*, *G. mizquensis* (Fig. 2-40 C, D).

Hirsuto, with long, rather stiff trichomes, usually in the positions >35 to 90 degrees with respect to the surface. The trichomes multicellular, uniseriate, with the basal and uppers with straight and firm cells, cover highly surface with regular spaces. This type the indumentum is characteristic of few species as *G. lanigera* and *G. macrocephala*, but is founded also in the stems of *G. fuscipellita*.

Glabrous, without trichomes, the most the species usually are glabrous only in speciphic part, because always have some trichomes, but usually *G. umbellate*, *G. radiata*, *Blutaparon* ssp. do not have trichomes in the leaves.

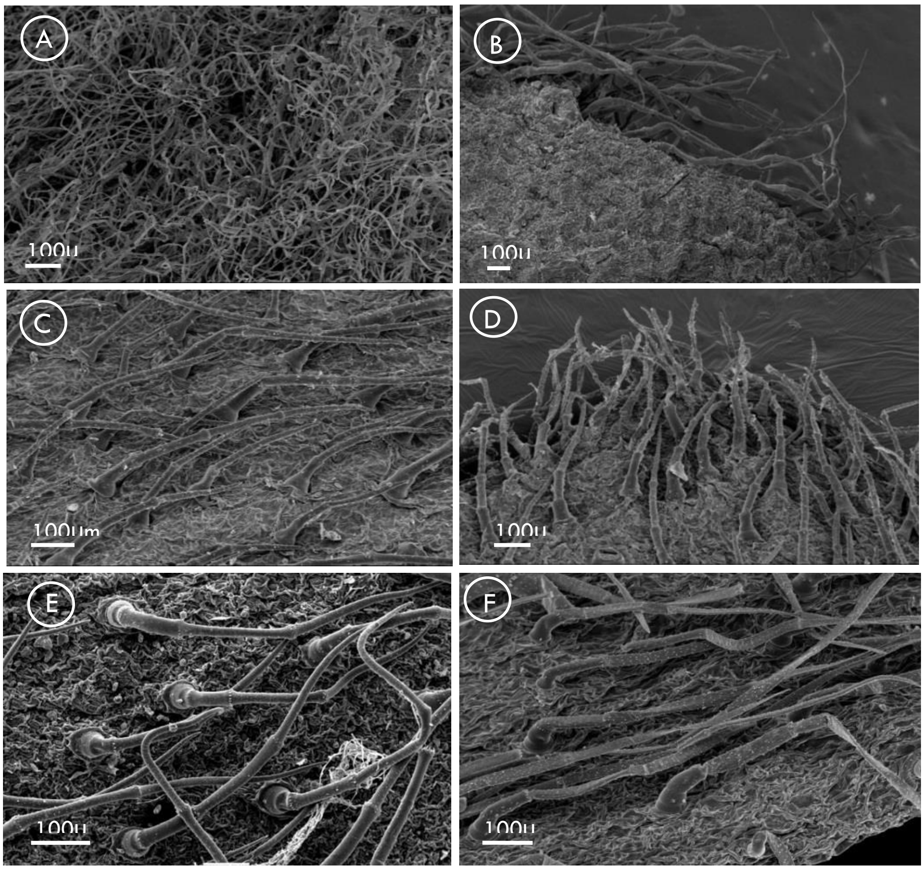


Fig. 2-40. Indumentum: A) Tomentose, *G. tomentosa* [voucher Ortuño, 1235, (LPB, B)]. B) Lanate, *G. meyeniana* [Zenteno, 10099 (B, LPB)]. C) Appressed, *G. mizqueensis* [Borsch & Ortuño, 3584 (B, LPB)]. D) Appresed, *G. mizqueensis* [Borsch & Ortuño, 3584 (LPB, B)]. E) & F) Villous. *G. potosiana* [Borsch & Ortuño, 3716 (B, LPB)], *Gomphrena* sp. nov. (Spec. 7), [Ortuño, 3584 (LPB)].

The leaves may present different density of indumentum in the different sides of the leaf, in many species it is common that the present higher density, in the lower part, and the upper side are glabrous or with fewer trichomes, as in *G. boliviana*, *G. bicolor*, *G. canescens*, *Guilleminea densa* and *G. prostrata*. The involucral leaves exhibit more differences, especially where the leaves are smaller than the inflorescence, e.g. *G. haenkeana*, *G. trollii*, some species having only or more trichomes in the margin as in *G. bicolor*. It is also frequent that when they acquire mature there is a loss of the trichomes this happens in those species that have basal leaves such as *G. tomentosa*, *G. macrocephala*.

2.4. Distribution and important characters and their states in *Gomphrena* s.str. related with the close genera and species (+ character matrices)

The taxa samples are listed in the Apendix 3-1 (Chapter 3), the matrix with codes regards to characters (1-22) (for ancestral character reconstruction at genus level chapter 3) are included in the Table 2-4, the names of each character and character state are develop in the text above. For the Chapter 4, more related into the bolivians species the number of character ascending to115, all of them are listed in the digital appendix 2-1, with the respective state of characters.

This two different data set was introducing in the software Xper^2 in independiently files, because the propose for each data are different. The sofware Xper^2, help to organize better the data is possible include register photoghaps and definitios of the diferent an is possible to see easily wich the caracters are particular of each species, and is a interactive key, one of the result of this software is the list of descriptors with the discriminating power, where the program is shows the classification the descriptor according to their ability to discriminate the different species incorporate into the data base. This discriminating power is given by the Xper2 index provided by the software itself. It allows for the calculation method to remark the descriptors whose states allow better identification of concerned taxa. A descriptor is then more efficient if it exists in at least two exclusive modalities within the studied species group. The best descriptors are those which have the highest index. The index of Xpert ^{2} range from 0 to 1. It is calculated by the ratio between the number of couples with no common values and the total number of couples. A descriptor with little or no discriminating power can however become very decisive when the state of the descriptor which conditioned its applicability is verified (http://www.infosyslab.fr) (Abotsi 2015).

Here to propose some characters shared by all the group of species of *Gomphrena s. str.* (synapomorphy) that help with the complex delimitation, and distinguish them of the other genus related and *Gomphrena* polyphyletic. The lineage has complex delimitation of point of view taxonomic history and morphologically because the genus includes higth number species with a wide distribution. Reason why here to explore different vegetative and floral morphological characters to define and support a news conception from the genus based in phylogenetic results acquired until now, (see chapter one and three), to arrived a better evolutionary understanding of the genus, and proposed a new scenario. Traditional taxonomic and morphological studies (see chapter one) of the genus have been based almost exclusively in floral characters, however, contemporaneous authors explored other characters inside the Amaranthaceae family include micromorphological characters, all are cited at the beginning of this chapter (Carolin 1978, Borsch 1998, Eliasson 1998, Fank-De-Carvalho). Is evident that the construction from a new conception of *Gomphrena* s. str. will be require more work in the future, for example it is necessary to explore more into the architectonical characters that requires more summarized and discussed some of principal morphological characters, selected through values with a representative index from the list of the descriptors with high discriminatory power extracted with the program Xper². It must be considered that characters were introduced in the program, independently, we have two tables. studies with life specimens for follow the development of the plants for understand better the models of growing of the species and the evolutions implications (Barthelemy & Caraglio 2007).

the results from the list of descriptors with the power of discrimination from the first part of the morphological study, used here to make a wide comparison of *Gomphrena* s. str. in relationship with related genera, in which the vegetative characters presents the index with mosth high value is the character eight, arrangement of paracladia (0.8, fig. 2, 7 and 8), which is constituted as the most important character related with the dispositions of the branched systems and the inflorescens in *Gomphrena*, these characters are related to the architecture of the plants few explored at the moment (Acosta et al 2009) and could be useful to clarify the difference between some species and understand variations within them. Nevertheless, this characters no corroborate the delimitation of *Gomphrena* s. str., due to polyphyletic *Gomphrena* s.l. share the same state o character that those *Gomphrena* s. str. e.g. *G. mandonii* (polyphyletic) and *G. celosioides* (*Gomphrena* s. str.), they have the same character. Next, the apical leave subtending the paracladia (ALSP) with index 0.63 (Fig. 2-9 and 2-10), this character doesn't support in the delimitation of the species of *Gomphrena* s. str., though most of the 9 species of *Gomphrena* s. str. have ALSP, it is noted that *G. tomentosa* lack of this character, at the same of the genera related to Froelichia, Pedernesia, Xerosiphon, and the polyphyletic species of *G. rupestris, G. mollis, G. protrata, Guilleminea densa* (sin ALSP). However, the importance of this character (homoplastic) in this study, is that some species

Table. 2-4. Taxon samples with the matrix coded 1-22, the characters names and number of character states are develop in the text above.

Code	Taxon	Number Character																					
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
AC154	*Pedersenia volubilis* Borsch, T. Ortuño & M. Nee	1	1	0	2	1	0	1	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0
AC008	*Hebanthe occidentalis* (R.E. Fr.) Borsch & Pedersen	1	1	0	2	1	0	1	0	0	1	0	0	1	0	6	1	0	0	0	0	0	1
AC019	*Gomphrena elegans* Mart.	1	1	0	2	1	1	0	1	0	0	0	0	1	0	4	2	0	0	1	3	1	
AC099	*Gomphrena mandonii* R.E.Fr.	1	1	0	2	1	1	0	1	0	0	0	0	1	1	2	2	0	0	1	2	1	0
AC105	*Pfaffia fruticulosa* Suess.	1	1	0	2	1	1	0	1	0	0	0	0	1	1	4	3	0	0	0	0	0	0
AC101	*Xerosiphon aphyllus* (Pohl ex Moq.) Pedersen	1	1	0	2	0	1	1	0	0	0	0	0	1	0	3	3	1	3	0	0	0	2
AC016	*Froelichia floridana* (Nutt.) Moq.	0	1	0	2	0	1	1	0	0	1	1	0	1	1	2	3	1	2	0	0	0	2
AC462	*Gomphrena mollis* Mart.	1	1	0	2	0	1	0	1	0	0	0	2	1	3	2	2	0	0	1	4	1	2
AC464	*Gomphrena rupestris* Nees	1	1	0	2	0	1	0	1	0	0	0	2	1	3	2	2	0	0	1	4	4	2
AC461	*Gomphrena agrestis* Mart.	1	1	2	2	0	1	0	1	2	0	1	1	1	3	2	3	0	0	1	3	1	2
AC1029	*Gomphrena lanigera* Pohl.	1	1	0	2	0	1	0	1	2	0	1	1	1	3	1	3	0	0	1	1	1	2
AC007	*Gomphrena macrocephala* A. St.-Hil.	1	1	0	2	0	1	0	1	2	0	1	1	1	4	1	3	0	0	1	1	1	2
AC932	*Gomphrena celosioides* Mart.	1	1	0	2	1	1	0	1	2	0	1	1	1	3	2	2	0	0	1	2	1	2
AC1182	*Gomphrena celosioides Mart.*	1	1	0	2	1	1	0	1	2	0	1	1	1	3	2	2	0	0	1	2	1	2
AC141	*Gomphrena haenkeana* Mart.	0	0	0	2	1	1	0	2	2	0	1	1	1	3	2	3	0	0	1	2	3	2
AC095	*Gomphrena flaccida* R.Br.	0	0	2	1	0	1	0	1	2	0	1	1	1	2	2	1	0	0	0	0	0	2
AC674	*Blutaparon vermiculare* (L.) Mears	1	2	0	1	1	1	0	3	1	0	1	1	1	0	5	1	0	0	0	0	0	2
AC677	*Lithophila muscoides* SW.	1	1	0	1	1	1	0	3	1	0	1	1	1	0	5	1	0	0	0	0	0	2
AC140	*Gomphrena boliviana* Moq.	0	0	0	1	1	1	0	2	2	0	1	1	1	1	2	3	0	0	1	0	2	2
AC1199	*Gossypianthus brittonii Standl.*	1	1	1	0	1	0	0	4	2	0	1	1	1	0	3	1	0	0	0	0	0	2
AC783	*Gomphrena meyeniana* Walp.	1	1	1	1	0	1	0	2	2	0	1	1	1	0	2	1	0	0	0	0	0	2
AC784	*Gomphrena meyeniana* Walp.	1	1	1	1	0	1	0	2	2	0	1	1	1	0	2	1	0	0	0	0	0	2
AC445	*Gomphrena radiata* Pedersen	0	0	1	0	1	0	0	4	2	0	1	1	1	0	2	1	0	0	0	0	0	2
AC1052	*Gomphrena tomentosa* (Griseb.) R.E. Fries	1	1	1	0	1	0	0	4	2	0	1	1	1	0	3	1	0	0	0	0	0	2
AC465	*Gomphrena prostrata* Mart.	1	1	0	0	1	1	0	1	0	0	1	0	1	0	2	1	0	0	0	0	0	2
AC931	*Guilleminea densa* (Willd.) Moq.	1	1	1	0	1	0	0	4	0	0	1	0	0	0	2	1	0	0	0	0	0	2
AC1214	*Guilleminea densa* (Willd.) Moq.	1	1	1	0	1	0	0	4	0	0	1	0	0	0	2	1	0	0	0	0	0	2
AC1169	*Guilleminea densa* (Willd.) Moq.	1	1	1	0	1	0	0	4	0	0	1	0	0	0	2	1	0	0	0	0	0	2

have been identified with a type of specialized ALSP in the case of *Gomphrena sp*. nov. (Spec. 7) that represent a clear example “peudantium” paracladia didn’t describe before in the family (Fig. 2-12T), the pesudantium is a vegetative adaptation of the most proximal apical leaves of the “peduncle” toward the paracladia, that achieve to the inflorescence the appearance of one flower. These pseudantial leaves could be have variations in the density and the type of the trichomes in the abaxial or adaxial sizes leaves, presence or absent considering also the margin, in some groups of andean species this character in the leaves are related with a peculiar type of short trichomas formed by ususlly tree or two superiors cells with ellipsoidal form (see Fig. 2-38) this type of trichomes are found only in the adaxial surface of the leaves, and in one of the new species (Spec. 7) have a intence dark yellows colours, this character was not describe in other studies of the genus, and constitute an interesting find in this study. Related with the floral characters, the androecium tube (see chapter 3) has a highest value (0.65). These characters are cataloged as one of the most variable into the family (Townsend 1993), they have high difference in the proportions that is the filament united into the androecium conform a cup or tube, and vary specially in the free portion of the filament because for the presence or not apical filaments appendix (with rounded, acute apex), and also the position where is attached the anther (Fig. 2-23 and 2-24). However, the result expose in the chapter 3, show clearly that this homoplastic character is a reason why can’t be delimiting the *Gomphrena* s. str., but result useful to support the identification of the species and boundaries for some groups and probably in future works to see how is the environmental factor produce these changes, but the closest exponation is related to the specific polinization.

The most relevant character for the determination of *Gomphrena* s. str. found in this study, since and evolutionary point of view as a sinapomorphic character, is the character twelve the morphological differences between inner and outer tepals, that show principaly diferences sizes between the inner (shorlty) and outer tepals (0.51, Fig. 2-18) Furthermore, most of the species of *Gomphrena* s. str., the inner tepals being also cymbiforms, except *G. tomentosa*, *G. radiata* and *G. umbellata* which are flat and envelops and suborbicular tepals, other characteristic are usually the tepals are carinated when the plant mature. Unlike to other genera and species of polyphyletic *Gomphrena* (*G. mandonii*, *G. rupestris*, *G. elegans*) that present tepals of similar size, and usually without differences between the them, additionally and higthly related with this last character, here is found that *Gomphrena* s. str, species has a peculiar tissue tepals with all a similar type of dermal cells, disposed conforming a membranous thick or thin sheet formed by elongated, tubular fibrous cells (Fig. 2-19). In general, in the tepals are visualized a middle nerve, with the exception of *Gossypiantus* (included inside the *Gomphrena*, see chapter 3) that have lateral nervesthat do not reach to the end of the sheet, meanwhile, the allied genera and polyphyletic *Gomphrena* present tepals with tissues formed by orbicular cells, rounded, arranged in several layers (sheet), and some have a middle nerve and two lateral nerves prolonged to the end of the sheet. The most similar tepals, in relation to the dermal tissue, are from *Guilleminea*, however this are tepals connate until the middle and to be linked the androecium in the internal part (Fig. 2-21), reason for why this identified character is different to the tepals Gomphrena s. str., supporting the diference between the tepals character to help delimit the species of the genus Gomphrena s. str. and that not has been explicitly described in any study.

the results from the list of the 114 descriptors with the power of discrimination from the second part of the morphological study, which has been focused to the distinction at specific level of the Bolivian species.

From the new characters includes the micromorfological character of the trichomes of the vetegetative (in the pseudaution leaves) and floral parts (tepals), where the trichomes stems (with always similar to the caulinar leaves) reach levels of 0.78, the trichomes in Gomphrena s. str. in general are very characteristic, being uniseriated, multicellular, unlike e.g. G. mollis presents dentritic trichoms, or candelabra in G. mandonii (Fig. 2-33), thay mean constitutes a character that has to be more explored at generic level, some character of the trichoms from ALSP have values index > 0.6, being an important character at species level by the variation founded and described in this work, like the type of cells that shapes trichoms, the ornamietation of the cuticules, the type of cellular intermocking junctions, the color, etc.. Inside the floral characters related to the apex, shape, color, the bract, bracteoles, tepals and androecium present highest values index. These characters and the difference between the Bolivians species are discussed very punctually in Chapter 4.

Chapter 3 *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

3.1. Introduction

Gomphrena L. is the largest genus of the Amaranthaceae with c. 120 species (Townsend 1993; Müller and Borsch 2005) and includes subshrubs as well as perennial and annual herbs, which occur in the New World tropics and subtropics (Holzhammer 1955, 1956; Eliasson 1988) and Australia (Palmer 1998). Considerable species diversity (c. 40 species; Zuloaga et al. 2008; Borsch et al. 2015) 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 regions continue to be discovered and described, many of them endemic (Ortuño and Borsch 2005, 2006). The Cerrado and Caatinga habitats in mid-western and northeastern Brazil also are diverse in *Gomphrena* (ca. 50 sp.; Siqueira 1992), whereas Central America and the desert regions of Mexico and North America harbour only ca. 20 species (Robertson and Clemants 2009). *Gomphrena* occurs disjunct also in the arid and semi-arid regions of western, central and north-eastern Australia, which, with 33 species (Palmer 1998), constitutes another center of diversity.

Linneaus (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 (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 androeceum tube appendages (Vrijdaghs et 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). *Froelichia* differs from all other Gomphrenoideae by tepals fused for more than half, with this tube developing two lateral wings at maturity (Eliasson 1988). 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 androeceum morphology that also occurs in some Australian species of *Gomphrena*. The currently widely used genus concept of *Gomphrena* (Townsend 1993; Hernández-Ledesma et 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 its two species and removed them from *Gomphrena* based on the difference that their tepals are united until the middle.

According to the resulting slightly narrower genus circumscription, *Gomphrena* is characterized by flowers with five free and symmetric tepals, a stigma with an elongated style and two filiform stigma branches and the five filaments being united into a tube to varying degrees, in some species almost completely (Townsend 1993; Eliasson 1988; Borsch 2000). Most species of *Gomphrena* further possess stamen appendages in an almost terminal position on each side of the filament which can lead to the impression of "sunken" anther insertion points in species with a completely fused androecial tube (Borsch and Ortuño 2005, 2006; Pedersen 1997, 2000). The genera *Gossypianthus* and *Lithophila* are morphologically similar to *Gomphrena* in terms of their gynoecia. *Lithophila* also shares these androeceum characteristics but the number of filaments and anthers is reduced to two or three (Eliasson 1988), whereas *Gossypianthus* has a shortly fused androecium cup, lacks appendages but the androeceum is fused to the tepals for the most part (Schinz 1934; Eliasson 1988).

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 and Borsch 2005; Sánchez-del Pino et al. 2009; Borsch et al. 2018). Following the *matK-trnK* study by Müller and Borsch (2005), who presented an overall phylogenetic analysis of the Amaranthaceae, Sánchez-del Pino et al. (2009) focused on the Gomphrenoideae through an increased taxon sampling. Based on combined *trnL-F* and *rpl16* sequence data three highly supported subclades of the Gomphrenoideae were found, and informally called as Alternantheroids, Gomphrenoids, and Iresinoids. The iresinoid clade contains the genus *Iresine* and is sister to the remaining Gomphrenoideae (Borsch et al. 2018). Alternantheroids and Gomphrenoids share the presence of metareticulate pollen (Borsch 1998; Borsch and Barthlott 1998) as a synapomorphy and were also called core Gomphrenoideae (Müller and Borsch 2005). The alternantheroid clade consists of the monophyletic genera *Alternanthera*, *Pedersenia* and *Tidestromia* (Sánchez-del Pino et al. 2009, 2012; Borsch et al. 2011), whereas all remaining genera of the core Gomphrenoideae are in the gomphrenoid clade.

Molecular trees of Sánchez-del Pino et al. (2009), Sage et al. (2007) and Bena et 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 lineage constituted by *Gomphrena* s.str. (including *G. globosa* as the type species of the genus), *Philoxerus*, *Lithophila*, *Gossypianthus* and *Guilleminea* is characterized by metareticulate pollen with strongly reduced tectum (Borsch 1998) whereas the other including *Hebanthe*, *Pfaffia*, and two species of *Gomphrena* (*G. elegans* and *G. vaga*) has metareticulate pollen with the tectum completely covering the mesoporia and possessing just small perforations or foveolae (Borsch 1998; Borsch and Pedersen 1997). However, in all these studies relationships within each of these two lineages remained largely unresolved.

This investigation focuses on the first lineage ["clade a" in Sánchez-del Pino et al. (2009)]. These authors published the so far best resolved trees with plastid *trnL-F* + *rpl16* sequences but included just 11 species. They basically found three lineages in a polytomy, among which one depicted *Gossypianthus* appeared sister to *Gomphrena boliviana*, another *Gomphrena flaccida* sister to *Blutaparon* + *Litophila*, and the third the remaining species of *Gomphrena*. Recently, Bena et al. (2017) added *trnL-F* sequences of a dozen further species from Argentina, but their trees largely 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 et 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 androeceum from species with “pseudostaminodes” alternating with the stamens to species with apical filament lobes such as *Gomphrena spp.* through varying degrees of fusion. Vrijdaghs et al. (2014) examined androeceum development in Gomphrenoideae and concluded that the androecial tube in 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 et al. (2014) only examined *Alternanthera*, *Iresine* and *Tidestromia* but no sample of *Gomphrena*. Acosta et 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 C_4 photosynthesis in *Gomphrena* and allies, which was previously analyzed in the whole Amaranthaceae s.str. by Sage et 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 et al. (2007) only included five *Gomphrena* species to map the evolution of C_4 photosynthesis on the tree of Amaranthaceae and revealed a common origin of C_4 in species of *Gomphrena* belonging to “clade a” alongside with *Philoxerus*, *Guilleminea* and *Froelichia*. This result was confirmed by Bena et al. (2017) who tested if the evolution of the C_4 pathway correlated with changes in macroclimatic niches and found that C_4 Gomphrenoideae specialized to dryer regions compared to their C_3 relatives and then expanded into colder environments. That is consistent with the current distribution of C_4 species of *Gomphrena* growing at high elevations of the Andes in Argentina and Bolivia (Sage et al. 2007; Borsch et al. 2015). Here we use a representative sampling of C_3 and C_4 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 Paleocene-Eocene thermal maximum (N.P. Barker et al. 2007a; Pennington and 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 and Crisp 2005; P.F. Barker et al. 2007b). Using data from published phylogenetic and biogeographic analyses, Sanmartín et 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 data sets, 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 C_4 photosynthesis on the basis of our new phylogenetic results and to test in how far a realigned genus *Gomphrena* is characterised by C_4 photosynthesis.

3.2. Material and Methods

3.2.1. Taxon sampling and composition of data sets

The first dataset comprises major entities of *Gomphrena* and allied genera (*Lithophila, Gossypianthus, Guilleminea, Philoxerus*) and also covers the other lineages of the Gomphrenoid clade sensu Sánchez del-Pino et 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 data set of plastid regions (*rpl16* intron, *matK* gene and *trnK* intron as well as the *trnL intron and the trnL-F* spacer; data set A) and a 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. macrocephala*) the *trnLF* and *rpl16* data came from Sánchez del-Pino et 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 *trnLF* from Sánchez del-Pino et al. 2009), as well as

Gomphrena mandonii (*matK-trnK*, morphology, this study), and *G. elegans* (*rpl16* and *trnLF* from Sánchez del-Pino et al. 2009).

The second data set includes a much higher number of samples (80 for plastid *matK-trnK* = data set B-1 and 82 for nrITS = data set B-2) with the aim to illuminate the overall tree space of the "*Gomphrena* clade" (= *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 distribution 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 were used for some species (*Gomphrena macrocephala*, *G. fuscipellita*, *Blutaparon vermiculare*, *G. ferruginea*, *Guilleminea densa*). *Gomphrena globosa* L. (type of the genus; Hernández-Ledesma et al. 2015) data. Voucher information and EMBL/GenBank accession number is provided in Appendix 3-1.

A third, extended *matK-trnK* data set (Data set 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 et 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 data set B-1 of this investigation with some terminals belonging to the same species not included to reduce polytomies.

3.2.2. DNA isolation and sequencing

Genomic DNA was isolated from silica-gel-dried leaf tissue or herbarium specimens using a triple CTAB extraction method (Borsch et al. 2003). The *matK-trnK, trnLF* and *rpl16* regions were selected because of their high phylogenetic structure (Borsch and Quandt 2009, Korotkova et al. 2011) and to achieve consistency with other Amaranthaceae data sets (Müller and Borsch 2005, Di Vincenzo et al. 2018, Borsch et al. 2018). They were amplified and sequenced using the primers given in Di Vicenzo (2018). In most cases two overlapping halves of the *matK-trnK* region were amplified. DNAs isolated from herbarium specimens often required to amplify shorter fragments, for which several internal primers (ACmatK100F, ACmatK200R, ACmatK1300R, ACmatK1250F)were taken from Müller & Borsch (2005) or newly designed for *Gomphrena* such as ACmatK442F (5'-AGT CAA AAG AGC GAT TGG G-3'), ACmatK602F (5'-CTT GTT TTG ACT GTA TCG C-3'), ACmatK465R (5'-TCT TAT AAC AAA ATA AGA TGG-3') and ACmatK631R (5'-ACA AAA GTA AAA ATA GAG G-3'). Primer ACmatK442F was also used as a forward sequencing primer to complement the pherograms made with ACmatK1400R that could not read over a large microsatellite located in the *trnK* intron several *Gomphrena* species about

90 nt upstream the *matK* start codon. The *rpl16* intron was amplified with flanking primers rpl16-1216F and rpl16-1516R, and an additional internal forward primer GOMrpl16-495F was used for sequencing (see Borsch et al. 2018 for primer sequences). The *trnL-F* region was either amplified as a whole using primers c and f (Taberlet et al. 1991) or in two parts when DNA was isolated from herbarium material with primers c and d as well as trnL460F (Worberg et al. 2007) and f. Primers d and trnL460F were used for sequencing.

The ITS region was amplified and sequenced with the universal primers ITS4 and ITS5 (White et al. 1990). In cases when the pherograms were not readable, mostly from herbarium specimens, the internal primers ACITS3F (5'-TTG GTGTGA ATT GCA GAA TCC C-3') and AC-ITS2R (5'-GAT GGT TCA CGGGAT TCT GC-3') designed by Müller (2002, unpubl., u) annealing to the 5.8 S gene were used to amplify and sequence shorter fragments.

The PCR profiles used for the chloroplast regions were as described in Borsch et al. (2018). PCR amplification of ITS was performed using the following reaction mix: 1.5 mM $MgCl_2$, 1X PeqLab Taq Buffer S (including $MgCl_2$),0.25 mM each dNTP, 0.8 pmol primer, 0.03 U/ul Taq polymerase(PeqLab, Erlangen Germany) and 0.8 ng/ul DNA template. Betaine was added to a final concentration of 1 M. The PCR was performed in a Mastercycler (Eppendorf, Hamburg, Germany).

Primer dimers and unspecific PCR products were separated from the targeted bands using a 1.5% NEEO agarose gel (Carl Roth, Germany) running for 3 h at 100 volts. Gel extraction was performed using the AveGene Gel/PCR DNA Fragments Extraction Kit (AveGene life science Corporation). The quality and quantity of the purified PCR product were measured with a NanoDrop spectrophotometer. Cycle sequencing, fragment purification, and direct automated sequencing was performed by Macrogen Inc. (Seoul, South Korea).

3.2.3. Alignment and coding of length mutational events

Sequences were edited and aligned manually using PhyDE (Phylogenetic Data Editor) version 0.9971 (Müller et al., 2012), using a motif alignment approach (Morrison 2009, Ochoterena 2009) following the rules by Löhne and Borsch (2005). Positions of uncertain homology (mutational hotspots) were excluded from the analysis (exact delimitation see Table 3-1). Indels were then coded automatically using the Simple Indel Coding method (Simmons and Ochoterena, 2000) as implemented in SeqState 1.40 (Müller, 2005a).

3.2.4. Phylogenetic analyses

Maximum Parsimony 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 ModelTest 2 (Darriba et al. 2012) and using the Akaike information criterion (Akaike, 1974). The best fitting model was TVM+G for *trnL-F* and *rpl16* and GTR+G for *matK-trnK (*data sets A and B-1). The substitution model found for ITS was SYM+G (Table 3-1).

Bayesian inference (BI) was carried out using MrBayes 3.2 (Ronquist et 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 combined 27-taxon plastid dataset was set in Mr. Bayes as nst=6 and rates=gamma with rate–matrix parameters, state frequencies, gamma-shape parameter, and proportion of invariable sites unlinked across partitions. The convergence and effective sample size (ESS) of each replicate were checked using Tracer v. 1.5.0 (Rambaut et al., 2013).

Maximum Likelihood (ML) analysis was performed using RAxML GUI 1.3 version 7.2.8 with 1000 bootstrap replicates and the setting described in Stamatakis et al. (2008). 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.

3.2.5. Assessment of morphological characters and ancestral character state reconstruction.

In most cases, herbarium specimens corresponding to the samples also used for the molecular analyses were used to assess the morphological characters. A set of 22 morphological characters was defined (see Chapter 2) covering vegetative, inflorescence and floral morphology as well as presence of metareticulate pollen (Borsch & Barthlott 1998). Characters used in previous studies of Amaranthaceae (e.g. Holzhammer 1955, Pedersen 1976, 1990, 1999, Eliasson 1988; Borsch & Pedersen 1997) were re-analysed, compared with the observed variation, and relevant results on comparative morphology and ontogeny, in order to arrive at clear definitions of characters, reflecting a hypothesis of homology, and their states. The selection of characters also considered their previous use as diagnostic features for the various generic concepts that were applied to *Gomphrena* and allies. The respective character data were obtained in majority by examining the herbarium specimens under a stereo microscope. Others were obtained from the literature, such as in *Froelichia* (Acosta et al. 2009). Pollen data came from Borsch (2008), and an extended survey of *Gomphrena* pollen (T. Ortuño, T. Borsch, unpubl. data).

The 22 morphological characters were scored for the same species as in the 27-taxon combined plastid dataset (data set A). The matrix is provided as Appendix 3-2 at the end of this chapter. To depict the ancestral states the maximum clade credibility tree from the Bayesian analysis is used, which was identical in topology to the Bayesian Majority rule consensus and the best ML trees. Ancestral states were reconstructed in a ML framework using BayesTraits, version 2.0 (Pagel et al. 2004) sampling 1000 randomly selected trees after the burn in generated by BEAST using the parameters already established for the analysis with MrBayes but constraining *Pedersenia* as sister to a monophyletic ingroup. Commands for BayesTraits were generated by TreeGraph2 (Stöver & Müller 2010). Ancestral state probabilities were imported into TreeGraph2 to simultaneously visualize them on the branches, adding current states on terminal branches. The goal was to illustrate the taxonomic distribution of characters and their states, to detect synapomorphies for major clades within *Gomphrena* and allied genera and to provide hypotheses of ancestral character states.

3.2.6. Evolution of C_4 photosynthesis

To assess the type photosynthetic pathway, delta C13 values were taken from Sage et al. (2007). Many of the specimens studied there are also included into our phylogenetic analysis. Some additional specimens were examined for Kranz anatomy, which all were close relatives of taxa previously studied for isotopes. Presence of C_4 versus C_3 was then coded as a binary character. Ancestral states were reconstructed as reported for the other morphological characters. The large Maximum Parsimony (MP) matK-trnK and nuclear ITS trees constructed by PAUP. More elaborate analysis of ancestral states plastid versus ITS because of topical incongruence of the *G. mollis/ruprestris* lineage; extended molecular data set from other analyses in gomphrenoideae to test the effect of coding in alternantheranthoids /Pedersenia is C3 but some *Alternanthera* are C4.

3.2.7. Molecular clock dating

Dating was carried out with BEAST 1.8.0 (Drummond et al. 2012) using the broad Amaranthaceae-Chenopodiaceae *matK-trnK* data set C. Because no fossils for the Gomphrenoideae are known, the same three fossil calibration points used by Di Vincenzo et 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 et al. 2010). Age distribution priors for fossil primary calibration points were set as “exponential” (Ho and Philips 2009), whereas the three secondary calibration points (using age estimates of Bell et al. 2010) were included with “normal” age distributions equal to the 95% highest posterior densities interval (HPD) of Bell et al. (2010). Thus, 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 Acalyphoid clade as recently carried out by Di Vincenzo et 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 Mio. Generations for two MCMC runs. Adequate parameter sampling was checked with Tracer 1.4.0 (Rambaut and Drummond 2007). The combined pos-burn in tree distribution of both runs was then summarized as a maximum clade credibility tree using TreeAnnotator 1.8.0 (Drummond et al. 2012).

3.2.8. Generation of the distribution map

The distribution map of the coastal species (*Blutaparon verniculare* and *B. portulacoides*) was produced in ArcGIS 10.3 program, based on the data obtained from the labels of samples reviewed of the National Herbarium of Bolivia (LPB), the herbarium of the Darwinion institute (SI) in Buenos Aires Argentina, Herbarium of Berlin (B), Herbarium of the State University of Feira of Santana-Bahia Brasil. In addition, the database included the online registers of Tropicos-MOBOT (MO). Jardim Botânico do Rio de Janeiro (JABOT) specimens from Brazil; African Plant

Database (CJB, www.ville-geneve.ch). The georeferenced data was used "DECIMAL DEGREES" format and all de coordinate was verified Google earth, in ArcGIS 10.3 program.

3.3. Results

3.3.1. Characteristics of the sequence data sets

Statistics of the multiple sequence alignments for the 27 samples of *trnL-F*, *rpl16, matK-trnK* the individual and consensus information are in Table 3-1. The length of alignment of 27 samples in *trnL-F*, *rpl16, matK-trnK* region had 1082, 1150, 2499 characters, were excluded 8 Hotspots (HS) with 93 characters, 4 HS (103 characters) and 3 HS (66 characters) respectively. The *trnL* intron matrix starts at position 13 (first twelve nt trimmed off). Number of parsimony informative characters was 91 in *trnL-F*, 118 in *rpl16,* and 178 in *matK-trnK*. In the combined short tree, alignment length was 4857 bp without the HS and including the indel-coded characters. Number of parsimony-informative characters was 387. The alignment of data set A and the matrix including indels as used in analysis is provided in the electronic Appendix E-1 at the end of the thesis The alignment of *matK-trnK* for 80 samples had 2510 characters including the 45 indels, excluded 3 HS with 424 characters. 238 are the parsimony informative character. The alignment of data set B-1 and the matrix including indels as used in analysis is provided in the electronic Appendix E-2 at the end of the thesis The ITS with 82 samples the number of 722 characters plus 81 indels. 269 are parsimony informative characters (Table 3-1). The alignment of data set B-2 and the matrix including indels as used in analysis is provided in the electronic Appendix E-3 at the end of the thesis.

3.3.2. Molecular phylogenetic trees

The combined plastid tree (*matK-trnK*, *trnLF*, *rpl16*; Fig. 3-1) 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 parsimony, Bayesian and likelihood. 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 The trees inferred from the extended *matK-trnK* dataset (Fig. 3-2) show the same principal lineages but several of them are revealed with more diverse crown groups. These are a central and southern Andean dry Puna and Prepuna *G. radiata -umbellata-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. macrocephala* ranging from the Cerrado to the Chaco is extended by *G. cardenasii*, an endemic from the Cerrado-Chiquitania of Bolivia and thus comprises species "core C_4 *Gomphrena* clade"

(Fig. 3-1). Within the latter, a clade comprising *Gomphrena meyeniana* sister to *G. radiata* plus *G. tomentosa, Gossypianthus* and *G. boliviana;* a clade of *Lithophila, Philoxerus* and *G. flaccida* from Australia; a clade of *Gomphrena haenkeana* and *G. celosioides;* and a clade with *G. agrestis*, *G. lanigera* and *G. macrocephala*. *Xerosiophon* and *Froelichia* are successive sisters to the "*Gomphrena* clade".

The trees inferred from the extended *matK*-*trnK* dataset (Fig. 3-2) show the same principal lineages but several of them are revealed with more diverse crown groups. These are a central and southern Andean dry Puna and Prepuna *G. radiata -umbellata-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. macrocephala* 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 South-Eastern 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 a Mexican *G. nitida* appears unresolved to them (Fig. 3-2).

Table 3-1. Sequence statistics of the combined tree cpDNA combined *matK-trnK+rpl16+trnLF* (data set A) and the extended tree *matK-trnK* (data set B-1), (C) and ITS (data set B-2).

Genomic region	***matK-trnK*[a]**	***rpl16*[a]**	***trnL-F*[a]**	**Combined cpDNA**	***matK-trnK*[a]**	**ITS**
number taxa	**27**	**25**	**27**	**27**	**80**	**82**
Length of the alignment	2499	1150	1082	4731	2508	644
Hotspots (positions in alignment)	373-381 584-563 605-686 963-988 2628-2645 2778-2810	477-517, 576-591, 1015-1024, 1065-1104	73-82, 184-202, 305-310, 342-345, 406-423, 522-544, 858-868, 1117-1129	All the Hospots included in the each T aling combined	355-363 488-518 560-619 864-889	374-533 762-810
Total number of indels	40	54	45	139	44	84
Total number of characters in matrix[1]	2539	1204	1127	4870	2553	728
Variable substitution characters	435	249	211	895	512	391
Informative substitution characters	178	117	91	386	253	271
Informative indel characters	12	22	21	55	15	39
Model (AIC)	GTR+G	TVM+G	TVM+G	GTR+G	GTR+G	SYM+I+G
CI substitutions without indels	0.863	0.858	0.870	0.859	0.848	0.529
RI substitutions without indels	0.855	0.881	0.868	0.861	0.934	0.806
RC substitutions without indels	0.738	0.756	0.755	0.739	0.792	0.426
tree length substitutions without indels	510	267	216	998	617	960
CI substitutions+indels	0.866	0.845	0.844	0.850	0.848	0.554
RI substitutions+indels	0.859	0.861	0.837	0.848	0.932	0.81
RC substitutions+indels	0.744	0.727	0.706	0.721	0.79	0.448
tree length substitutions+indels	553	335	275 (32 trees)	1170	669	1067

[1] Including the corresponding indel coded matrix.

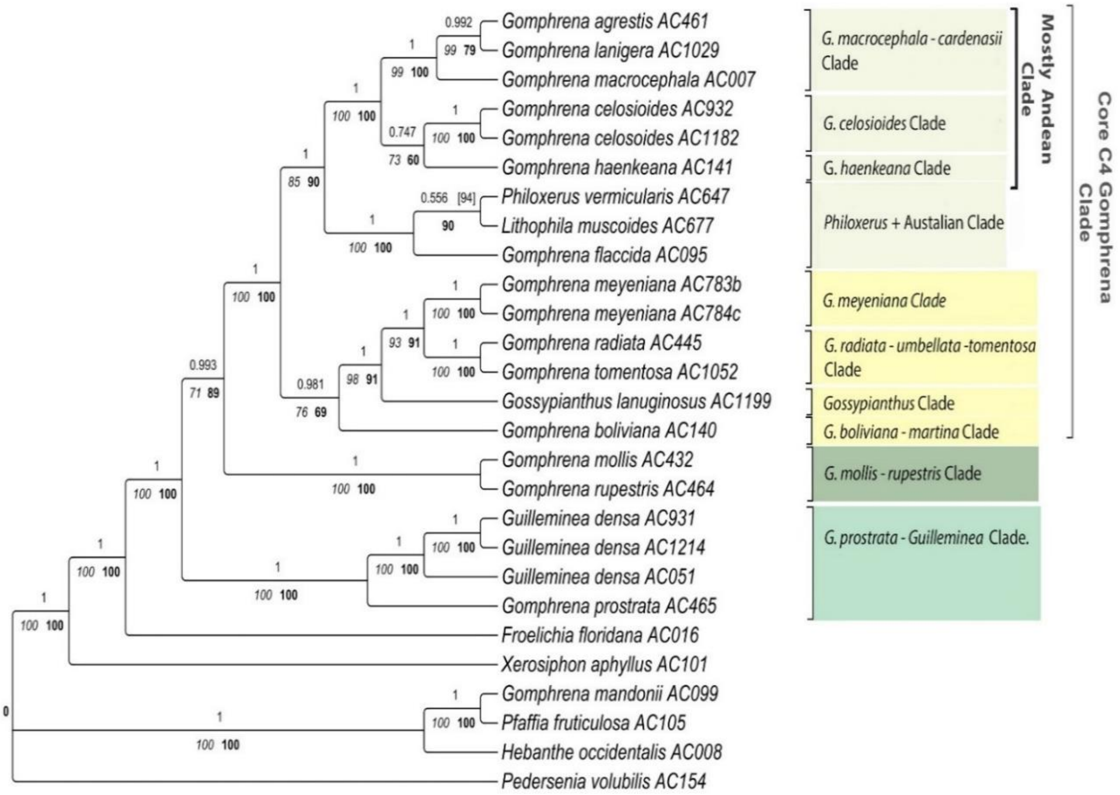


Fig. 3-1. Cladogram reconstructed from the combined matrix of *matK-trnK+rpl16+trnLF* sequence data including indels. The majority rule consensus tree obtained from MrBayes is depicted. Support values shown above branches are posterior probabilities; below are JK percentages from parsimony (left) and BS percentages from likelihood reconstruction (right).

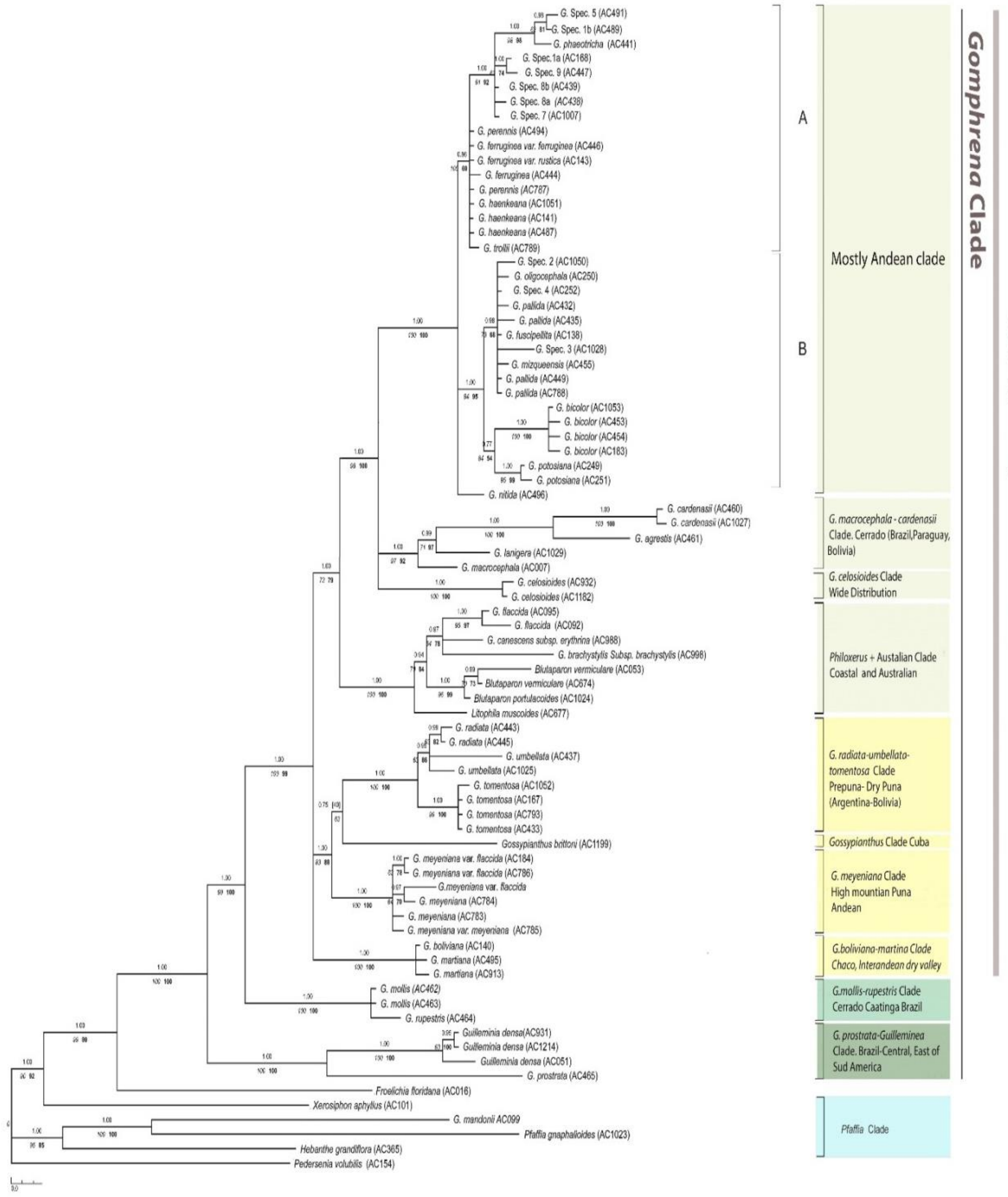


Fig. 3-2. Extended phylogeny of *Gomphrena* based on *matK*-*trnK*. The Bayesian topology is shown as phylogram. Support values shown above branches are posterior probabilities; below are JK percentages from parsimony (left) and BS percentages from likelihood reconstruction (right). Major subclades ("phylogenetic species groups") are annotated as well as the geographic origin (country, department) of the respective samples. Note that there is a diverse clade that is mostly constituted by Andean species with two further sub-clades (A and B).

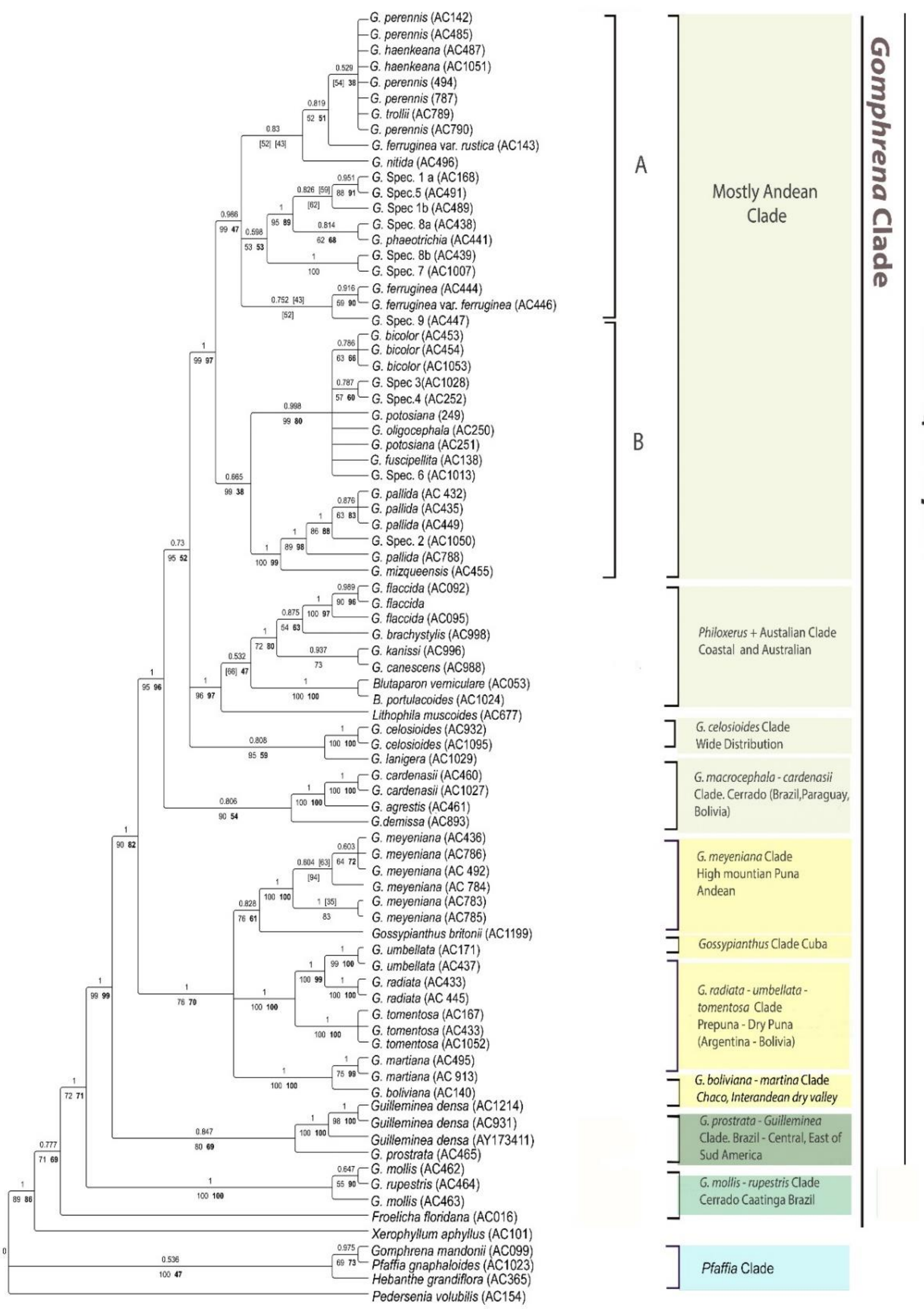


Fig. 3-3. Extended phylogeny of *Gomphrena* based on *nrITS*. The Bayesian topology is shown as cladogram. Support values shown above branches are posterior probabilities; below are JK percentages from parsimony (left) and BS percentages from likelihood reconstruction (right). The same names of the principal clades are annotated on the right as in Fig. 3-2.

The ITS data (Fig. 3-3) 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* lineage. The Australian species of *Gomphrena* clade are also retrieved with high support as close relatives to *Philoxerus* and *Lithophila* (Fig. 3-3).

3.3.3. Morphological characters

Six characters describe the habit and vegetative morphology in *Gomphrena* and allies were defined (see Table in Chapter 2; this includes a discussion about homology). Character 1 is a complex trait (lyfe cycle) which is relevant because of many annuals. Characters 7 and 8 relate to inflorescences. The paracladia in *Gomphrena* (Fig. 3-4) 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. 3-4). 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). Character 11 (type of photosynthesis) is here understood as a complex character, which includes morpho-anatomical as well as physiological and biochemical features. Two characters 12 and 13 refer to floral morphology, whereas characters 14 to 22 describe the variation of the androeceum in detail.

3.3.4. Evolution of morphological characters

Ancestral state probabilities for vegetative characters and floral morphology are depicted as pie charts in Fig. 3-5 (characters 1, 2, 3, 4, 5, 6, 8, 9, 12 and 13 are illustrated in this summary figure). For characters 7 and 10 individual character state reconstructions in Appendix 3-3. Note that heteromorphic tepals with the inner three 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 (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* (Fig. 3-4 terminal states).

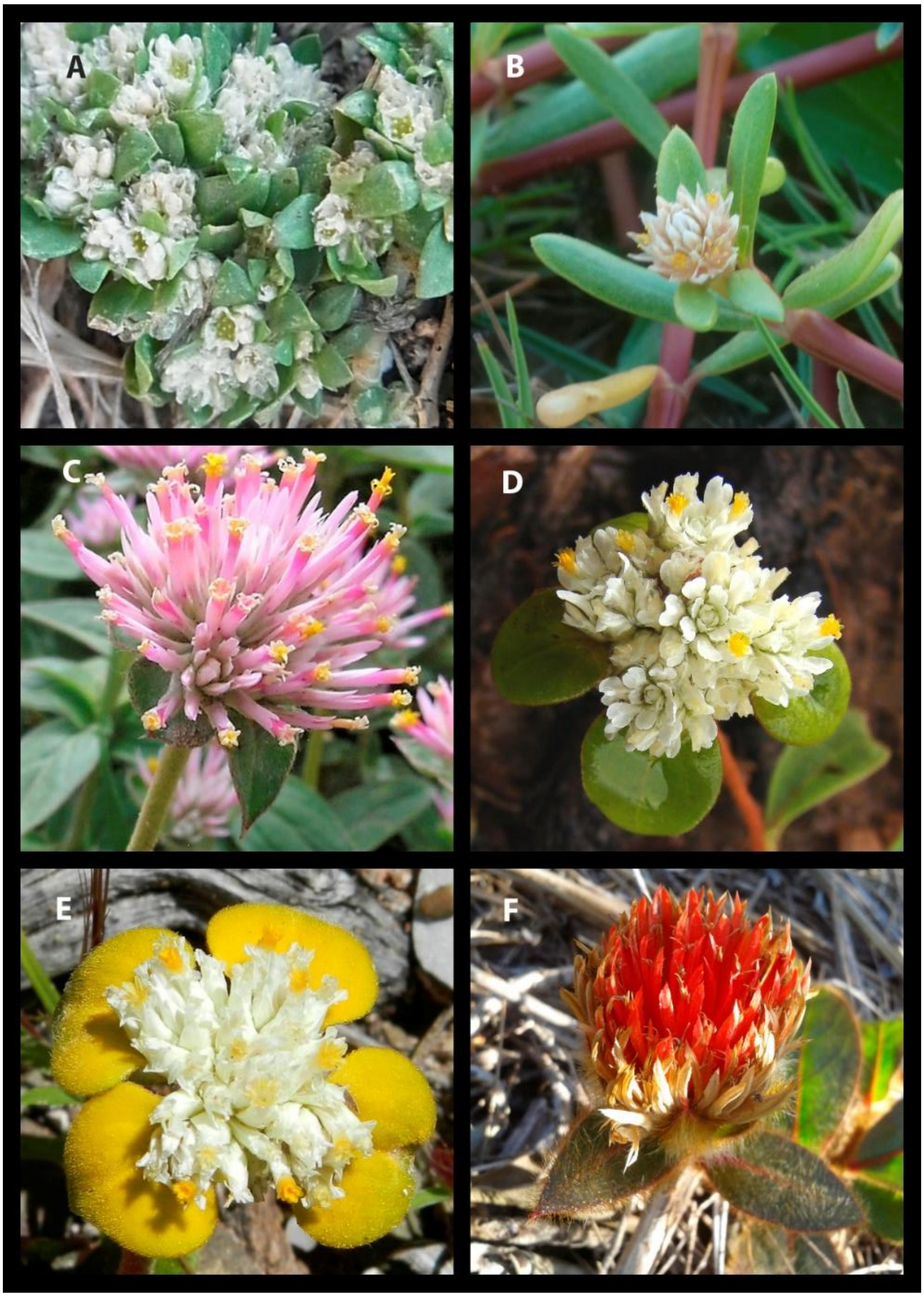


Fig. 3-4. Inflorescence morphology of *Gomphrena*: Flowers are arranged in partial florescences (paracladia), which can be subtended by various kinds of leave organs (Character 9). A) Cauline leaves subtending partial florescences absent, state (0). in *Guilleminea densa*. B) Two opposite and unspecialized cauline leaves, state (1) in *Philoxerus portulacoides*. C) With broadend, often stellately arranged (4-) 5 (-6) pseudantial leaves arranged in a whorl, state (2) in *G. haenkeana* (photo T. Borsch, and D) in *G. pallida*. E) With these pseudanthial leaves having bright yellow colour in *Gomphrena sp. nov.* (Spec. 7); and F) with 5-10 specialized, narrow leaves that are very different from the cauline leaves, state (3) in *G. macrocephala* (photo #. Fank-de-Carvalho).

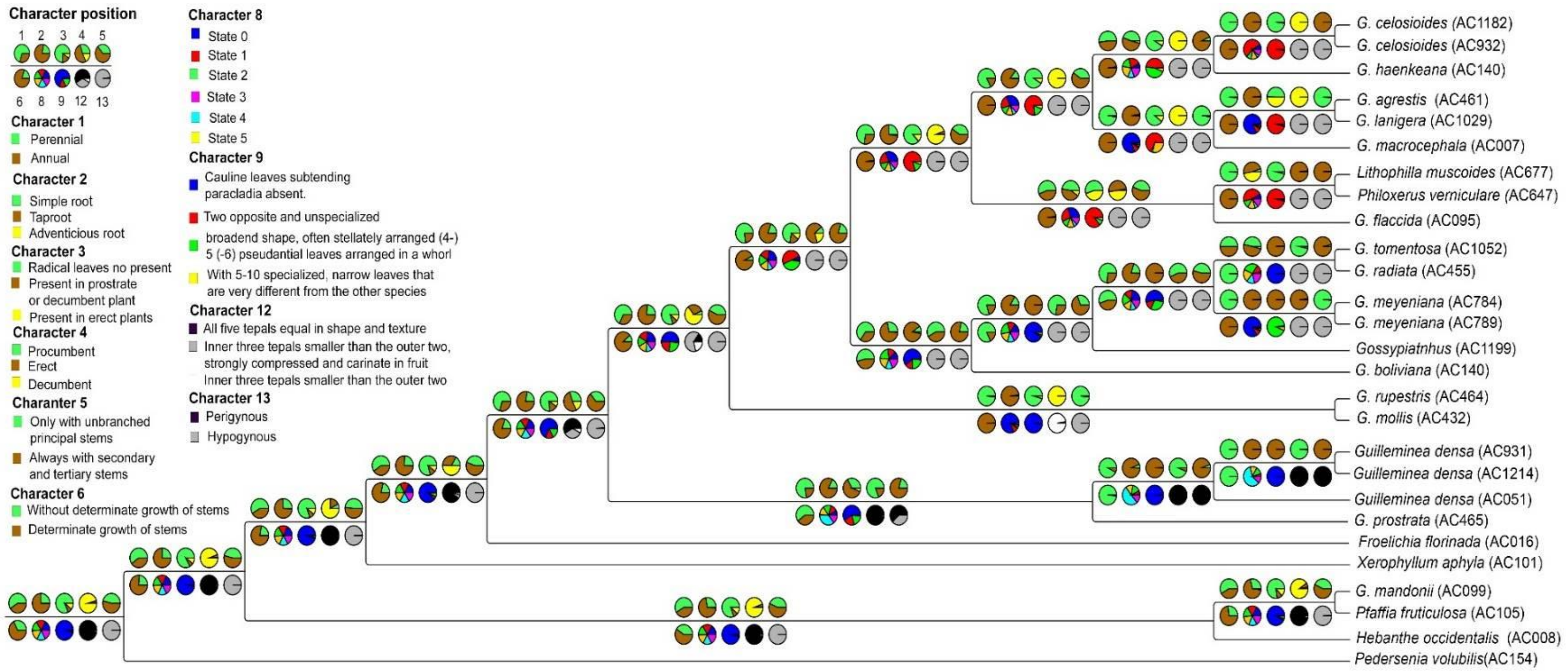


Fig. 3-5. Evolution of vegetative. Character 1: lyfe cycle, character 2: Type of Root, character 3: Radical leaves, character 4: Orientation of growth of the stems, character 5: Vegetative branching system, Character 6: Determinate vs. indeterminate growth of stems, character 8: Arrangement of paracladia State 0: Paracladia are often solitary and terminal on the main vegetative axes, state1: or as well on principal lateral branches, state 2: Solitary paracladia can appear in the axes of one of the cauline leaves, and in terminal parts of major branches of the plant there can be elongated or very reduced axes often only appearing in one of the leaves axils. State 3: paracladia are strongly condensed appear in a terminal whorl, character like structure with a terminal partial florescence surrounded by usually 5 (3-6) paracladia without visible axes, state 4: Guilleminea with a regular assymetric arrangement of a big paracladium arising from the axillary bud of a large cauline leaf and a very condensed structure with multiple branching orde. State 5: The paracladia are 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. Inflorescence. Character 9: Apical leaves subtending paracladia. Floral morphology. Character 12: Morphological differences between inner and outer tepals, character 13: Perigynous versus hypogynous flowers. The ancestral state reconstruction carried out with BayesTraits is depicted on the maximum clade credibility tree obtained by Bayesian Inference (identical topology to the majority rule tree) of the combined plastid data set. States of the current samples are shown on the terminal branches. Pie charts were omitted for some deep nodes with minor changes and for characters 7 and 10 where changes appeared not be relevant for Froelichia, Hebanthe, Pedersenia and Xerosiphon, all of which are well-defined distant genera (see Appendix 3-2 and 3-3). In Gomphrena and relatives (see also Chapter 2 for the definition of characters and their states as well as the full matrix in appendix 3-2.

3.3.5. Evolution of C_4 photosynthesis

The reconstruction of ancestral characters states of the presence and absence of C_4 photosynthesis in the small plastid tree shokkkw that the C_4 photosynthesis appeared in the common ancestor of the *Gomphrena* clade with *Froelichia* and *Xerosiphon*. (Fig. 3-8). The C_4 photosynthesis then was lost in the C_3 - *G. mollis- rupestris* clade.

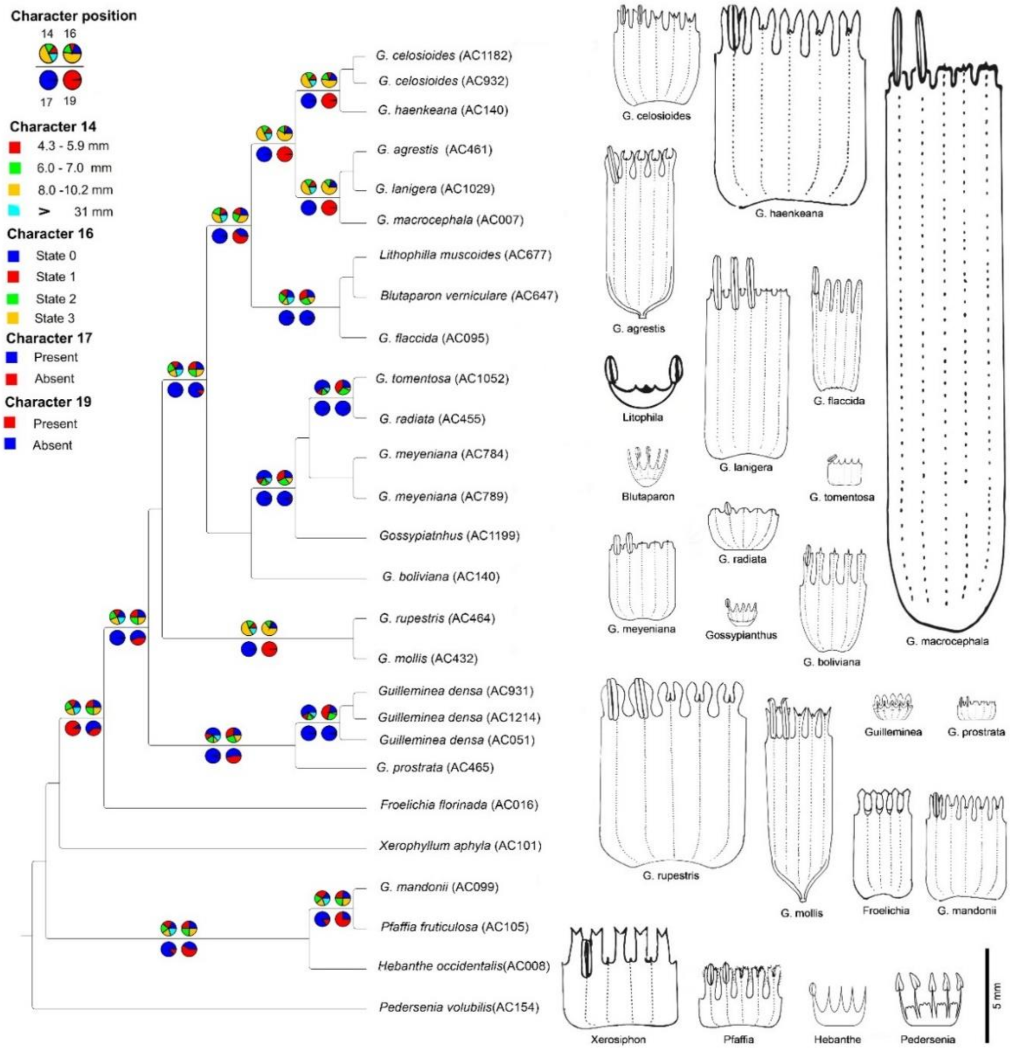


Fig. 3-6. Evolution of the androecium in Gomphrena and related genera reconstructed over a Bayesian maximum credibility tree based on the combined plastid dataset (27-taxon data set).The position of the character it is showing in the left where the meaning of the character 14 is the length of the androecial tube; character 16 shape of the androecial tube where the state 0: no present. State 1: Broadly cup-shaped with distinctly spaced filaments and distinct horizontall margin. State2: More or less broadly cup-shaped with V-shaped connection between filaments. State 3: More or less broadly cup-shaped with U -shaped connection between filaments. The character 17: Presence of androecial tube appendages. Character 19: Presence of filament appendages tube. The illustrations of androecium characters belong to the voucher (are in the righ); look for a way to map character state transformations of all respective androecium characters over the tree [chars 14, 16, 17, 19 are selected to be illustrated in this Figure, whereas chars 15, 18, 20, 21 will be in an appendix 3-2.

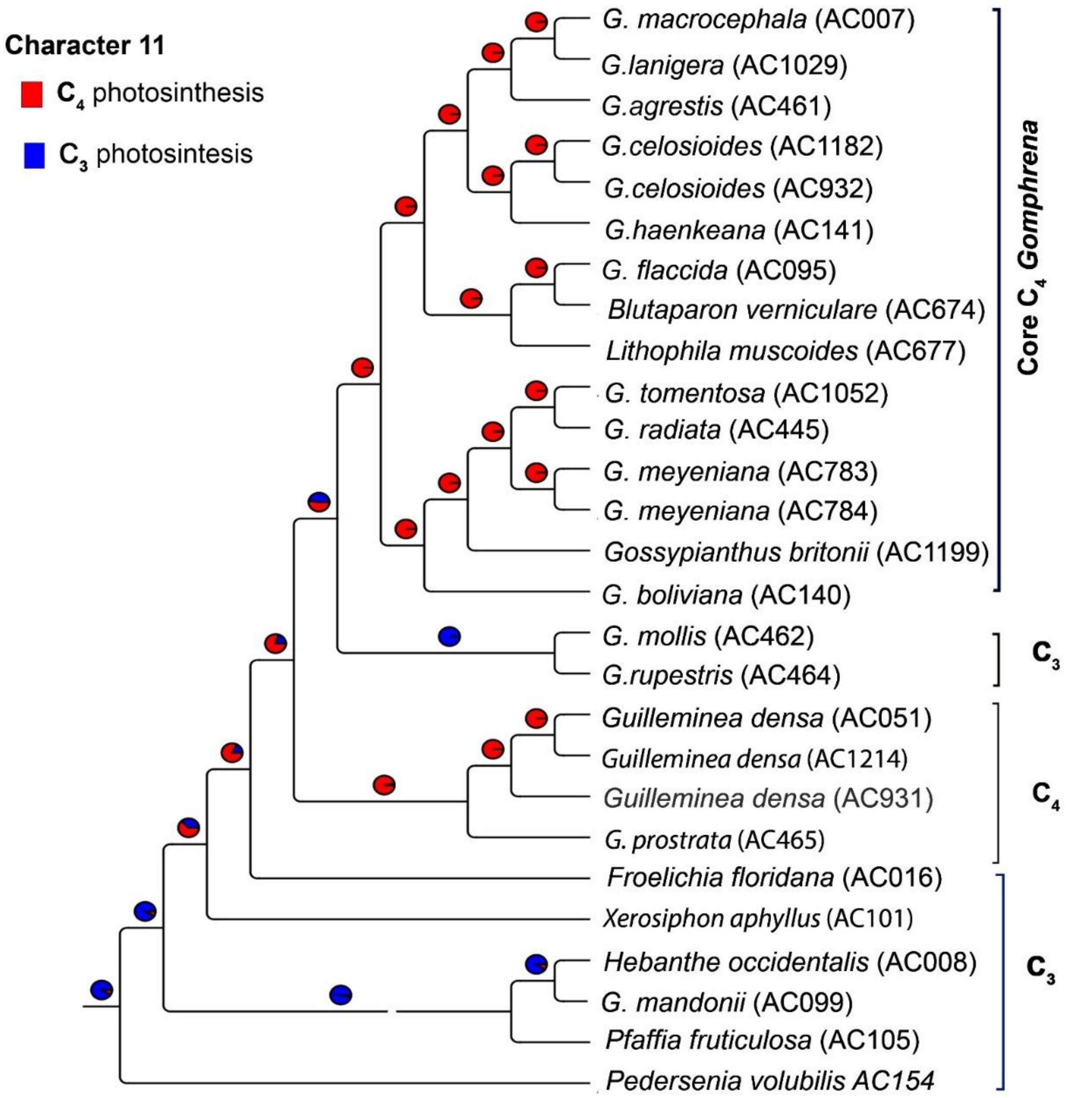
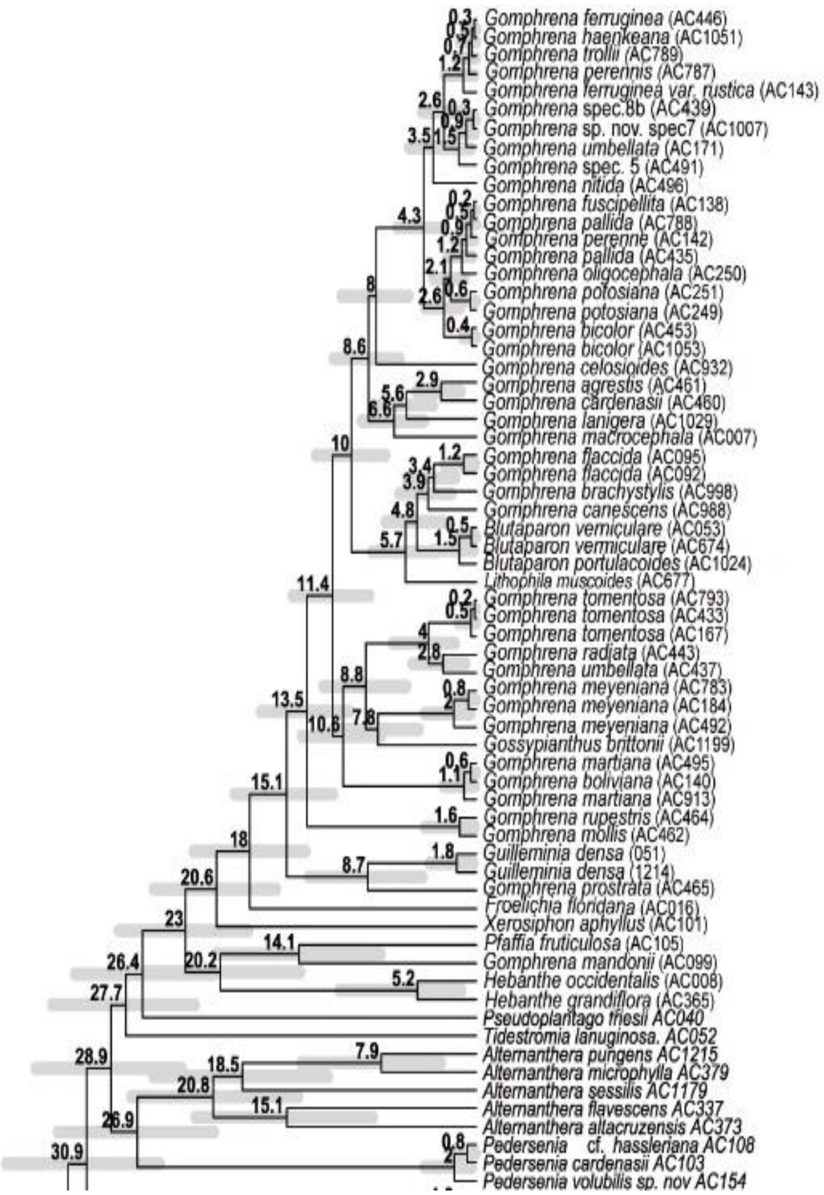


Fig. 3-7. Pie charts depict the evolution of C_4 photosynthesis in *Gomphrena* in the wider context of the Gomphrenoideae. The core C_4 *Gomphrena* clade including, *Lithophila*, *Gossypianthus*, and *Philoxerus* constitutes the most diverse C_4 lineage in Amaranthaceae. The *G. mollis*- *G. rupestris* clade is reconstructed to reversed back to C_3- *Pedersenia* are include into outgroup.

3.3.6. 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. 3-8; 21.16-43.22 95% HPD, node number 14 in Appendix 3-5), whereas the *Gomphrena* clade (see Figs 3-1, 3-2 (node 21, 15.1 Ma, 8.92-23.6, 95% HPD, see Appendix 3-5) and the less inclusive core C_4 *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 than the speciose Andean subclades 1 and 2. Figure 3-7 shows the divergence times calculated in this study.



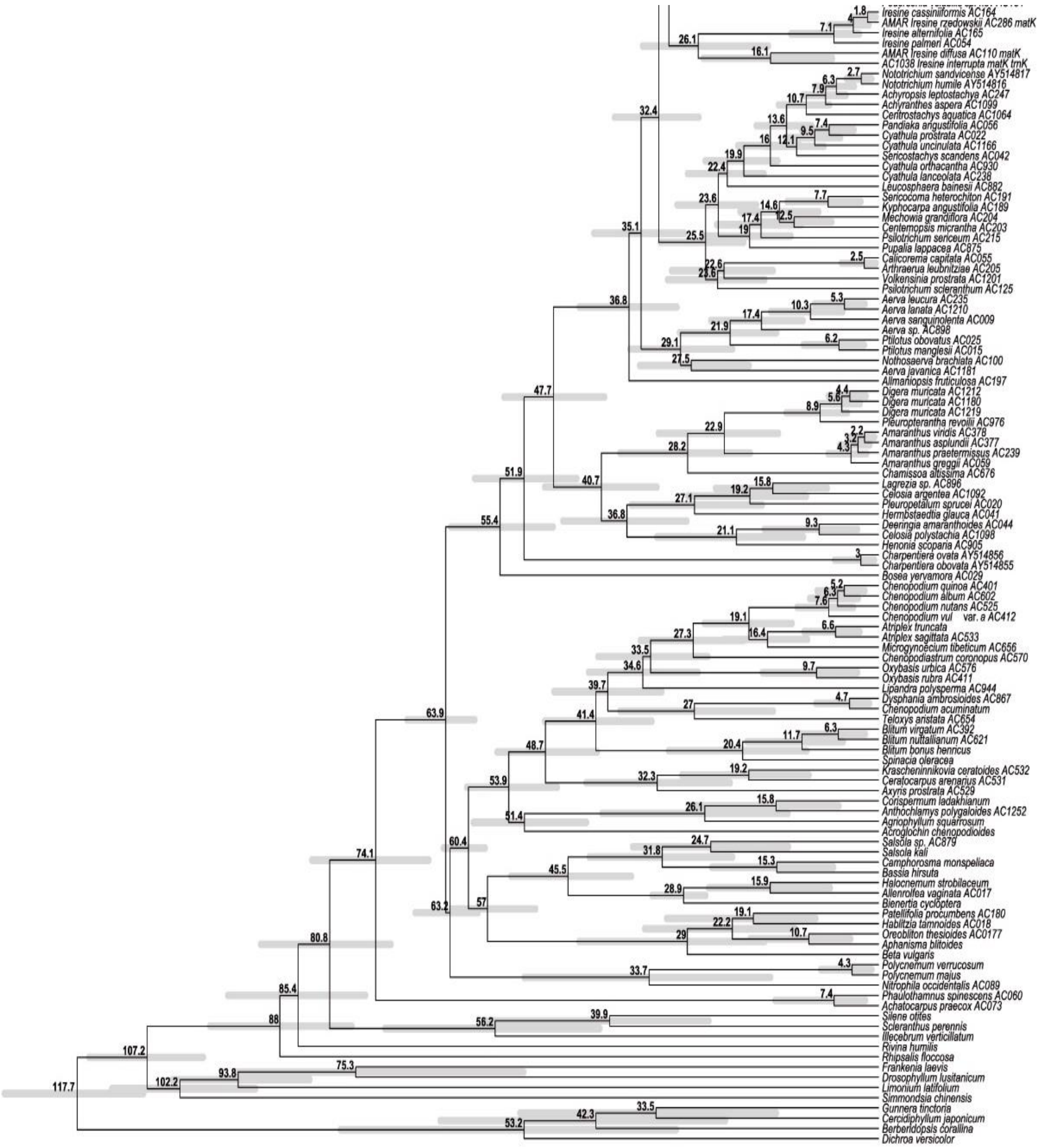


Fig. 3-8. Overview on the evolution of *Gomphrena* in time and space resulting from BEAST analysis.

3.4 Discussion

3.4.1. 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 (Figs. 3-1, 3-2). The deep nodes received maximum support under parsimony, Bayesian, and likelihood in *matK*-*trnK* alone (Fig. 3-2) as well as plastid regions combined (Fig. 3-1). 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 et al. (2009) based on *trnLF* and *rpl16* sequences alone. The trees recovered from nrITS are largely congruent, although they remain inconclusive on the branching order of *Froelichia* and *Xerosiphon* (Fig. 3-3). The clade that includes the majority of *Gomphrena* species in addition to *Xerosiphon* and *Froelichia* is characterized by metareticulate pollen with the tectum reduced to distal bands (see also Borsch et al. submitted) and depicts *Guilleminea*, *Gossypianthus*, *Philoxerus* and *Lithophila* nested among other species of *Gomphrena*. This clade of *Gomphrena* with the latter four satellite genera is here annotated as the *Gomphrena clade* (Fig. 3-1, Fig. 3-2 and Fig. 3-3), 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 13 species in Sánchez del-Pino et al. (2009). Our trees inferred from plastid and nrITS sequence data congruently reveal ten lineages within the *Gomphrena* clade (see Figs. 3-1, 3-3). 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*+*trnLF* sequence data shows only moderate support for the second-branching position of the *Gomphrena mollis*-*G. rupestris* clade under maximum parsimony (71% JK) and maximum likelihood (89% BS; Fig. 3-1). The signal of the *trnK*-*matK* partition alone (Fig. 3-2) for this topology is much stronger. The nrITS partition depicts the *Gomphrena mollis*-*rupestris* clade in a switched position, branching before the *Gomphrena 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 tepals, and the five tepals 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 androcial tube, the anthers attached between two small filament appendices, and five tepals 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. *G. 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 (Figs. 3-1, 3-3).

3.4.2. Evolution of vegetative morphology in *Gomphrena* and allied genera

Vegetative characters tend to be homoplastic rather than exhibiting synapomorphies for major clades (Fig. 3-5). The annual life cycle (character 1) thereby was derived multiple times from perennial ancestors, and is depicted as an independent transition in four lineages of the core C_4 *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* (Scrophulariaceae; Datson et 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 et al., 2010), whereas aereal 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, taproots of *Guilleminea* or *G. tomentosa* and relatives are tuberose as a drought adaptation strategy. Whereas taproots originated in the ancestor of the *Gomphrena* clade, this state got lost again with shifts to annual life forms (e.g. *G. radiata*). The taproots of Cerrado species like *G. macrocephala* or *G. lanigera* have been observed to store of fructanose (Fank-de-Carvalho et al., 2015), which is a further response to the environmental stress of the dry season and to fires where the soil temperature can raise to > 70°C. The adventitious roots of *Philoxerus* (character 2, state 2) evolved independently, and allow the plants to spread in the wet sand of coastal habitats. Roots of this species show tolerance to salinity (Bove, 2011) and Cordazzo and Seeliger (2003) have proven the regeneration capacity of *P. portulacoides* from fragments of the adventitious root.

Radical leaves has evolved independently three times in different lineages of the *Gomphrena* clade. We coded two different states regarding to their different morphology in plants with prostrate versus erect stems. The clade *G. tomentosa* and *Guilleminea densa*, are developed on a reduced main stem that is then curved postrate or decumbent, making up one or few layers of leaves that develop at ground level, covering a wide radial surface. On the other hand, species such as *G. lanígera*, *G. agrestis* and *G. fláccida* have erect stems which are hardly branched, but develop a radical rosette of long-lived leathery leaves, often with a dense indumentum.

Ancestral character state reconstruction shows that procumbent and decumbent stems are derived from erect ones, and evolved two times independently within the core C_4 *Gomphrena* clade (in the *Lithophila* + *Philoxerus* clade; and in the ancestor of *G. tomentosa*, *G. meyeniana* plus *Gossypianthus*) and a third time in the ancestor of *G. prostrata* and *Guilleminea* (Fig. 3-5). In the latter two clades plants grow in dry and hot environments where procumbent and decumbent stems protect them from wind, and reduce evapotranspiration. This corresponds to the evolution of radical leaves. In *Guilleminea* they are small and lost when the plants grow (Mears 1967), whereas in *Gossypianthus* they are persistent and more prominent, a similar quality also present in *G. tomentosa*, *G. radiata* and *G. meyeniana* which all belong to the same clade (Figs. 3-2, 3-3, 3-5).

Complex branched main stems are the rule in woody species (character 5, state 1) such as *Hebanthe*, *Pedersenia* or *Pfaffia fruticosa* and are ancestral in Gomphrenoideae (Fig. 3-5). 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*, *G. flaccida*, *G. mollis*, *G. agrestis*, and *G meyeniana*). Among the species of *Gomphrena*, *G. tomentosa* presents undetermined 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.

3.4.3. Evolution of inflorescence and floral morphology, especially the androeceum in *Gomphrena* and allied genera

The ancestral inflorescence in Gomphrenoideae was a head-like paracladium with densely arranged solitary flowers (character 7, state 0) appearing terminal on a more or less elongated axis, without any specialized subtending leaf organs (character 9; Fig. 3-5). 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 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 states (character 8 with 6 states). Whereas all states reach nearly equal probabilities to be ancestral at deeper nodes (Fig. 3-5), 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. 3-5). In fact, all relatives of *G. boliviana* (the *G. boliviana-martiana* clade) and of *G. haenkeana* in the two Andean subclades A and B (see Figs. 3-2, 3-3) possess the same states, so that the two species depicted in Fig. 3-5 are good representatives for their respective clades with a whorl-like arrangement of 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, some populations of which have been found to possess yellow-colored pseudanthial leaves (Fig. 3-4). Then in the *Gomphrena boliviana-martiana* clade, and a third time in *Gomphrena meyeniana* that grows with a short upright stem at high elevations in the Andes (Figs. 3-4, 3-5). 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. *Gomphrena macrocephala* 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. 3-6), 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. macrocephala* which is a typical Chaco species (Pedersen 1976). This pattern of inflorescence evolution indicates that there is a trend towards 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 et al 2014). Their arrangement results in two external, one intermediate, and two inner tepals which can vary in size and texture (Character 12). The state with the inner three tepals smaller than the outer two, which are cimbiform, compressed and carinate in fruit is resolved as synapomorphy for the core C_4 *Gomphrena* clade (Fig. 3-5). In *Guilleminea* perigynous flowers are derived as the only genus in Gomphrenoideae (character 13).

Differences in the morphology of the androceum 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*, *Pedersenia* or *Xerosiphon* (Fig. 3-6) to “apical filament lobes” present in many species of *Gomphrena* (e.g. *G. haenkeana*, Fig. 3-6). Vrijdaghs et al. (2014) investigated the ontogeny of the androeceum in Gomphrenoideae and found that the androeceum 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. This is consistent with the observation that the Amaranthaceae-Chenopodiaceae-clade generally has a single whorl of antesepalous stamens without any trace of staminodes (Ronse de Craene 2013). To the contrary, our reconstruction of ancestral states shows that the presence of androecial tube appendages (character 17, Fig. 3-6) is ancestral in Gomphrenoideae. They were lost independently in the core C_4 *Gomphrena* clade and the *Pfaffia*-clade. Moreover, filament appendages have arisen twice within the *Gomphrena* clade and a third time in the *Pfaffia*-clade (Fig. 3-6), and thus only occur in clades without appendages alternating with stamens. These results are in line with Vrijdaghs et al. (2014) who found these appendages in Amaranthaceae and Chenopodiaceae to develop from individual primordia from the rim of the androecial tube and confirm our hypothesis that androecial tube appendages and filament appendages are two different, non-homologous characters. Vrijdaghs et al. (2014) further suggested the androecial tube appendages to be part of an insect-pollination syndrome, functioning as floral nectaries. Moreover, the presence of filament appendages (character 19, Fig. 3-6), which are derived in some species of *Gomphrena* goes in line with large and showy flowers (e.g. *G. haenkeana*) as well as elongated androecial tubes, the extreme of which are the up to 30 mm long tubes in *G. macrocephala*. Floral evolution in the *Gomphrena mollis-rupestris* lineage is therefore convergent to *G. haenkeana*, *G. macrocephala* and allies. Based on scattered observations, *Gomphrena* and allies seem to be pollinated by insects. During fieldwork for this study, moths were observed visiting flowers of *Gomphrena pallida* that introduced their proboscid through the androceum tube, and butterflies were reported to pollinate the Australian *G. splendida* (Barrett and Palmer 2015). The position, length and shape of filament appendages (characters 20 to 22) is highly homplastic (Appendix 3-4). On the other hand, *Lithophila muscoides* has true staminodes, which result from the general reduction of the androceum. This species was classified as an own genus based on this feature and its specific Caribbean habitat (Swartz 1783; Bentham and Hooker 1880) but it is deeply nested within *Gomphrena*.

3.4.4. Overall phylogenetic relationships and diversification of the core C4 Gomphrena clade

The extended taxon sampling based on plastid *matK-trnK* (Fig. 3-2) and nrITS (Fig. 3-3) sequence data revealed the same principal lineages of *Gomphrena* and allies as in the analysis of combined plastid markers (Fig. 3-1) but indicates that the majority of species of the more extensive taxon set belong to a large "mostly Andean clade" that receives maximum statistical support in all analyses. In the 27-taxon set this clade is just represented by *G. haenkeana* (Fig. 3-1). The increased taxon sampling also reveals the Gomphrena boliviana-martiana clade, the high Andean Gomphrena meyeniana clade and a more extensive central to south Andean *Gomphrena radiata-tomentosa* clade also comprising G. umbellata based on evidence from *matK-trnK* (Fig.3-2) and nrITS (Fig. 3-3). Sequence data from *matK-trnK* alone show the *Gomphrena boliviana-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-tomentosa* clade and the *Gomphrena 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 *Gomphrena-macrocephala-cardenasii* clade that consists of lowland species occurring in the Chaco (*G. macrocepala*; Pedersen 1976), Cerrado (*G. agrestris*, *G. demissa*; Siqueira 1992); *Gomphrena lanigera* campo rupestres in Brazil but reaching the eastern parts of Bolivia (Siqueira 1992, Borsch et al. 2015), although ITS inconsistently depicts the latter species as sister to *G. celosioides* (the respective nodes are not well supported, Fig. 3-3). 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 and its samples appear on a long branch in the *matK-trnK* tree (Fig. 2). The other two major lineages within the core *Gomphrena* C_4

clade are the clade comprising all Australian species of *Gomphrena* plus *Philoxerus* and *Lithophila* (the *Philoxerus* + Australian clade) and *Gomphrena celosioides*, the specimens of which appear as a rather isolated clade (Figs. 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 data set (Fig. 3-1), 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 (Figs. 2, 3), both of which predominantly comprise perennial and annual species from dry valleys and prepuna habitats (from 2500 to 4000 m NN) of the central Andes, with the exception of *G. perennis*, which is a morphologically variable species extending from the Chaco and Bosque Tucumano-Boliviano to the Andean dry valleys (Borsch, Ortuño & Nee 2015; Borsch and Ortuño 2008). *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 *G. 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 Potosi (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* (Figs. 3-2, 3-3). 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 innerandean 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 mya [0.7-7.1 and 0.2-5.0 95% HPD, respectively; Fig. 3-8] and the annual lineages appear to be not much older than 1 mya.

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 taproot, flower heads few to solitary on inflorescence axes arising from a stout, almost invisibly short stem, bracteoles without crest and stames almost completely fused into a staminal tube lacking filament appendages Holzhammer (1955, 1956; see also Fig. 3-6). Our molecular phylogenetic data that depict the *G. meyeniana* clade as a highly supported lineage with a crown group diverging on a long stem (Figs. 3-2, 3-3) 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 within most individuals 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-umbellata-tomentosa* clade appears well supported in plastid and nuclear trees (see Fig. 3-2 and 3-3). In both trees it comprises two subclades, the first of which includes all the *G. tomentosa* specimens, and the second subclade includes *G. umbellata* and *G. radiata*. However, both species are only resolved as monophyletic with ITS, whereas *matK-trnK* only resolves the two samples of *G. radiata* as sisters. The main morphological difference between the species is the life form, where *G. tomentosa* is perennial (Fries 1920, Hunziker 1977), while *G. radiata* and *G. umbellata* are annual (Pedersen 1976; Remy 1846; respectively). The last mentioned species lives in sandy places at high elevations (2800 to 4400 m NN), and is largely reduced to upper cauline leaves and the apical leaves subtending paracladia (the stems are under the sand). In all these species the filament is long fused into a tube and the free part is one conspicuous linear filament appendices, without of two lateral filament appendices. Based on the absence of lateral appendices Fries (1920) proposed the *Chnoanthus* group, later elevated to a section by Holzhammer (1956). Fries (1920) hypothetized 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 on the end of this series. Currently is clear that the lateral filament appendices in *Gomphrena* are homoplastic and do not follow the "evolutionary line proposed by Fries (1920; see 3.4.3). However, the section *Chnoanthus* within Gomphrena as currently circumscribed can be maintained, because it is consolidated as a monophiletic group. Moreover, Bena et al. (2017) generated *trnLF* 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 added the sequences to a dataset of Gomphrenoideae and 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. 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 mode elevation by the late Miocene (Gregory-Wodzicki 2000; Garzione et al. 2008; Jiménez et 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* (Fabaceae) with a crown group age of about 1.5 mya (Hughes & Eastwood 2006) the Andean diversification within *Gomphrena* started somewhat earlier (crown group ages of 2.6 mya [0.7-7.1 and 0.2-5.0 95% HPD, respectively) for the Andean subclades A and B, and 2 mya for the *G. meyaniana* clade). The youngest crown group within *Gomphrena* (*G. meyeniana* and allies) exclusively grows above 3000 m (up to 4700 m; Borsch & Ortuño 2008; Borsch et al. 2015) whereas members of Andean subclades A and B are often range-restricted in dry innerandean 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 et al. 2007) in particular in the Eastern Cordillera (Bolivia and NW 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 *Gomphrena 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. The species of *Lithophila* and *Philoxerus* appear morphologically similar but differ mainly in the number of stamens with two and five, respectively (Eliasson 1988). Their filaments are united in forming a cup, and in this species the lateral filament appendices are absent as in the *G. radiata- umbellata- tomentosa* clade (see above). To the contrary, the Australian species have a highly variable filaments and lateral filament appendices (Townsend 1993). The Australian species differ from the all the Neotropical species mainly in the sizes of the stigma, appearing markedly longer (Palmer 1998). However, all the species of the *Philoxerus* + Australian clade share the main morphological characteristics of the core C_4 *Gomphrena* clade (see other parts of the discussion) so that it is proposed here to include the two genera into *Gomphrena*.

3.4.5. 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. 3-8 and Appendix 3-5). Therefore, a Gondwanan vicariance hypothesis (Upchurch 2008, N.P. Barker et 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. 3-9 an overview on the global distribution of the core C4 *Gomphrena* clade (pale yellow signature) as well as *Blutaparon* (dot map for each of the three currently accepted species) is presented. *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 (Figs. 3-2, 3.3). The possible first branch of the *Philoxerus*+Australian *Gomphrena* clade is *Lithophila* (Figs. 3-2, 3-3), which is endemic to all Carribean 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 et al. (2007) inferred this as a frequent pattern, apparently facilitated by westwards 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 and 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 also, 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 et 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 such as the warm South Ecuatorial Current, which then leads over into the East Australian current and which were present since about 6 Ma. 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.

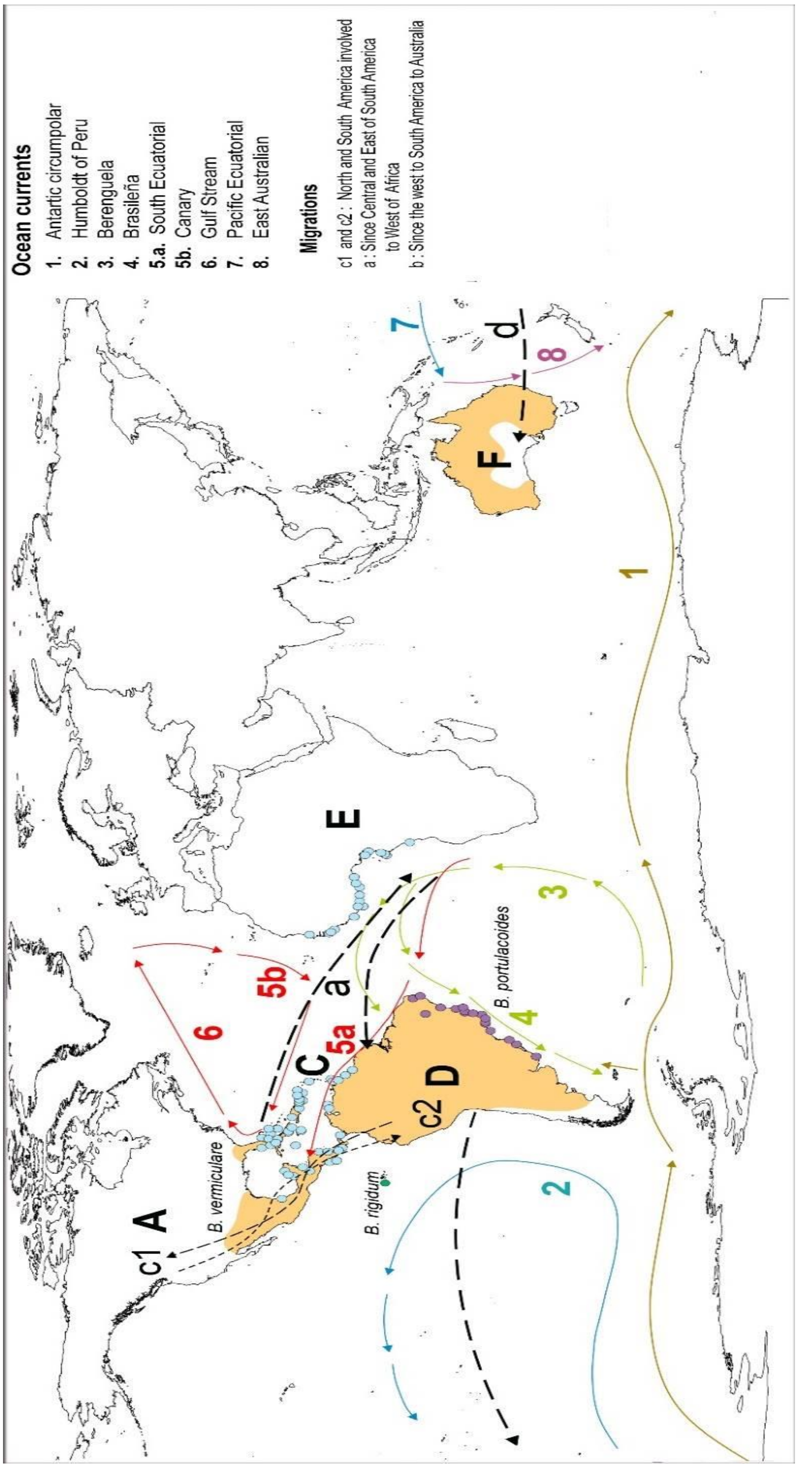


Fig.3-9. Map of distribution of *Blutaparon* and the native range of *Gomphrena* sensu stricto in the Americas and Australia. The names of the current and the was taken of the https://www.britannica.com/acience/ocean-current and Dijkstra, H. 2008. For the world map the shp was taken of the http://download.geofabrik.de/.

3.4.6. C₄ 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 *Blutaparon*, *Froelichia*, *Guilleminea*, *Lithophila*, and *Tidestromia* (Sage et al. 2007). Our results show that the C_4 species of *Gomphrena* (Figs. 3-2, 3-3, 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. 3-7). 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. The only exception are the two C_3 species *Gomphrena mollis* and *G. rupestris* that belong to the core *Gomphrena* clade in which they share the morphology of pollen with reduced tecta (Appendix 3-2, Table 3-2 and Chapter 2).

Ancestral character state reconstruction using the chloroplast trees (Fig. 3-7) indicates that C_4 photosynthesis arose in the common ancestor of the core *Gomphrena* clade but reversed back to C_3 in the lineage of *G. mollis* and *G. rupestris*. Unlike the species of the core C_4 *Gomphrena* clade, *G. prostrata* and *Guilleminea densa* species parenchyma has a complete radial sheath (Estelita-Teixeira and Handro 1984, Fank-de-Carvalho et al. 2015, Filippa & Espinar 1993). This structural differentiation in the radial parenchyma indicates that there could be a gradual process in acquiring this character. Ancestors *G. mollis* and *G. rupestris* lack radial parenchyma sheath so it is clear that these suffered a reversal. The same is inferred for *Xerosiphon*. However, the sampling in the 27-taxon tree represents the Alternantheroid clade only by *Pedersenia*, which is C_3, although C_4 photosynthesis also occurs within the two other genera of this clade, namely in *Alternanthera* and *Tidestromia*. Since the phylogenetic position of *G. mollis* and *G. rupestris* is inferred incongruently from the nuclear ITS sequence data to branch directly after *Froelichia*, we repeated the ancestral character state reconstruction for this scenario. Sage et al. (2007) mapped the taxonomic distribution of C_4 photosynthesis using a *matK-trnK* tree of the Amaranthaceae under parsimony and depicted three C_4 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 plesiomorpic condition in the monophyletic genus *Alternanthera* was later confirmed to be C_3 in a much more detailed study by Sanchez del-Pino et al. (2012) whereas C_4 was considered to be derived within their clade B3. As a result of our improved taxon sampling and a more detailed approach to reconstruct ancestral character states in this investigation, our picture of C_4 evolution in the Gomphrenoideae changed to a scenario involving three independent origins, the largest of which is the here newly described core *Gomphrena* clade, and two reversals back to C_3 (*Gomphrena mollis-rupestris* and *Xerosiphon*). Amaranthaceae s.str. like the chenopod lineages (Kadereit et al. 2012) therefore exhibits multiple gains and losses of C_4. It is noteworthy that one of the lineages for which we estimate a reversal to C_3 is hypothesized to have evolved in a reticulate pattern.

Recently, Bena et al. (2017) studied macroclimatic niche limits and C_4 evolution in Gomphrenoideae. The authors compiled available plastid sequences from GenBank (mostly from Müller & Borsch 2005, Borsch et al. 2012, Sage et al. 2007, Sánchez del-Pino et al. 2009 and

2012) and added new *trnLF* sequences from ten species. However, they did not obtain any significant statistical support on nodes within in the Gomphrenoids (sensu Sánchez del-Pino et al. 2009) which may be explained by the patchiness of their matrices, and also, they did not sample relevant taxa like *G. mollis* or *G. rupstris*, thus limiting conclusions on the origin of C4 in Gomphrenoideae. Nevertheless, the general conclusion of Bena et al. (2017) that C4 Gomphrenoideae, unlike C_4 grasses, shifted 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* C_4 clade plus *Froelichia* is inferred as 18 Ma (10.2-28.4 95% HPD; the stem diverged from C_3 *Xerosiphon* at 20.6 Ma [11.8-32.9 95% HPD]), and thus is slightly younger than the earliest inferred gain of C_4 in the crown group of Salsoloideae/Camphorosmoideae (Kadereit et al. 2012). The stem of the C_4 clade within *Alternanthera* originated at 18.5 Ma (7.8-33.7 95% HPD) and the C_4 genus *Tidestromia* diverged at 27.7 Ma (19.3-38.9 95% HPD). *Tidestromia* is very different morphologically to the other extant genera and C_4 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 C_4 originiated in *Gomphrena* and other Gomphrenoideae in roughly the same time interval than in Chenopodiaceae s.str. subsequently to the drop of CO_2 concentrations at Eocene-Oligocene boundary (Christin et al. 2011, Kadereit et 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 NN) and *Gomphrena meyeniana* (2600-4000 m NN) and allies probably constitute the highest populations of any C_4 plant, thereby being competitive in subarid as well as humid puna vegetation.

3.4.7. Towards 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 and Green (1929). *Gomphrena globosa* is included in the molecular trees of Sanchez del-Pino et al. (2009) in a position that corresponds to the mostly Andean clade (Figs. 2, 3) and thus belongs to the core C_4 *Gomphrena* clade.

Martius (1826) then treated 57 species of *Gomphrena* with detailed descriptions and also described the genera *Pfaffia*, *Hebanthe* and *Serturnera* (Martius, 1826). 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 (1836) 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 (1894), Holzhammer (1955; 1956) and Townsend (1993), and confirmed by more recent investigations using molecular and morphological characters (Borsch and Pedersen, 1997; Müller and Borsch, 2005; Sanchez del-Pino et 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 Sanchez-del Pino et 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 Figs. 1-3).

Genus 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 C_4 *Gomphrena* clade. As currently classified (Eliasson 1988, Townsend 1993, Hernández-Ledesma et al. 2015) they represent cases of segregate genera that show morphological adaptions to specific habitats. Morphological synapomorphies of the core C_4 *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 *Guillemina* is different. The species of *Guilleminea* could represent a convergent origin of a procumbent habit in relation to *Gossypianthus* and the *Gomphrena radiata-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 progess 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 et al. 2015). 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* wheras 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 et 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 androeceum 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).

3.5 Taxonomic treatment

Gomphrena L., Sp. Pl. 1: 224. (1753). Lectotype: *Gomphrena globosa* L., designated by Standley, N. Amer. Fl. 21: 147 (1917).

= *Lithophila* Sw., Prodr. 14 (1788). syn. nov. Type: *Lithophila muscoides* Sw.

= *Blutaparon* Raf., New Flora 4: 45. (1838 [dated 1836]). syn. nov. Type: *Blutaparon repens* Raf., nom. illegit. (based on *Gomphrena vermicularis* L.), lectotype designated by Mears, J. A. 1982. Taxon 31(1): 113 (1982).

= *Gossypianthus* Hook. Icon. Pl. 3: pl. 251. (1840). syn. nov. Type: *Gossypianthus rigidiflorus* Hook.

Gomphrena muscoides (Sw.) [to be published as a new combination]

Basionym: *Lithophila muscoides* Sw., Prodr. [O. P. Swartz]: 14. 1783-1787

Type: Ind. Occ. Navaza island, Swartz, O.P. s/n (HT: S S-R-3294, IT: LD 1756579, BM 000993153).

≡ *Iresine muscoides* (Sw.) Kuntze, Nov. Gen. Sp. Pl. 2: 542. 1891

≡ *Alternanthera muscoides* (Sw.) Benth. & Hook. f.

= *Alternanthera caribaea* Moq., A.DC., Prodr. ser. 13, (2): 354. 1849.

Type: Guadeloupe,W.I; Beaupertuis s.n.; 1839 (HT: P P00622601)

= *Achyranthes linearifolia* Sw. ex Wikstr., Symb. Antill. 5(2): 338. 1907.

Type: Saint Barthelemy, Forsström, J.E. s.n. (HT: S S-R-34)

= *Lithophila muscoides* Sw. subsp. *macrantha* Urb. var. *platyphylla* Urb. Symb. Antill. 5: 339. 1907.

Gomphrena radicata (Hook.f.) [to be published as a new combination]

Basionym: *Alternanthera radicata* Hook.f., Trans. Linn. Soc. London 20: 261-262. 1847. Type: Ecuador, Galapagos, Chatham Island, C. Darwin s.n. (HT: K K000583052, IT: CGE)

≡ *Lithophila radicata* (Hook.f.) Standl., J. Wash., Acad. Sci. 5: 396. 1915

= *Alternanthera acaulis* Anders., Galapagos Veg. 164. 1854.

Type: Ecuador, Galapagos, Chatham Island, Anderson, N.J. s.n. (HT: S-R-219)

= *Alternanthera scirpoides* Hook.f., Gen.Pl. [Bentham & Hooker f.] 3(1): 39, in bs. 1880

Lectotype: Ecuador, Galapagos, Chatham Island, Captain Wood s.n. (LT: K000583050, designated by Turner in Ann. Bot. Fenn. 53: 288. 2016).

≡ *Lithophila scirpoides* (Hook. f.) Schinz, Nat. Pflanzenfam. 2 (16c): 84. 1934

Gomphrena subscaposa (Hook. f) [to be published as a new combination]

Basionym: *Alternanthera subscaposa* Hook.f., Trans. Linn. Soc. London 20: 189. 1847.

Lectotype: Darwin s.n. Galapagos Islands, Charles Island, 1835 (HT: K 00583053. IT M: 0241869)

≡*Iresine subscaposa* (Hook.f.) Kuntze, Nov.Gen.Sp. Pl. 2: 542. 1891

≡ *Lithophila subscaposa* (Hook. f.) Standl., J. Wash. Acad. Sci. 5: 396. 1915

Gomphrena brittonii (Standl.) [to be published as a new combination]

Basionym: *Gossypianthus brittonii* Standl., Contr. U.S. Natl. Herb. 18: 92. 1916

Type: Cuba, Santa Clara, rocky hill in a palm plantation, 4.1912, Britton & Cowell 13318 (HT: NY00073684).

≡ *Guilleminea brittonii* (Standl.) Mears, Sida 3(3): 150. 1967

= *Gossypianthus heterophyllus* Ekman & Suess., Repert. Spec. Nov. Regni Veg. 35: 317. 1934

Type: Cuba, Matanza, Ponce, sterile Örtlichkeiten, Ekman, E.L. 17079 (HT: S S-R-2462).

= *Gossypianthus jackianus* Ekman & Suess., Repert. Spec. Nov. Regni Veg. 35: 317. 1934

Type: Cuba, Matanzas, Canasi, locis siccissimis, 5.1923, Ekman, E.L. 16507 (HT: B 10 0242403).

Gomphrena rigidiflora (Poir.) [to be published as a new combination]

Basionym: *Paronychia lanuginosa* Poir., Lam., Encycl., Suppl. 4: 303. 1816, non *Gomphrena lanuginosa* Span. (1841)

Type: Dominican Republic, Poiteau P.A. s/n (HT: P P00610545).

Gossypianthus lanuginosus Moq., A. DC., 13 (2): 337. 1849,

≡ *Guilleminea lanuginosa*(Poir.) Hook, Benth. & Hook., Gen. Pl. 3: 37. 1880

= *Gossypianthus lanuginosus* var. *sheldonii* Uline & Bray, Bot. Gaz. 20:342-1895.

Lectotype: United States. Oklahoma, (Indian Territory) near Cash (Cache) Creek, Jul 1891, CS. Sheldon n° 170 (LT: US US00102749, GH)

≡ *Gossypianthus sheldonii* (Uline & W.L.Bray) Small, Fl. S.E.U.S.: 394. 1903

≡ *Guilleminea lanuginosa* var. *sheldonii* (Uline & Bray) Mears, Sida 3:149, 1967

= *Gossypianthus rigidiflorus* Hook, Icon. Pl. 3: t. 251. 1840

Type: United States, Texas, Drummond 262 (HT: K!, IT: GH GH00037091)

≡*Guilleminea lanuginosa* var. *rigidiflora* (Hook.) Mears, Sida 3: 149. 1967

Gomphrena* *lanosa* (Moq.) var. *tenuiflorus (Hook.) [to be published as a new combination]

Type: United States of America, Texas, Drummond 262 (HT: K 000848066).)

≡*Gossypianthus tenuiflorus* Hook, Icon. Pl. 3: 251. 1840

≡*Gossypianthus lanuginosus* var. *tenuiflorus* (Hook.) Henrickson in 12: 321. 1987

≡*Guilleminea lanuginose* var. *tenuiflora* (Hook.) Mears, Sida 3(3): 147. 1967.

Gomphrena portulacoides (A. St.-Hil.) [to be published as a new combination]

Type: Brazil Southeast, Province de Rio de Janeiro. Bord de la mer; 1816-1821, A. St.-Hil. A2-304-N82 (HT: P P00622606).

≡*Philoxerus portulacoides* A. St.-Hil., A.St.-Hil. Voy. Distr. Diam. 2: 436 (-437). 1833

≡*Iresine portulacoides* (A. St.-Hil) Moq., in DC, Prodr. 13(2): 341. 1849

≡*Blutaparon portulacoides* (A. St.-Hil.) Mears, Taxon ser. 31, (1): 115. 1982

Gomphrena rigida (B.L. Rob. & Greenm.) [to be published as a new combination]

Type: Ecuador, Republic of, Islands Galapagos orchilla Bay, James Bay Island, 1891, Baur's G. 387. (HT: GH GH00036970).

≡*Alternanthera rigida* B.L. Rob. & Greenm., Amer. J. Sci. Arts 3: 143. 1895

≡*Achyranthes rigida* (B.L. Rob. & Greenm.) Standl., J. Wash. Acad. Sci. 5: 74. 1915

≡*Lithophila rigida* (B.L. Rob. & Greenm.) Standl., J. Wash. Acad. Sci. 5: 396. 1915

≡*Philoxerus rigidus* (B.L. Rob. & Greenm.) Howell, J. Wash. Acad. Sci. 5: 396. 1915

≡*Blutaparon rigidum* (B.L.Rob. & Greenm.) Mears, Taxon ser. 31, (1). 1982

Gomphrena vermiculare L.

Lectotype: “AMARANTHOIDES Corassavicum humile Cepeae folio” in Hermann, Parad. Bat.: unnum. t. [7], 2 unnum. figs. ad p. 15 at bottom. 1698. Designated by Iamonico & Sánchez–del Pino; Taxon 63(2) April 2014: 403-404.

≡*Blutaparon vermiculare* (L.) Mears

≡*Gomphrena vermiculare* L. in Sp. Pl. 1: 224. 1753

≡*Illebrum vermicularis* (L.) L.,Sp. Pl., ed. 2: 300. 1762

≡*Achyranthes vermicularis* A. Eaton, Man. Bot. N. Amer., ed. 5, 91: 2. 1829

≡*Blutaparon breviflorum* Rafinesque, New Fl. (Rafinesque) iv: 45. 1836

≡*Blutaparon repens* Rafinesque, New Fl. (Rafinesque) iv: 46. 1836

≡*Caraxeron vermicularis* Rafinesque, Fl. Tell.: 38. 1837

≡*Iresine vermicularis* (L.) Moq. in A. DC., 13 (2): 340. 1849

≡*Cruzeta vermicularis* (L.) M. Gómez in Anales Inst. Segunda Ens.Habana 2: 213. 1896

≡*Lithophila vermicularis* (L.) Uline ex Millsp., Publ. Field Columb. Mus., Bot. ser. 2: 39. 1900

≡*Philoxerus vermicularis* (L.) J.E. Sm. Sp. Pl. 1: 224. 1753.

Appendix 3-1. Specimens used in phylogenetic analysis and reconstruction of ancestral character states including voucher information and EMBL/GenBank Accession numbers for sequences. The columns to the right refer to the inclusion of a specimen in the respective analysis. The "Combined Tree" is based on combined *trnLF+rpl16+matK-trnK* sequence data. For *matK-trnK* it includes the same sequences as in the large *matK-trnK* tree (column next to the right). All sequences newly generated in this study are marked by "X". Those sequences that were published in previous papers (not belonging to this thesis) and which were downloaded from EMBL/GenBank are presented with their accession number.

Code	**Species names**	**Field/garden origin**	**Voucher**	**Combined Tree**	***matk -trnK***	**nrITS**	**List of evolution and otime**	**GenBank number**
AC007	*Gomphrena macrocephala* A. St.-Hil.	Paraguay	Zardini 45564 (B)	X		X	X	AY514802 (*)
	Gomphrena macrocephala A. St.-Hil	Paraguay	Hil.-Schinini&Dematteis 33318(NY)	X				EF688760 (**)
AC016	*Froelichia floridana* (Nutt.) Moq.		BG Bonn 03615-90, Th. Thiel s.n.	X	X	X	X	AY514799 (*)
	Froelichia floridana (Nutt.) Moq.	USA	Fryxell 1847	X				EF688751 (**)
AC019	*Gomphrena* mandonii R.E.Fr..	Bolivia	S.G.Beck 18720 (B, LPB)	X	___	_____		AY514801
	Gomphrena elegans Mart.	Bolivia	M. Nee 34257 (NY)	X				EF688755 (**)
	Gomphrena elegans Mart.	Bolivia	M. Nee 34257	X				EF688684 (***)
	Guilleminia densa (Willd.) Moq.		Mc Cauley. R.A. & Ballard, H.E.					AY173411 (****)
AC051	*Guilleminia densa* (Willd.) Moq.	Sud Africa (RSA), Gauteng	Th. Borsch, K. Müller & D. Pratt 3437 (BONN, ISC)	X		X	X	AY514803 (*)
	Guilleminia densa (Willd.) Moq.	México	Flores Olvera et al. HF 02-24, ventura 2889 (MEXU)	X				EF688764 (**)
	Guilleminia densa (Willd.) Moq.	México	Flores Olvera et al. HF 02-24, ventura 2889 (MEXU)	X				EF688693 (***)
AC0008	*Hebanthe occidentalis* (R.E. Fr.) Borsch & Pedersen	Paraguay	Zardini 45377 (B, MO)	X		X	X	AY514800 (*)
	Hebanthe occidentalis (R.E. Fr.) Borsch & Pedersen	Bolivia	Nee & Saldias 47054	X				EF688767 (**)
	Hebanthe occidentalis (R.E. Fr.) Borsch & Pedersen	Bolivia	Nee & Saldias 47054	X				**EF688697 (***)**
AC053	*Blutaparon vermiculare* (L.) Mears	USA/ Texas	Th. Borsch, K. Müller & D. Pratt 3444 (B, ISC)	X	X	X	X	AY514798 (*)

	Blutaparon vermiculare (L.) Mears		Liogier 34352 (NY)	X				EF688748 (**)
	Blutaparon vermiculare (L.) Mears		Liogier 34352 (NY)	X				EF688676 (***)
AC092	*Gomphrena flaccida* R.Br.	Australia	SJ 8830		X	X	X	
AC095	*Gomphrena flaccida* R.Br.	Australia	SJ 8776	X	X	X	X	
	Gomphrena fláccida R.Br.	Australia	Fryxell et al. 4748	X				EF688756 (**)
	Gomphrena fláccida R.Br.	Australia	Fryxell et al. 4748	X				EF688685 (***)
AC099	*Gomphrena mandonii* R.E.Fr.	Bolivia	St Beck 18170 (LPB, B)	X	X	X	X	AY514801 (*)
AC101	*Xerosiphon aphyllus* (Pohl ex Moq.) Pedersen	Brazil	Splett, S. 701 (B)	X	X	X		
	Xerosiphon aphyllus (Pohl ex Moq.) Pedersen	Brazil	Fonseca et al. 1303	X				EF676100 (**)
	Xerosiphon aphyllus (Pohl ex Moq.) Pedersen	Brazil	Fonseca et al 1303	X				EF688729 (***)
AC105	*Pfaffia fruticulosa Suess.*	Bolivia	Borsch, Th., 3522 (LPB, B)	X	____	___	X	
AC138	*Gomphrena fuscipellita* T. Ortuño & T. Borsch	Bolivia	Th. Borsch & T. Ortuño, 3594 (LPB, B)		X	X		AM887525 (*)
AC140	*Gomphrena boliviana* Moq.	Bolivia, Cochabamba, Tapacari	Th. Borsch & T. Ortuño, 3577 (LPB, B)	X	X	X	X	
	Gomphrena boliviana Moq.	Bolivia	Fortunato & Adelqui 5526	X				EF688683 (***)
	Gomphrena boliviana Moq	Bolivia	Fortunato & Adelqui 5526	X				EF688754 (**)
AC141	*Gomphrena haenkeana* Mart.	Bolivia, Cochabamba, Tapacari	Th. Borsch & T. Ortuño, 3572 (LPB, B)	X		X		
	Gomphrena haenkeana Mart.	Bolivia	Nee et al. 52178 (NY)	X				EF688759 (**)
	Gomphrena haenkeana Mart.	Bolivia	Nee et al. 52178 (NY)	X				EF688688 (***)
AC142	*Gomphrena perennis* L.	Bolivia, Cochabamba, Mizque	Th. Borsch & T. Ortuño, 3590 (LPB, B)		X		X	
AC143	*Gomphrena ferruginea* var. *rustica* Pedersen	Bolivia, Tarija	Th. Borsch & T. Ortuño, 3650 (LPB, B)		X	X		AM887524 (*)
AC154	*Pedersenia volubilis* Borsch, T. Ortuño & M. Nee	Bolivia Santa Cruz	Th. Borsch & J. Coimbra 3537 (LPB, B)	X	X	X		
AC167	*Gomphrena tomentosa* (Griseb.) R.E. Fries	Bolivia /Tarija	Th. Borsch & T. Ortuño, 3649 (LPB, B)		X	X	X	
AC168	*Gomphrena* (Spec. 1 a)	Bolivia/Tarija	Th. Borsch & T. Ortuño, 3648 (LPB, B)		X	X		
AC171	*Gomphrena umbellata* J.Rémy	Bolivia/Potosi	J. Wood 10741 (LPB, K)		X		X	
AC183	*Gomphrena bicolor* Mart.	Bolivia/Cochabamba	Th. Borsch & T. Ortuño, 3558 (LPB, B)			X		
AC184	*Gomphrena meyeniana var. flaccida*	Bolivia, Cochabamba, Tapacari	Th. Borsch & T. Ortuño, 3561 (LPB, B)			X	X	
AC249	*Gomphrena potosiana* Suess. & Benl.	Bolivia, Potosi, T. Frias	Th. Borsch & T. Ortuño, 3716 (B, LPB)		X	X		
AC250	*Gomphrena oligocephala* J.Rémy	Bolivia, Chuquisaca, Yamparaez, Candelaria	Th. Borsch & T. Ortuño, 3760 (B, LPB)		X	X		
AC251	*Gomphrena potosiana* Suess. & Benl.	Bolivia/Potosi	Th. Borsch & T. Ortuño, 3672 (LPB, B)		X	X	X	
AC0252	Gomphrena (Spec. 4)	Bolivia	Th. Borsch & T. Ortuño, 3766 (B, LPB)		X	X		

AC365	*Hebanthe grandiflora* (Hook.) Borsch & Pedersen	Mexico	Th. Borsch, 3882 (B)		X	X	X	FR870370.1 (*)
AC432	*Gomphrena pallida* (Suess.) Pedersen	Bolivia, Potosí, Nor Chichas	Th. Borsch, T. Ortuño & R. P. Lopéz 3719 (B, LPB)		X	X		
AC433	*Gomphrena tomentosa* (Griseb.) R.E. Fries	Bolivia, Potosí, Nor Chichas	Th. Borsch, T. Ortuño & R. P. Lopéz 3722 (LPB, B)		X	X	X	
AC435	*Gomphrena pallida* (Suess.) Pedersen	Bolivia, Potosí, Nor Chichas	Th. Borsch, T. Ortuño & R. P. Lopéz 3724 (LPB, B)		X	X	X	
AC436	*Gomphrena meyeniana* Walp.	Argentina/JuJuy, Yavi	Th. Borsch, T. Ortuño & R. P. Lopéz 3726 (B, LPB)		X			
AC437	*Gomphrena umbellata* J. Rémy	Argentina /Jujuy	Th. Borsch, T. Ortuño & R. P. Lopéz 3727 (B, LPB)		X	X	X	
AC438	*Gomphrena* Spec. 8a	Argentina /Jujuy	Th. Borsch, T. Ortuño & R. P. Lopéz 3731 (LPB)		X	X	X	
AC439	*Gomphrena* Spec. 8b	Argentina , Jujuy	Th. Borsch, T. Ortuño & R. P. Lopéz 3733 (B, LPB)		X	X	X	
AC441	*Gomphrena phaeotrichia* Pedersen	Argentina, Salta	Th. Borsch, T. Ortuño & R. P. Lopéz 3738 (B, LPB)		X	X		
AC443	*Gomphrena radiata* Pedersen	Argentina, Salta	Th. Borsch, T. Ortuño & R. P. Lopéz 3740 (LPB, B)		X	X	X	
AC444	*Gomphrena ferruginea* Pedersen	Argentina, Salta	Th. Borsch, T. Ortuño & R. P. Lopéz 3743 (LPB, B)		X	X		
AC445	*Gomphrena radiata* Pedersen	Argentina, Salta	Th. Borsch, T. Ortuño & R. P. Lopéz 3749 (LPB, B)	X	X	X	X	
AC446	*Gomphrena ferruginea* Pedersen var. Ferruginea	Argentina	Th. Borsch, T. Ortuño & R. P. Lopéz 3751(LPB, B)		X	X	X	
AC447	*Gomphrena* Spec. 9	Argentina, San Isidro, isolated population	Th. Borsch, T. Ortuño & R. P. Lopéz 3753 (LPB, B)		X	X		
AC449	*Gomphrena pallida* (Suess.) Pedersen	Bolivia, Potosi, Saavedra	Th. Borsch, T. Ortuño & R. P. Lopéz 3755 (LPB, B)		X	X		
AC453	*Gomphrena bicolor* Mart.	Bolivia, Cochabamba, Arani	Th. Borsch & T. Ortuño, 3580 (LPB, B)		X	X	X	
AC454	*Gomphrena bicolor* Mart.	Bolivia, Cochabamba, Arani	Th. Borsch & T. Ortuño, 3581(LPB, B)		X	X		
AC455	*Gomphrena mizqueensis* T. Ortuño & T. Borsch	Bolivia/Cochabamba,	Th. Borsch & T. Ortuño, 3584 (LPB, B)		X	X		
AC460	*Gomphrena cardenasii* Standl. ex E. Holzh.	Bolivia, Santa Cruz, Chiquitos	J. Wood 18813 (B, K, LPB)		X	X		
AC461	*Gomphrena agrestis* Mart.	Brazil , MG de 7 km Itacambira	B. Stannard, J. D. P. Oliveira, M. L. Kawasaki, R. M. Harley 36152 (LPB, B)	X	X	X	X	
AC462	*Gomphrena mollis* Mart.	Brazil , Bahia, Paramirin	R. M. Harley 27179	X	X	X	X	
AC463	*Gomphrena mollis* Mart.	Brazil, Bahia, Paramirin	R. M. Harley 27021		X	X		
AC464	*Gomphrena rupestris* Nees	Brazil , Bahia, rio cotas	R. M. Harley 26990 (MO)	X	X	X	X	
AC465	Gomphrena *prostrata* Mart.	Brazil , Bahia, Agua Quente, Pico das almas	R. M. Harley 26995 (MO)	X	X	X	X	
AC485	*Gomphrena perennis* L.	Bolivia/Cochabamba,	Th. Borsch & T. Ortuño, 3618 (LPB, B)		X			
AC487	*Gomphrena haenkeana* Mart	Bolivia, Santa Cruz, Caballero	Th. Borsch & T. Ortuño, 3627 (LPB, B)		X	X		

AC489	*Gomphrena* (Spec 1b)	Bolivia/Tarija	Th. Borsch & T. Ortuño, 3647 (LPB, B)		X	X		
AC491	*Gomphrena* (Spec. 5)	Bolivia/Tarija	Th. Borsch & T. Ortuño, 3657(LPB, B)		X	X	X	
AC492	*Gomphrena meyeniana Walp.*	Bolivia, Tarija, Mendez	Th. Borsch & T. Ortuño, 3663 (LPB, B)		X	X	X	
AC494	*Gomphrena perennis* L.	Bolivia, Santa Cruz, Andrez Ibañez	Th. Borsch, Ibisch 3529 (LPB, B)		X	X		
AC495	*Gomphrena martiana* Mart.	Bollivia, Santa Cruz, Andrez Ibañez	Th. Borsch, J. Coimbra 3535 (LPB, B)		X	X	X	
AC496	*Gomphrena nitida* Roth.	México, Oaxaca	Th. Borsch et al. 3773 (MEXU, B)		X	X	X	
AC674	*Blutaparon vermiculare* Gillies ex Moq.	Cuba	W. Greuter et al 26916 (B, HAJB)	X		X	X	
AC677	*Lithophila muscoides* SW.	Cuba	W. Greuter et al 26915 (B, HAJB)	X	X	X	X	
	Lithophila muscoides SW.	West Indies-Islas Turks and Caicos	Correll 43425 (NY)	X				EF688780 (**)
	Lithophila muscoides SW	West Indies-Islas Turks and Caicos	Correll 43425 (NY)					EF688710 (***)
AC783	*Gomphrena meyeniana* Walp. *var. Meyeniana*	Bolivia, La Paz a Cochabamba, Japo	Th. Borsch & T. Ortuño 3952 (LPB, B)	X	X	X	X	
AC784	*Gomphrena meyeniana* Walp. *var. Meyeniana*	Bolivia, La Paz a Cochabamba, Japo	Th. Borsch & T. Ortuño 3953 (LPB, B)	X	X	X		
AC785	*Gomphrena meyeniana* Walp. *var. Meyeniana*	Bolivia, La Paz a Cochabamba, Japo	Th. Borsch & T. Ortuño 3954 (LPB, B)		X	X		
AC786	*Gomphrena meyeniana var. flaccida Pedersen*	Bolivia, La Paz a Cochabamba, Japo	Th. Borsch & T. Ortuño 3955 (LPB, B)		X	X		
AC0787	*Gomphrena perennis* L.	Bolicia (Sucre- Morochata)	T. Ortuño, R.P.Lopez & R. Rios 1211 (B, LPB)		X	X	X	
AC0788	*Gomphrena pallida* (Suess.) Pedersen	Bolivia, Sucre, Sorona)	T. Ortuño, R.P.Lopez & R. Rios 1217 (B, LPB)		X	X		
AC0789	*Gomphrena trollii Suess.*	Bolivia, Potosi, Nor Chichas	T. Ortuño, R.P.Lopez & R. Rios 1255 (B, LPB)		X	X	X	
AC0790	*Gomphrena perennis* L.	Bolivia, Chuquisaca, Camargo	T. Ortuño, R.P.Lopez & R. Rios 1236 (B, LPB)		X			
AC0793	*Gomphrena tomentosa (Griseb.) R.E. Fries*	Bolivia (Sucre- Camargo)	T. Ortuño, R.P.Lopez & R. Rios 1235 (B, LPB)			X	X	
AC0893	*Gomphrena demissa* Mart.	Brazil , Bahia, Río de Contas.	Harley, R.M. 26991 (SPF,CEPEC, B)		X			
AC0913	*Gomphrena martiana Mart.*	Bolivia (Chuquisaca-Sud Cinti)	S. Fuentes 120 (B, LPB)		X	X	X	
AC0931	*Guilleminia densa* (Willd.) Moq.	Süd-Afrika (RSA), Gauteng	K. Müller 881 (B, PRE)	X	X	X		
AC0932	*Gomphrena celosioides* Mart.	Süd-Afrika (RSA), Gauteng	K. Müller 882 (B, PRE)	X	X	X		
AC0988	*Gomphrena canescens* R.Br. subsp. erythrina J. Palmer	Australia, Fortescue Botanical District	P.S. Short 4273 (MEL, AD,BRI,CANB,NSW,PERTH)		X	X	X	
AC0993	*Gomphrena flaccida* R.BR	Australia, Norlangie	M. Lazarides 8882 (NSW)		X			
AC0996	*Gomphrena kanisii* J. Palmer	Australia, South of Newman	G. Errington 468, et al. (NSW)		X			
AC0998	*Gomphrena brachystylis Subsp. brachystylis*	Australia, Timber Creek	Evans M, 3118 (NSW, DNA, BRI,CANB,K)		X	X	X	
AC1007	*Gomphrena* (Spec7)	Bolivia, Potosi, Sud Chichas, Tupiza	Ortuño, T. 1677 (LPB, B)		X	X	X	
AC1013	*Gomphrenna* (Spec 6)	Bolivia, Potosi, Torotoro	Huaylla, H 3647 (LPB, B)		X			
AC1023	*Pfaffia gnaphalioides* Mart.		Wood, J. 22738 (LPB, B)		X	X		
	Pfaffia tuberosa (Moq. Ex DC) Hicken		Pedersen 1010 (NY)					EF688785 (**)
	Pfaffia jubata Mart.	Brazil	Uhlmann 88 (NY)	X				EF688716 (***)

AC1024	*Blutaparon portulacoides* (A. St.-Hil.) Mears	Uruguay	Beck, StG. 33571 (LPB, B)		X	X	X
AC1025	*Gomphrena umbellata* J. Rémy	Bolivia, Oruro, Jirira	Acho, J. 2 (LPB, B)			X	
AC1027	*Gomphrena cardenasii* Standl. ex E. Holzh.	Bolivia, Santa Cruz, Chiquitos	Wood, J. 20678 (LPB, B)		X	X	
AC1028	*Gomphrena* (Spec3)	Bolivia, Chuquisaca, Cerro Chataquila	Wood, J. 22568 (LPB, B, K)		X	X	
AC1029	*Gomphrena lanigera* Pohl	Bolivia, Santa Cruz, Velasco, Meseta de Caparuth	Wood, J. 19964 (LPB, B, K)	X	X	X	
AC1050	Gomphrena (Spec 2 a)	Bolivia, Potosi, Charcas, Toro Toro	J. Wood 22662 (B, K, LPB)		X	X	
AC1051	*Gomphrena haenkeana* Mart.	Bolivia, Cochabamba, Tapacari	T. Borsch, T. Ortuño & S. Fuentes 3963 (LPB, B)		X	X	X
AC1052	*Gomphrena tomentosa* (Griseb.) R.E. Fries	Bolivia, Potosi, Sud Chichas, Tupiza	Beck, StG. 33662, (LPB, B)	X	X	X	
AC1053	*Gomphrena bicolor* Mart.	Bolivia	T. Borsch, T. Ortuño & S. Fuentes 3961 (LPB, B)		X	X	X
AC1095	*Gomphrena celosioides* Mart.	Ethiopia	M. Wondafrash 2215 (ETH, B)		X		
AC1182	*Gomphrena celosoides* Mart.	Kenya	V. Di Vincenzo, P. Kamau, M. Wondafrash, M. Mbale 317 (EA, B, ETH)	X		X	
AC1199	*Gossypianthus brittonii* Standl.	Cuba, Villa Clara, 9-9-2012	I. Castaneda N-UCLV 10185 (UCLV)	X	X	X	X
AC1214	*Guilleminia densa* (Willd.) Moq.	Ethiopia	V. Di Vincenzo, A. Hailu 180 (B, ETH)	X	X	X	X
AC1169	*Guilleminia densa* (Willd.) Moq.	Kenya	V. Di Vincenzo, P. Kamau, M. Wondafrash, M. Mbale 284 (EA, B, ETH)	X			

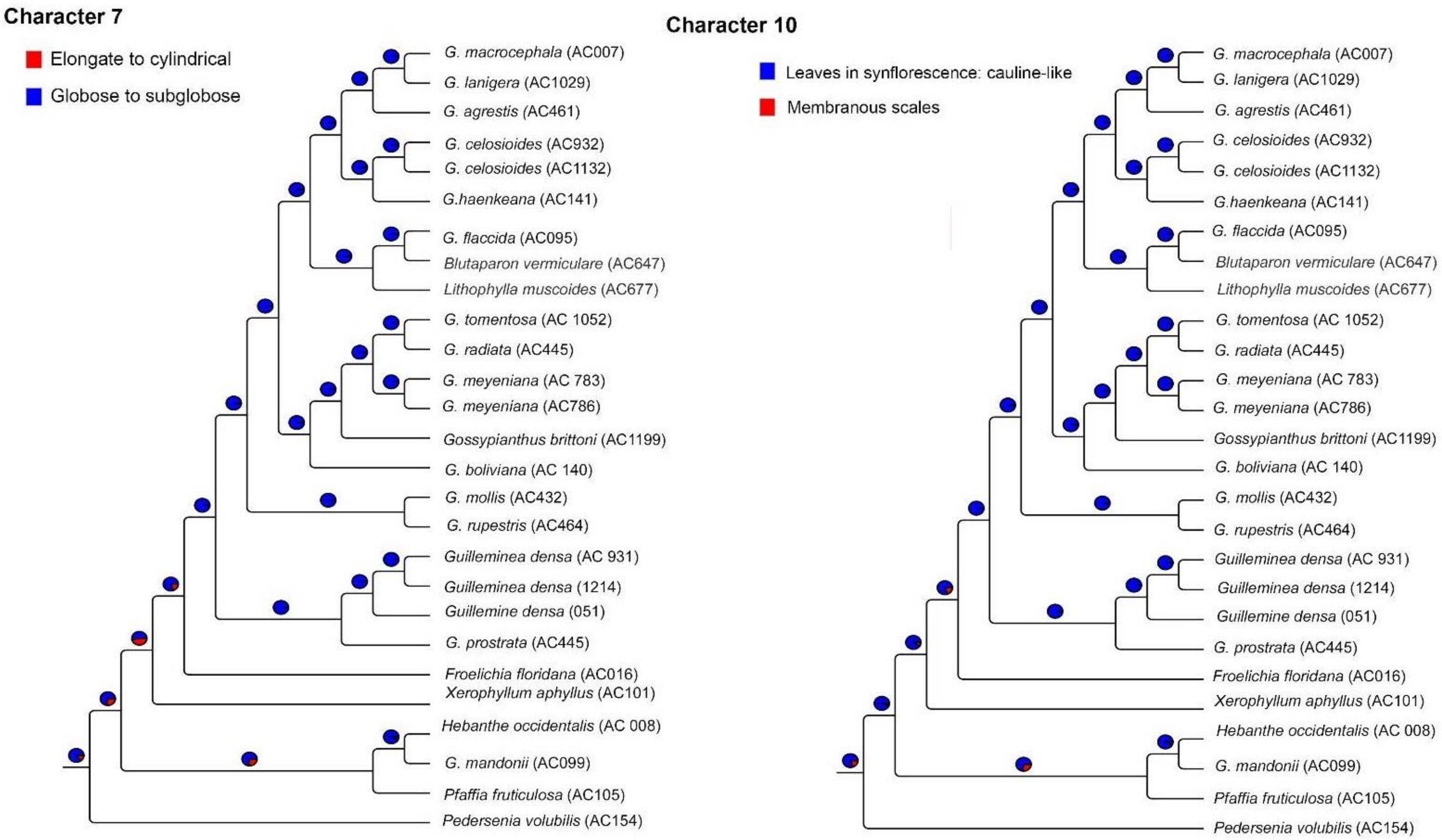
matK-trnK (*);
trnL-trnF (**);
rpl16 (***);
ITS: (****)

Appendix 3-2. Matrix of morphological characters including C4 photosynthesis. For the description of the 22 characters and the states see chapter two.

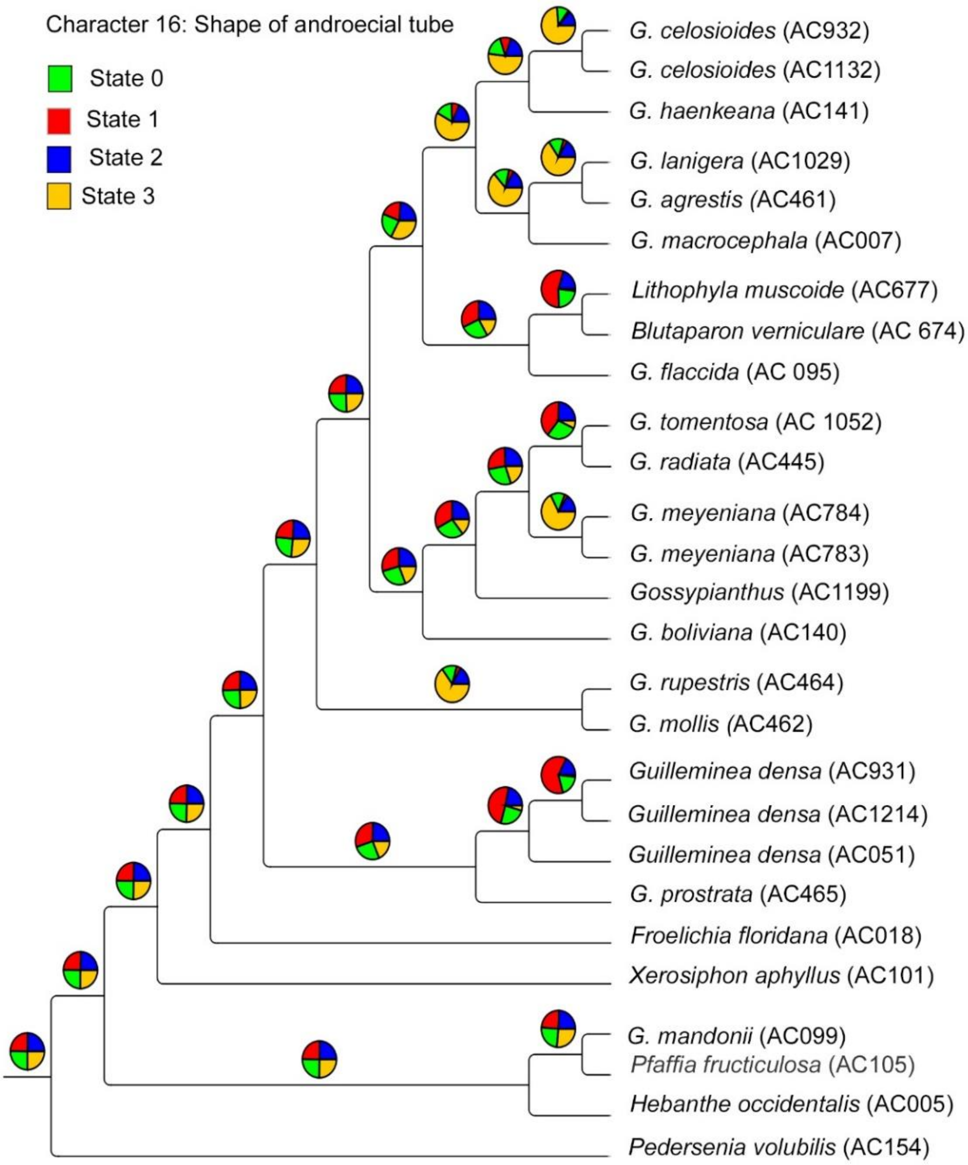
Code	Taxon	Field/garden origin	Voucher/ Number Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
AC154	*Pedersenia volubilis* Borsch, T. Ortuño & M. Nee	Bolivia Santa Cruz	Th. Borsch & J. Coimbra 3537 (LPB, B)	1	1	0	2	1	0	1	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0
AC0008	*Hebanthe occidentalis* (R.E. Fr.) Borsch & Pedersen	Paraguay	Zardini 45377 (B, MO)	1	1	0	2	1	0	1	0	0	1	0	0	1	0	6	1	0	0	0	0	0	0
AC019	*Gomphrena elegans* Mart.	From Bot. Gard. Meise 07-4052 (BONN)	Th. Borsch 3545 (B)	1	1	0	2	1	1	0	1	0	0	0	0	1	0	4	2	0	0	1	1	3	1
AC099	*Gomphrena mandonii* R.E.Fr.	Bolivia	St Beck 18170 (LPB, B)	1	1	0	2	1	1	0	1	0	0	0	0	1	1	2	2	0	0	1	1	2	1
AC105	*Pfaffia fruticulosa Suess.*	Bolivia	Borsch, Th., 3522 (LPB, B)	1	1	0	2	1	1	0	1	0	0	0	0	1	1	4	3	0	0	0	0	0	0
AC101	*Xerosiphon aphyllus* (Pohl ex Moq.) Pedersen	Brazil	Splett, S. 701 (B)	1	1	0	2	0	1	1	0	0	0	0	0	1	0	3	3	1	3	0	0	0	0
AC016	*Froelichia floridana* (Nutt.) Moq.	BG Bonn 03615-90	Th. Thiel s.n.	0	1	0	2	0	1	1	0	0	1	1	0	1	1	2	3	1	2	0	0	0	0
AC462	*Gomphrena mollis* Mart.	Brazil, Bahia, Paramirin	R. M. Harley 27179	1	1	0	2	0	1	0	1	0	0	0	2	1	3	2	2	0	0	1	1	4	1
AC464	*Gomphrena rupestris* Nees	Brazil, Bahia, rio cotas	R. M. Harley 26990 (MO)	1	1	0	2	0	1	0	1	0	0	0	2	1	3	2	2	0	0	1	1	4	4
AC461	***Gomphrena agrestis* Mart.**	Brazil, MG de 7 km Itacambira	B. Stannard, J. D. P. Oliveira, M. L. Kawasaki, R. M. Harley 36152	1	1	2	2	0	1	0	1	2	0	1	1	1	3	2	3	0	0	1	1	3	1
AC1029	*Gomphrena lanigera* Pohl	Bolivia	Wood, J. 19964 (B, where else?)	1	1	0	2	0	1	0	1	2	0	1	1	1	3	1	3	0	0	1	1	1	1
AC007	***Gomphrena macrocephala* A. St.-Hil.**	Paraguay	Zardini 45564 (MO, B)	1	1	0	2	0	1	0	1	2	0	1	1	1	4	1	3	0	0	1	1	1	1

AC0932	*Gomphrena celosioides* Mart.	Süd-Afrika (RSA), Gauteng	K. Müller 882 (B, PRE)	1	1	0	2	1	1	0	1	2	0	1	1	1	3	2	2	0	0	1	1	2	1
AC1182	*Gomphrena celosoides* Mart.	Kenya	V. Di Vincenzo, P. Kamau, M. Wondafrash, M. Mbale 317 (EA, B, ETH)	1	1	0	2	1	1	0	1	2	0	1	1	1	3	2	2	0	0	1	1	2	1
AC141	*Gomphrena haenkeana* Mart.	Bolivia, Chuquisaca, Camargo	Ortuño, T. , Lopez, R.P., Rios, R. 1236 (B, LPB)	0	0	0	2	1	1	0	2	2	0	1	1	1	3	2	3	0	0	1	1	2	3
AC095	*Gomphrena flaccida* R.Br.	Australia	SJ 8776	0	0	2	1	0	1	0	1	2	0	1	1	1	2	2	1	0	0	0	0	0	0
AC674	*Blutaparon vermiculare Gillies ex Moq.*	Cuba	W. Greuter et al 26916 (B, HAJB)	1	2	0	1	1	1	0	3	1	0	1	1	1	0	5	1	0	0	0	0	0	0
AC677	*Lithophila muscoides SW.*	Cuba	W. Greuter et al 26915 (B, HAJB)	1	1	0	1	1	1	0	3	1	0	1	1	1	0	5	1	0	0	0	0	0	0
AC140	*Gomphrena boliviana Moq.*	Bollivia, Santa Cruz, Andrez Ibañez	Th. Borsch, J. Coimbra 3535 (LPB, B)	0	0	0	1	1	1	0	2	2	0	1	1	1	1	2	3	0	0	1	1	0	2
AC1199	*Gossypianthus brittonii Standl.*	Cuba, Villa Clara, 9-9-2012	I. Castaneda N-UCLV 10185 (UCLV) (E.L. Ekman 16333 B)	1	1	1	0	1	0	0	4	2	0	1	1	1	0	3	1	0	0	0	0	0	0
AC783	*Gomphrena meyeniana* Walp. *var. meyeniana*	Bolivia, La Paz a Cochabamba, Japo	Th. Borsch, T. Ortuño 3954 (LPB, B)	1	1	1	1	0	1	0	2	2	0	1	1	1	0	2	1	0	0	0	0	0	0
AC784	***Gomphrena meyeniana* Walp. *var. meyeniana***	Bolivia, La Paz a Cochabamba, Japo	Th. Borsch, T. Ortuño 3954 (LPB, B)	1	1	1	1	0	1	0	2	2	0	1	1	1	0	2	1	0	0	0	0	0	0
AC445	*Gomphrena radiata* Pedersen	Argentina, Salta	Th. Borsch, T. Ortuño, R. P. Lopéz 3749	0	0	1	0	1	0	0	4	2	0	1	1	1	0	2	1	0	0	0	0	0	0
AC1052	***Gomphrena tomentosa* (Griseb.) R.E. Fries**	Bolivia, Potosi, Sud Chichas, Tupiza	Beck, St G. 33662 (LPB,B)	1	1	1	0	1	0	0	4	2	0	1	1	1	0	3	1	0	0	0	0	0	0
AC465	*Gomphrena prostrata* Mart.	Brazil, Bahia, Agua Quente, Pico das almas	R. M. Harley 26695 (B)	1	1	0	0	1	1	0	1	0	0	1	0	1	0	2	1	0	0	0	0	0	0
AC0931	*Guilleminia densa* (Willd.) Moq.	Süd-Afrika (RSA), Gauteng	K. Müller 881 (B, PRE)	1	1	1	0	1	0	0	4	0	0	1	0	0	0	2	1	0	0	0	0	0	0
AC1214	*Guilleminia densa* (Willd.) Moq.	Ethiopia	V. Di Vincenzo, A. Hailu 180 (B, ETH)	1	1	1	0	1	0	0	4	0	0	1	0	0	0	2	1	0	0	0	0	0	0
	Guilleminia densa (Willd.) Moq.	Bolivia	T. Ortuño s/n (LPB)	1	1	1	0	1	0	0	4	0	0	1	0	0	0	2	1	0	0	0	0	0	0

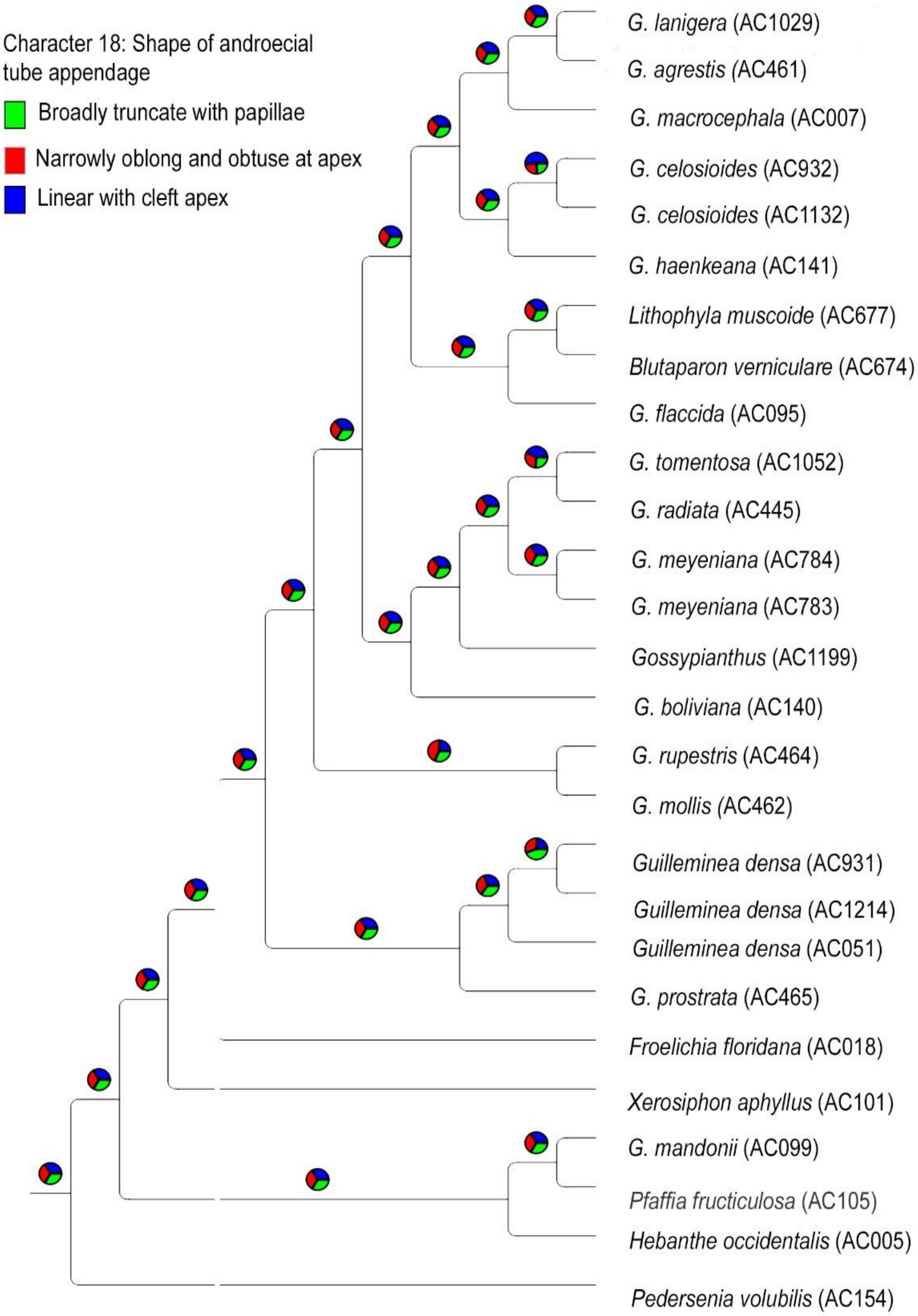
Appendix 3-3: Ancestral states of morphological characters 7 and 10 in Gomphrena and allies reconstructed over the 27-taxon tree. This character was not illustrated in Fig. 3-5.



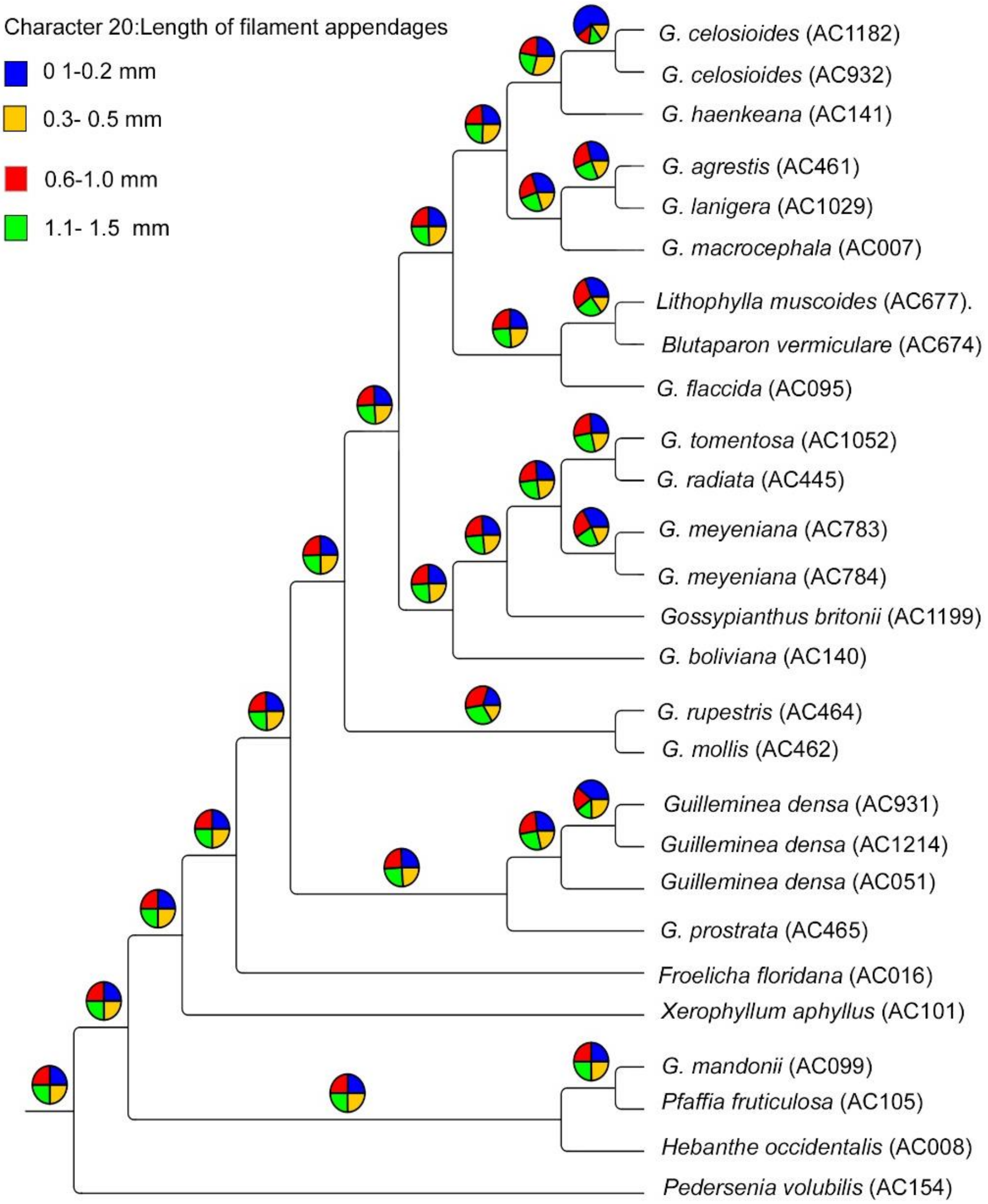
Appendix 3-4. Ancestral states of morphological characters 16: Shape of androecial tube, **state 0:** Four different states can be distinguished: broadly cup-shaped with distinctly spaced linear filament, **state 1**: more or less broadly cup-shaped with V-shaped connection between gradually narrowing filament, **state 2:** more or less broadly cup-shaped with U -shaped connection between more or less abruptly narrowing filament, **state 3** filaments broadly linear with narrowly U-shaped connection between filaments; in Gomphrena and allies reconstructed over the 27-taxon tree. This character was not illustrated in Fig. 3-5.



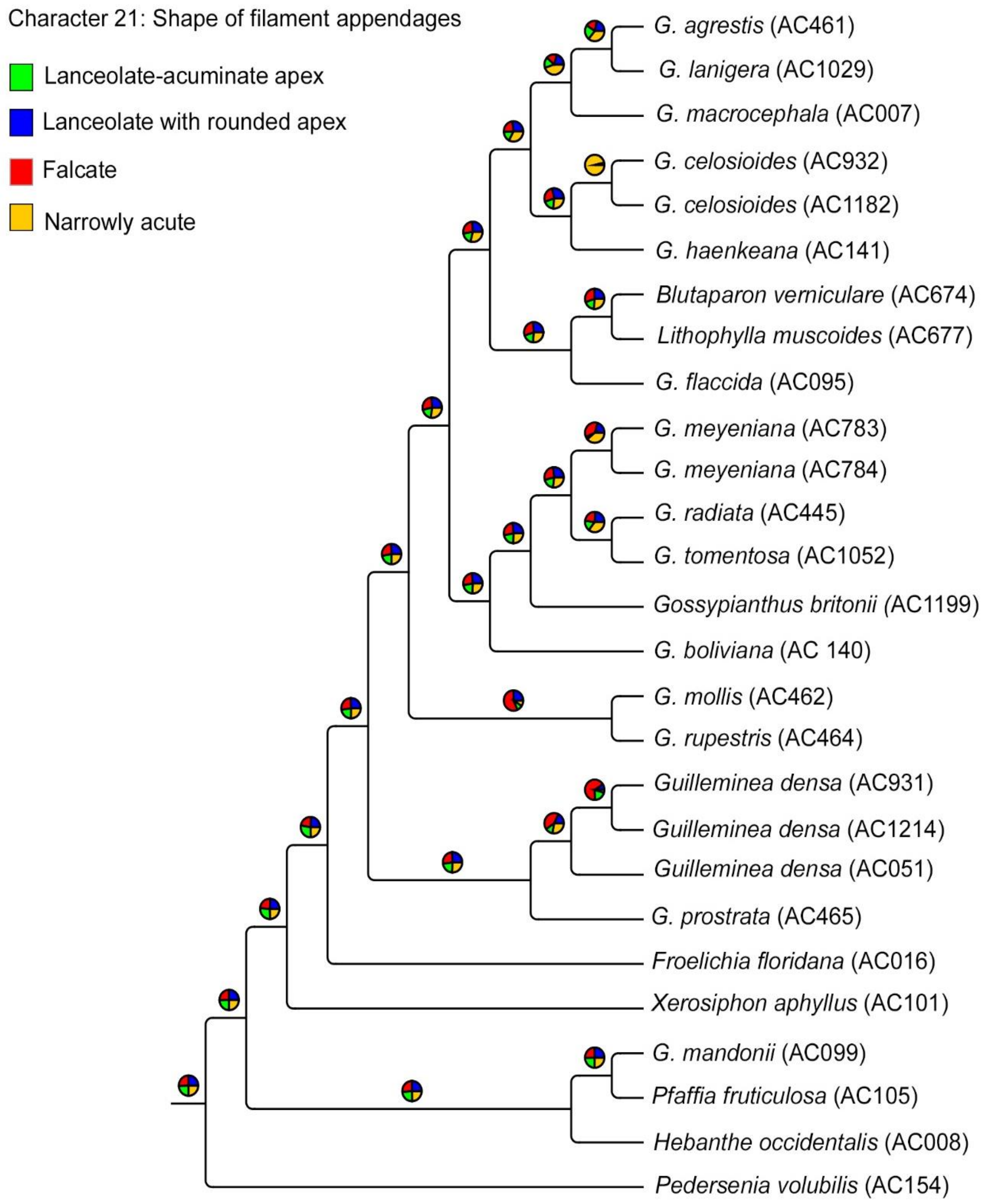
Appendix 3-5 Ancestral states of morphological characters 18: Shape of androecial tube appendages in Gomphrena and allies reconstructed over the 27-taxon tree. This character was not illustrated in Fig. 3-5.



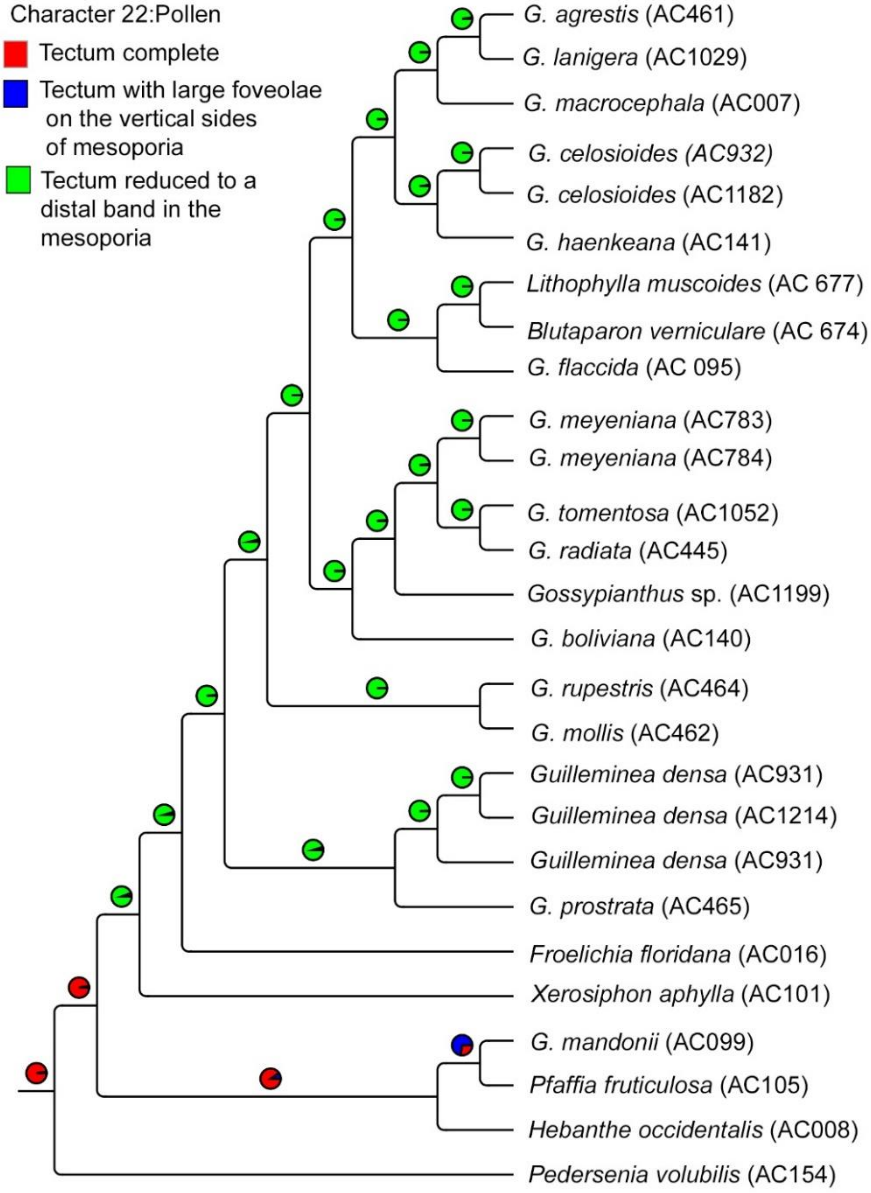
Appendix 3-6. Ancestral states of morphological characters 20: Length of filament appendages in Gomphrena and allies reconstructed over the 27-taxon tree. This character was not illustrated in Fig. 3-5.



Appendix 3-7. Ancestral states of morphological characters 21: Shape of filament appendades in Gomphrena and allies reconstructed over the 27-taxon tree. This character was not illustrated in Fig. 3-5.



Appendix 3-8. Ancestral states of morphological characters 22: Pollen in Gomphrena and allies reconstructed over the 27-taxon tree. This character was not illustrated in Fig. 3-5.



Appendix 3-9. Statistical values for all nodes of the Maximum credibility tree of BEAST analysis of the extended *matK-trnK* dataset (data set C). The node numbers correspond to the tree that is showed in the next appendix.

node	length_range_MIN	length_range_MAX	height_95%_HPD_MIN	height_95%_HPD_MAX	rate_95% MIN	rate_95%_HPD_MAX	length_95%_HPD_MIN	length_95%_HPD_MAX	rate	length	rate_median	length_median	height_median	rate_range_MIN	rate_range_MAX	height range_MIN	height range_MAX	height	posterior
1	NA	NA	107.79	128.2	NA	NA	NA	NA	1	0	NA	NA	117.54	NA	NA	96.08	145.83	117.74	1
2	0	39.88	99.05	115.8	0	0	0.02	21.09	0	10.49	0	10	107.25	0	0.01	90.72	123.7	107.25	1
3	5.17	39.24	77.25	98.08	0	0	8	27.93	0	17.69	0	17.3	87.81	0	0.01	70.56	108.62	87.97	1
4	0	18.87	75.24	95.45	0	0	0	7.48	0	3.09	0	2.6	85.11	0	0.01	69.75	105.68	85.43	0.62
5	0.16	22.61	71.5	90.61	0	0	0.87	10.28	0	4.99	0	4.45	80.5	0	0.01	66.72	106.19	80.81	1
6	0.63	24.45	65.96	83.13	0	0	1.29	13.1	0	6.75	0	6.15	73.75	0	0.01	62.37	98.15	74.08	1
7	2.18	32.35	59.22	69.15	0	0	3.73	17.97	0	10.22	0	9.69	63.48	0	0.01	57.75	83.48	63.85	1
8	1.11	23.07	47.73	62.76	0	0	2.32	13.69	0	7.55	0	7.14	55.51	0	0.01	38.34	74.27	55.43	1
9	0.2	16.81	44.26	59.23	0	0	0.55	7.43	0	3.51	0	3.12	51.97	0	0.01	35.63	69.97	51.92	1
10	0.44	17.19	40.19	54.92	0	0	0.93	8.48	0	4.26	0	3.89	47.69	0	0.01	33.34	65.15	47.66	1
11	2.41	27.27	29.55	43.89	0	0	4.78	17.39	0	10.87	0	10.66	36.6	0	0.01	24.28	52.85	36.79	1
12	0	11.59	28.44	41.76	0	0	0	5.4	0	2.11	0	1.69	34.82	0	0	22.73	50.05	35.05	0.66
13	0.01	16.5	26.35	38.72	0	0	0.18	6.04	0	2.62	0	2.22	32.21	0	0.01	21.83	45.31	32.4	0.92
14	0	10.12	24.98	37.1	0	0	0.01	3.96	0	1.56	0	1.25	30.76	0	0.01	21.16	43.22	30.89	0.9
15	0.09	11.23	23.24	34.79	0	0	0.26	4.57	0	2.09	0	1.82	28.84	0	0.01	19.62	42.84	28.87	0.99
16	0	9.92	22.2	33.46	0	0	0	2.79	0	1.04	0	0.8	27.65	0	0.01	19.29	38.93	27.65	0.44
17	0	9.07	20.78	31.68	0	0	0.07	3.73	0	1.59	0	1.34	26.34	0	0.01	18.13	37.21	26.37	0.66
18	0.39	11.76	17.99	28.23	0	0	0.96	6.49	0	3.44	0	3.2	22.96	0	0.01	14.39	33.94	23.05	1
19	0.18	9.77	15.8	25.45	0	0	0.44	4.76	0	2.36	0	2.15	20.5	0	0.01	11.84	32.87	20.61	1
20	0.25	10.86	13.48	22.31	0	0	0.59	5.03	0	2.64	0	2.43	17.87	0	0.01	10.2	28.36	17.96	1
21	0.26	11.54	11.32	19.07	0	0	0.86	5.41	0	2.89	0	2.69	14.97	0	0.01	8.92	23.62	15.07	1
22	0.02	9.6	10	17	0	0	0.18	3.39	0	1.6	0	1.42	13.37	0	0.01	8.11	21.34	13.47	1

23	0.11	8.87	8.45	14.5	0	0	0.44	4.07	0	2.03	0	1.85	11.36	0	0.01	6.69	18.78	11.44	1
24	0.07	6.04	7.16	12.67	0	0	0.17	2.72	0	1.27	0	1.11	9.86	0	0.01	5.68	16.94	9.96	1
25	0.74	11.69	3.12	8.23	0	0	1.56	7.21	0	4.26	0	4.16	5.6	0	0.01	2.02	12.41	5.7	1
26	0	5.71	2.61	7.18	0	0	0	2.46	0	0.96	0	0.77	4.69	0	0.01	1.69	11.24	4.79	0.88
27	0	7.12	1.94	6.07	0	0	0	2.28	0	0.92	0	0.75	3.8	0	0.01	1.31	8.67	3.92	0.95
28	0	4.3	1.64	5.47	0	0	0	1.57	0	0.52	0	0.35	3.34	0	0.01	1.03	8.42	3.42	0.27
29	0.13	8.35	0.09	2.54	0	0	0.46	4.31	0	2.26	0	2.13	1.01	0	0.01	0.03	5.68	1.16	1
30	0.16	9.64	0.21	3.4	0	0	0.64	5.82	0	3.21	0	3.12	1.35	0	0.01	0.06	7.41	1.54	1
31	0	6.25	0.01	1.29	0	0	0.01	2.68	0	1.04	0	0.82	0.38	0	0.01	0	4.27	0.5	1
32	0.04	6.29	6.06	11.24	0	0	0.16	2.91	0	1.38	0	1.23	8.5	0	0.01	4.66	16.66	8.58	1
33	0	5.76	5.36	10.63	0	0	0	1.85	0	0.6	0	0.4	7.89	0	0.01	4	13.6	7.96	0.37
34	0.54	13.46	2.5	6.23	0	0	1.42	6.51	0	3.93	0	3.84	4.16	0	0.01	1.75	10.33	4.27	1
35	0	6.03	1.79	5.32	0	0	0	2.36	0	0.79	0	0.56	3.41	0	0	1.26	7.9	3.48	0.48
36	0.01	7.35	1.17	4.26	0	0	0.02	2.67	0	1.14	0	0.97	2.55	0	0.01	0.65	7.1	2.65	0.99
37	0.03	5.88	0.44	2.61	0	0	0.12	2.38	0	1.1	0	0.97	1.39	0	0.01	0.21	4.94	1.47	1
38	0	3.58	0.12	1.78	0	0	0	1.68	0	0.64	0	0.51	0.81	0	0	0.02	3.68	0.89	0.59
39	0	3.52	0	0.98	0	0	0	1.69	0	0.69	0	0.59	0.25	0	0.01	0	2.54	0.34	0.59
40	0	6.48	0.14	2.47	0	0	0	3.25	0	1.53	0	1.42	1.02	0	0	0.04	5.14	1.16	0.8
41	0	3.37	0.03	1.59	0	0	0	2	0	0.64	0	0.42	0.58	0	0	0.03	4.02	0.7	0.11
42	0	3.97	0.01	1.3	0	0	0	1.93	0	0.59	0	0.38	0.36	0	0.01	0.01	3.79	0.48	0.09
43	0	4.42	0	0.87	0	0	0	1.76	0	0.54	0	0.32	0.15	0	0	0	3.01	0.26	0.17
44	0.06	6.17	1.28	4.04	0	0	0.21	2.94	0	1.41	0	1.27	2.54	0	0.01	0.78	6.68	2.61	1
45	0.3	6.08	0.01	1.06	0	0	0.69	3.42	0	1.97	0	1.89	0.35	0	0.01	0.01	3.02	0.43	1
46	0	4.15	0.94	3.37	0	0	0	1.62	0	0.56	0	0.39	2.02	0	0.01	0.35	4.95	2.08	0.44
47	0.01	5.55	0.32	2.24	0	0	0.03	2.3	0	1.04	0	0.92	1.15	0	0.01	0.16	3.85	1.23	1
48	0	2.71	0.19	1.73	0	0	0	1.17	0	0.4	0	0.28	0.79	0	0.01	0.1	3.25	0.86	0.16
49	0	3.28	0.01	1.14	0	0	0	1.42	0	0.49	0	0.36	0.41	0	0.01	0.01	2.35	0.48	0.23
50	0	3.26	0	0.73	0	0	0	1.25	0	0.45	0	0.34	0.18	0	0.01	0	2.48	0.25	0.24
51	0.05	6.32	0.01	1.53	0	0	0.33	3.11	0	1.65	0	1.56	0.49	0	0.01	0	3.58	0.61	1
52	0.13	6.98	4.13	9.05	0	0	0.28	3.48	0	1.73	0	1.58	6.49	0	0.01	2.49	12.88	6.56	1
53	0	5.9	3.4	8.03	0	0	0.03	2.27	0	0.99	0	0.85	5.5	0	0.01	2.09	11.99	5.57	0.98

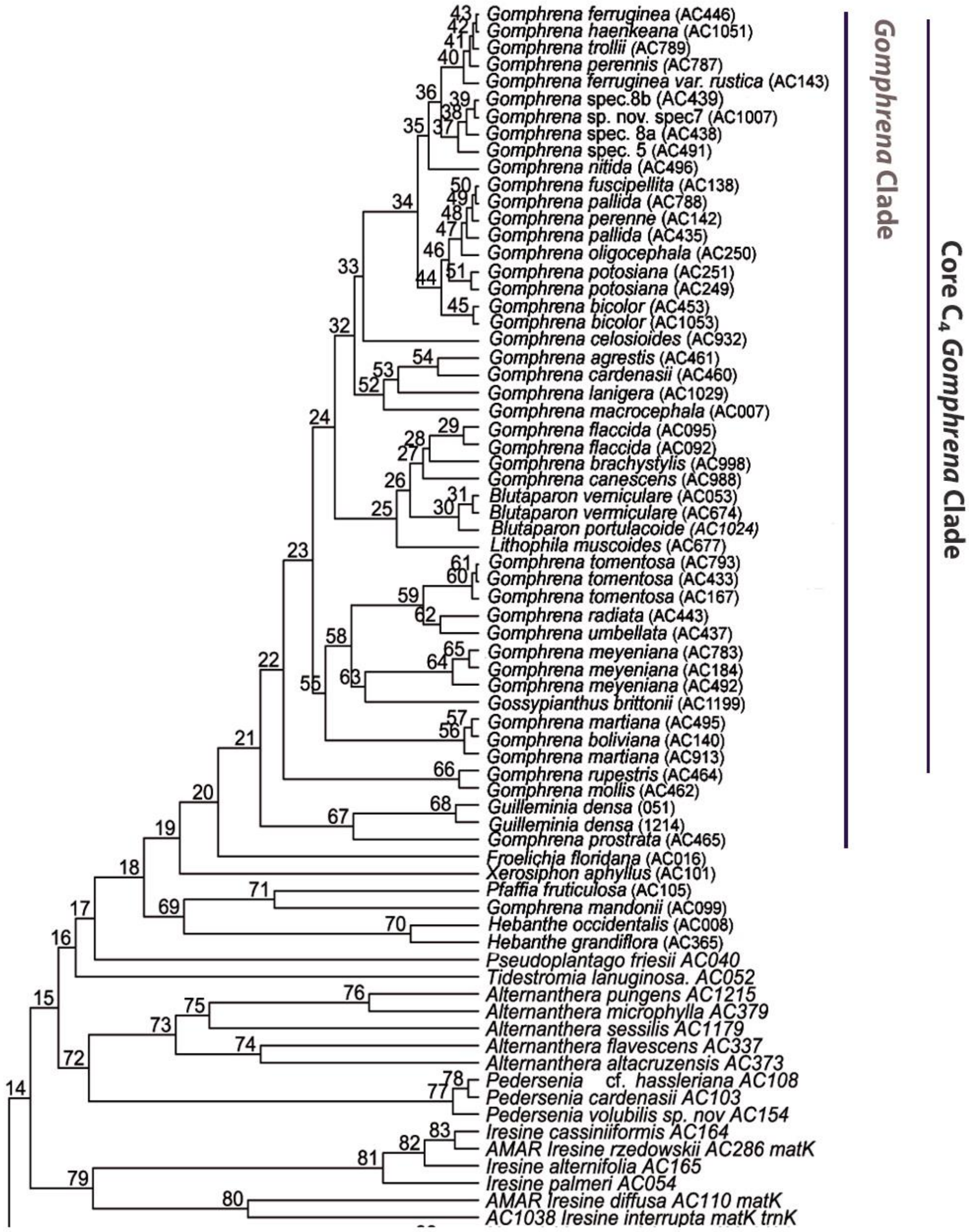
54	0.42	8.72	1.22	4.72	0	0	0.96	4.68	0	2.71	0	2.57	2.77	0	0.01	0.69	7.64	2.87	1
55	0	8.86	7.53	13.78	0	0	0	2.56	0	0.81	0	0.52	10.5	0	0	4.92	17.45	10.56	0.48
56	3.6	18.31	0.11	2.62	0	0	6.35	13.24	0	9.8	0	9.74	0.96	0	0	0.03	8.07	1.14	1
57	0	7.78	0	1.41	0	0	0	1.98	0	0.66	0	0.44	0.44	0	0.01	0	4.19	0.56	0.45
58	0.05	9.44	5.53	12.07	0	0	0.14	4.83	0	2.15	0	1.87	8.73	0	0.01	3.49	15.81	8.79	1
59	0.4	12.55	1.7	6.58	0	0	1.31	7.68	0	4.37	0	4.24	3.78	0	0.01	0.77	10.85	3.95	1
60	0.44	10.69	0.01	1.4	0	0	1.14	6.02	0	3.4	0	3.23	0.42	0	0	0	4.12	0.54	1
61	0	3.63	0	0.63	0	0	0	1.06	0	0.33	0	0.22	0.13	0	0.01	0	1.8	0.2	0.33
62	0	7.28	0.87	5.03	0	0	0	2.93	0	1.17	0	0.93	2.62	0	0	0.35	8.84	2.79	0.98
63	0	7.25	4.53	11.29	0	0	0	2.92	0	0.92	0	0.58	7.76	0	0	2.92	13.5	7.81	0.37
64	0.64	13.97	0.46	4.08	0	0	2.58	9.88	0	6.2	0	6.14	1.77	0	0	0.2	8.45	1.98	1
65	0	7.61	0.02	1.99	0	0	0	3.29	0	1.27	0	1.02	0.63	0	0	0	5.1	0.79	0.73
66	3.95	19.98	0.09	4.04	0	0	7.71	15.94	0	11.84	0	11.85	1.31	0	0	0.03	12.87	1.63	1
67	0.8	15.02	4.24	13.21	0	0	2.11	10.76	0	6.37	0	6.21	8.58	0	0.01	2.17	19.67	8.7	1
68	1.09	16.79	0.24	3.69	0	0	2.64	11.53	0	6.94	0	6.77	1.55	0	0.01	0.17	10.84	1.76	1
69	0.03	17.62	13.89	26.01	0	0	0.09	7.29	0	2.87	0	2.28	20.2	0	0.01	9.39	32.42	20.15	0.91
70	2.17	29.19	1.19	10.8	0	0	7.2	22.6	0	15.21	0	15.37	4.66	0	0	0.7	21.57	5.23	1
71	0.45	18.62	7.56	20.54	0	0	1.36	12.08	0	6.28	0	5.87	14	0	0.01	4.08	27.57	14.09	1
72	0	11.73	20.71	33.01	0	0	0	4.52	0	1.52	0	1.06	26.74	0	0.01	16.41	38.57	26.85	0.51
73	0.51	21.93	14.06	27.23	0	0	1.55	12.09	0	6.44	0	6.06	20.78	0	0	10.22	34.98	20.84	1
74	0.25	20.97	8.16	22.16	0	0	1.03	11.33	0	5.65	0	5.14	14.95	0	0.01	3.94	29.65	15.11	1
75	0	15.66	11.7	25.5	0	0	0	6.25	0	2.34	0	1.81	18.46	0	0.01	7.78	33.68	18.53	0.89
76	1.25	28.52	2.8	13.81	0	0	3.66	17.84	0	10.84	0	10.62	7.5	0	0	1.26	24.69	7.87	1
77	11.73	39.02	0.35	4.09	0	0	18.95	31.53	0	25.05	0	25	1.75	0	0	0.18	12.78	1.98	1
78	0	10.89	0.04	1.94	0	0	0	2.92	0	1.14	0	0.89	0.71	0	0.01	0.02	11.26	0.85	0.96
79	0	26.32	16.15	34.62	0	0	0	13.32	0	4.88	0	3.62	26.45	0	0	8.28	40.31	26.06	0.99
80	0.88	31.89	6.76	25.7	0	0	1.91	19.77	0	10.03	0	9.33	15.82	0	0	3.3	33.4	16.1	1
81	1.33	35.13	2.78	12.86	0	0	8.59	28.41	0	19.02	0	19.46	6.54	0	0	1.83	24.87	7.1	1
82	0.06	20.53	1.39	7.26	0	0	0.16	7.78	0	3.13	0	2.53	3.69	0	0.01	0.89	16.26	3.99	0.99
83	0.06	14.47	0.35	3.69	0	0	0.21	4.94	0	2.2	0	1.88	1.61	0	0.01	0.2	8.89	1.81	1
84	0.39	21.96	19.77	32.03	0	0	1.53	12.79	0	6.78	0	6.42	25.36	0	0.01	16.34	37.6	25.48	0.95

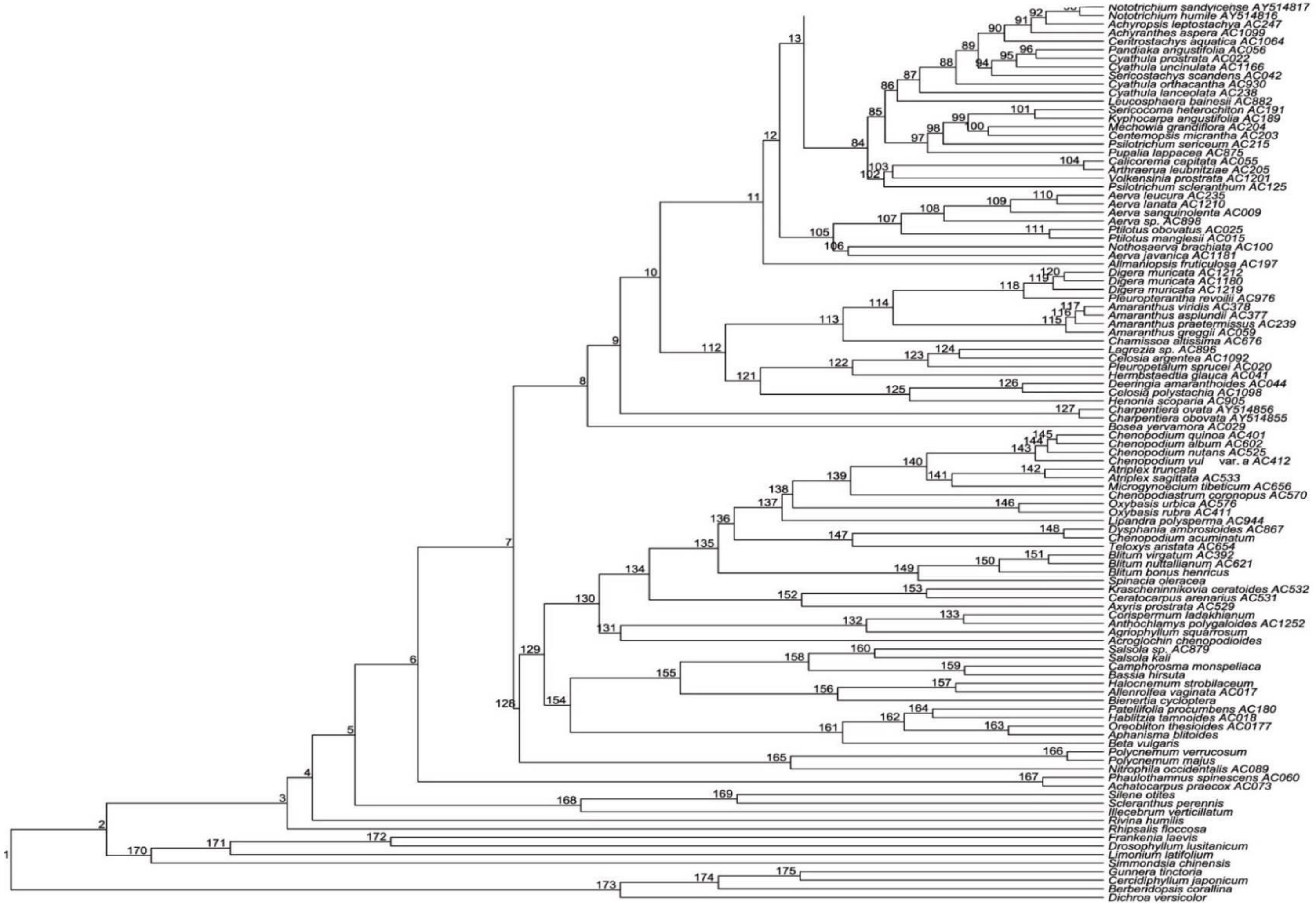
85	0	9.38	17.91	29.54	0	0	0.01	3.38	0	1.25	0	0.94	23.5	0	0.01	15.05	35.45	23.64	0.84
86	0	9.9	16.8	28.02	0	0	0	3.4	0	1.4	0	1.15	22.19	0	0	13.69	33.95	22.35	0.92
87	0.18	10.24	14.78	25.43	0	0	0.37	5.29	0	2.58	0	2.31	19.75	0	0.01	11.36	32.57	19.88	1
88	0.45	15.82	11.49	20.64	0	0	1.02	7.33	0	3.85	0	3.58	15.85	0	0.01	8.58	25.64	16.03	1
89	0.01	12.45	9.78	17.92	0	0	0.4	5.01	0	2.4	0	2.15	13.48	0	0.01	6.91	23.21	13.63	1
90	0.14	10.91	7.18	14.67	0	0	0.58	5.44	0	2.78	0	2.55	10.62	0	0.01	4.92	21.18	10.74	1
91	0.17	11.29	4.75	11.18	0	0	0.61	5.43	0	2.86	0	2.63	7.75	0	0.01	3.11	15.65	7.87	1
92	0.1	7.6	3.53	9.3	0	0	0.2	3.34	0	1.56	0	1.38	6.19	0	0.01	2.32	14.29	6.31	1
93	0.93	10.28	0.99	4.66	0	0	1.41	6.11	0	3.62	0	3.46	2.54	0	0.01	0.54	8.86	2.69	1
94	0	9.65	8.01	16.42	0	0	0	3.98	0	1.5	0	1.16	12	0	0	5.34	20.79	12.1	0.86
95	0.11	12.59	5.57	13.68	0	0	0.35	5.78	0	2.78	0	2.47	9.36	0	0.01	3.47	17.52	9.49	1
96	0.01	9.88	3.58	11.28	0	0	0.18	4.58	0	2.11	0	1.87	7.24	0	0.01	1.95	16.1	7.38	0.99
97	0.02	19.44	12.83	25.72	0	0	0.22	10.29	0	4.5	0	3.93	18.91	0	0	8.23	31.56	18.97	0.97
98	0	14.07	11.32	23.74	0	0	0	4.75	0	1.67	0	1.22	17.25	0	0.01	7.76	29.79	17.38	0.85
99	0.03	15.93	8.75	20.32	0	0	0.24	6.69	0	2.84	0	2.41	14.54	0	0	6.06	25.61	14.64	1
100	0.02	12	6.85	18.21	0	0	0.1	5.14	0	2.13	0	1.78	12.39	0	0.01	2.93	24.85	12.51	0.97
101	0.23	20.87	2.59	13.37	0	0	1.36	13.1	0	6.91	0	6.55	7.39	0	0.01	1.48	20.77	7.69	1
102	0	17.43	16.68	30.94	0	0	0	5.66	0	1.51	0	0.79	23.59	0	0	7.95	37.57	23.61	0.35
103	0	19.59	15.44	30.35	0	0	0	6.19	0	1.86	0	1.14	22.66	0	0.01	7.62	34.7	22.58	0.28
104	3.04	36.36	0.38	5.42	0	0	13.49	29.02	0	21.34	0	21.39	2.1	0	0	0.16	14.95	2.46	1
105	0.6	20.84	21.41	36.48	0	0	1.36	12.02	0	6.19	0	5.76	29.03	0	0	16.45	44.54	29.13	1
106	0	17.82	18.97	35.04	0	0	0	5.29	0	1.55	0	0.9	27.46	0	0	12.3	42.47	27.46	0.48
107	0.48	19.6	14.96	29.18	0	0	1.88	12.47	0	6.73	0	6.34	21.75	0	0.01	11.3	37.02	21.94	1
108	0.06	17.81	11.07	24.61	0	0	0.64	9.59	0	4.52	0	4	17.16	0	0.01	6.97	33.4	17.42	1
109	0.82	23.75	5.23	15.8	0	0	2.21	13.4	0	7.14	0	6.73	9.98	0	0.01	3.31	23.13	10.28	1
110	0.49	17.72	1.98	9.41	0	0	1.36	9.68	0	4.98	0	4.6	4.99	0	0.01	1.37	17.32	5.3	1
111	4.47	32.31	2.08	11.03	0	0	8.28	23.38	0	15.77	0	15.64	5.81	0	0.01	1.28	19.88	6.16	1
112	0.58	24.65	32.5	48.96	0	0	1.68	13.5	0	6.98	0	6.43	40.65	0	0.01	24.44	58.16	40.68	1
113	2.23	31.81	18.8	37.92	0	0	4.25	20.93	0	12.43	0	12.06	27.99	0	0.01	12.96	46.11	28.19	1
114	0.13	24.17	14.67	32.27	0	0	0.74	11.48	0	5.29	0	4.71	22.62	0	0.01	10.63	43.65	22.91	1
115	3.41	36.33	1.75	7.39	0	0	10.22	28.24	0	18.65	0	18.36	4.03	0	0	0.94	15.36	4.26	1

116	0	10.8	1.27	5.65	0	0	0	2.85	0	1.08	0	0.82	3.02	0	0.01	0.6	11.31	3.21	0.91
117	0	7.18	0.57	4.22	0	0	0.01	2.62	0	1.01	0	0.8	2.04	0	0.01	0.29	9.24	2.23	0.94
118	3.02	35.28	4.55	13.55	0	0	6.08	22.66	0	14.06	0	13.68	8.58	0	0.01	2.95	22.24	8.85	1
119	0.23	15.68	2.69	9.07	0	0	0.45	6.82	0	3.23	0	2.84	5.41	0	0.01	1.56	16.97	5.62	1
120	0	8.2	1.83	7.38	0	0	0	3.13	0	1.23	0	0.98	4.21	0	0.01	1.23	12.82	4.41	0.88
121	0.04	21.83	28.12	46.28	0	0	0.2	9.35	0	3.86	0	3.15	36.89	0	0.01	21.06	56.48	36.82	0.98
122	0.69	31.29	17.06	36.26	0	0	2.21	17.95	0	9.82	0	9.25	27	0	0.01	11.77	47.65	27.07	1
123	0.5	26.22	10.57	27.98	0	0	1.78	15	0	7.86	0	7.26	18.86	0	0.01	7.68	38.21	19.21	1
124	0.06	17.64	7.52	23.91	0	0	0.27	7.79	0	3.51	0	3.08	15.5	0	0.01	4.85	36.47	15.8	0.85
125	1.27	36.51	10.99	32.52	0	0	4.79	27.26	0	15.69	0	15.29	20.85	0	0.01	6.59	44.61	21.14	1
126	0.92	33.05	3.07	16.75	0	0	2.98	22	0	11.86	0	11.18	8.7	0	0.01	1.52	30.76	9.28	1
127	28.62	67.73	0.59	6.43	0	0	40.91	56.94	0	48.94	0	49.05	2.59	0	0	0.28	17.98	2.99	1
128	0	9.76	58.74	67.97	0	0	0	2.83	0	0.86	0	0.49	62.82	0	0	58.09	76.54	63.17	0.22
129	0.05	17.07	57.69	63.83	0	0	0.16	6.54	0	2.72	0	2.24	60.14	0	0.01	56.99	69.48	60.43	1
130	0.67	22.11	47.11	60.41	0	0	1.33	12.19	0	6.24	0	5.77	54.24	0	0.01	38.3	67.13	53.92	1
131	0	25.45	42.83	59.43	0	0	0	8.1	0	2.48	0	1.55	51.94	0	0	23.45	64.68	51.4	0.61
132	3.29	48.52	13.29	40.56	0	0	11.15	39.9	0	26.09	0	26.33	25.48	0	0.01	8.62	54.24	26.11	1
133	1.13	44.04	5.81	27.4	0	0	1.73	20.96	0	10.27	0	9.26	15.03	0	0	3.51	41.86	15.84	1
134	0.46	16.61	41.24	55.94	0	0	0.97	9.7	0	4.88	0	4.47	48.86	0	0.01	33.4	62.65	48.69	1
135	0.42	25.07	33.24	48.97	0	0	1.9	13.69	0	7.29	0	6.85	41.43	0	0.01	26.55	58.24	41.4	1
136	0	12.02	31.78	47.6	0	0	0.02	4.83	0	1.84	0	1.44	39.72	0	0.01	25	53.35	39.71	0.69
137	0.79	24.28	26.46	42.53	0	0	1.02	10.47	0	5.49	0	5.04	34.58	0	0.01	20.22	51.48	34.57	1
138	0	8.88	25.05	41.14	0	0	0	3.64	0	1.3	0	0.98	33.43	0	0.01	20.09	48.25	33.47	0.5
139	0.8	20.48	19.69	34.91	0	0	1.86	11.76	0	6.27	0	5.87	27.18	0	0.01	15.67	43.8	27.3	1
140	1.99	22.95	12.67	25.54	0	0	2.99	13.88	0	8.19	0	7.89	19	0	0.01	8.22	32.7	19.11	1
141	0.06	12.59	10.41	22.65	0	0	0.25	5.9	0	2.75	0	2.43	16.28	0	0.01	6.86	31.12	16.37	0.99
142	2.96	25.82	2.73	10.94	0	0	4.58	15.36	0	9.84	0	9.64	6.29	0	0.01	1.4	17.71	6.56	1
143	1.23	26.08	3.67	11.94	0	0	4.92	18.33	0	11.49	0	11.28	7.32	0	0.01	2.03	19.44	7.6	1
144	0	10.09	2.97	10.1	0	0	0.02	3.88	0	1.45	0	1.11	6.01	0	0	1.42	15.08	6.25	0.4
145	0.01	10.07	2	9.01	0	0	0.01	3.79	0	1.45	0	1.13	5.02	0	0.01	1.05	15.28	5.24	0.74
146	6.03	41.17	3.06	17.03	0	0	13.43	33.64	0	23.83	0	23.95	9.09	0	0	1.93	28.12	9.66	1

147	1.7	32.54	15.43	37.91	0	0	3.04	23.5	0	12.62	0	11.96	27.01	0	0	8.84	45.77	26.98	1
148	5.23	42.14	1.31	9.19	0	0	11.14	34.15	0	22.27	0	22.18	4.26	0	0.01	0.69	20.4	4.71	1
149	3	45.3	10.5	30.79	0	0	8.3	31.86	0	20.38	0	20.39	19.93	0	0	7.01	39.78	20.4	1
150	0.57	30.25	5.16	19.26	0	0	1.3	17.87	0	8.7	0	7.78	11.21	0	0.01	2.91	31.59	11.7	1
151	0.37	24.09	1.93	11.55	0	0	0.81	11.41	0	5.37	0	4.78	5.9	0	0.01	1.2	21.87	6.33	1
152	3.03	38.43	21.76	42.89	0	0	6.54	26.48	0	16.35	0	16.02	32.46	0	0.01	14.75	51.01	32.34	1
153	2.71	34.82	10.2	28.84	0	0	4.35	22.06	0	13.14	0	12.63	19.02	0	0.01	6.97	40.94	19.19	1
154	0.01	18.52	50.29	62.69	0	0	0.09	9.03	0	3.47	0	2.73	57.35	0	0.01	41.44	66.94	56.96	0.87
155	1.72	30.8	36.24	53.92	0	0	3.71	20.41	0	11.96	0	11.55	45.53	0	0.01	29.55	62.63	45.45	1
156	3.3	33.55	25.33	33.22	0	0	7.57	25.79	0	16.53	0	16.47	28.58	0	0	24.39	42.44	28.93	1
157	0.84	34.84	7.07	24.91	0	0	4.02	22.16	0	12.99	0	12.86	15.89	0	0.01	3.05	33.14	15.93	1
158	2.3	39.73	21.39	42.42	0	0	4.23	23.91	0	13.69	0	13.1	31.72	0	0.01	14.05	51.12	31.76	1
159	3.4	37.7	6.59	24.44	0	0	6.54	26.66	0	16.37	0	15.9	14.92	0	0.01	3.27	40.12	15.3	1
160	0.2	32.59	13.21	36.07	0	0	0.62	15.95	0	7.04	0	6.05	24.61	0	0.01	6.72	47.65	24.7	0.98
161	3	47.18	16.69	43.91	0	0	12.48	41.52	0	28.21	0	29.07	28.04	0	0	11.75	55.61	28.95	1
162	0.16	39.29	12.24	34.29	0	0	0.34	17	0	6.74	0	5.42	21.44	0	0.01	8.1	51	22.21	1
163	1.35	42.62	4.09	18.83	0	0	2.84	21.56	0	11.42	0	10.52	10.21	0	0.01	1.8	29.15	10.74	1
164	0	29.86	9.19	31.08	0	0	0	8.66	0	3.1	0	2.23	18.36	0	0.01	4.88	47.54	19.1	0.96
165	3.45	62.44	15.84	51.95	0	0	11.64	47.55	0	29.58	0	29.47	33.65	0	0	7.63	64.1	33.73	1
166	5.58	59.1	0.97	8.49	0	0	11.54	47.13	0	29.39	0	29.23	3.89	0	0	0.58	17.49	4.34	1
167	17.74	87.59	1.9	15.17	0	0	55.03	78.53	0	66.66	0	66.77	6.52	0	0	1.3	52.11	7.42	1
168	4.67	56.77	40.88	72.43	0	0	9.33	40.49	0	24.62	0	24.18	56.22	0	0.01	29.93	84.77	56.19	1
169	2.19	46.17	24.89	57.76	0	0	4.56	29.77	0	16.3	0	15.35	39.42	0	0.01	14.94	69.92	39.88	1
170	0	30.73	91.36	112.46	0	0	0	14.33	0	5.3	0	4.06	102.45	0	0	82.41	119	102.2	0.47
171	0.01	36.63	83.42	103.58	0	0	0.43	21.8	0	10.83	0	10.04	93.94	0	0.01	75.1	112.22	93.82	1
172	0.28	61.55	52.04	94.21	0	0	2.9	39.06	0	18.49	0	16.61	76.68	0	0.01	31.45	101.95	75.34	0.97
173	11.87	103.54	29.64	78.93	0	0	37.52	89.43	0	64.51	0	65.47	51.98	0	0	18.95	107.96	53.24	1
174	0.02	66.96	22.47	64.29	0	0	0.49	27.36	0	11.14	0	9.07	41.43	0	0.01	15.78	90.34	42.29	0.96
175	0.11	48.85	14.99	52.59	0	0	1.17	20.14	0	8.91	0	7.68	32.63	0	0.01	9.61	81.26	33.49	0.99

Appendix 3-10. Maximum clade credibility tree with node numbers.




Nototrichium sandvicense AY514817
Nototrichium humile AY514816
Achyropsis leptostachya AC247
Achyranthes aspera AC1099
Centrostachys aquatica AC1064
Pandiaka angustifolia AC056
Cyathula prostrata AC022
Cyathula uncinulata AC1166
Sericostachys scandens AC042
Cyathula orthacantha AC930
Cyathula lanceolata AC238
Leucosphaera bainesii AC882
Sericocoma heterochiton AC191
Kyphocarpa angustifolia AC189
Mechowia grandiflora AC204
Centemopsis micrantha AC203
Psilotrichum sericeum AC215
Pupalia lappacea AC875
Calicorema capitata AC055
Arthraerua leubnitziae AC205
Volkensinia prostrata AC1201
Psilotrichum scleranthum AC125
Aerva leucura AC235
Aerva lanata AC1210
Aerva sanguinolenta AC009
Aerva sp. AC898
Ptilotus obovatus AC025
Ptilotus manglesii AC015
Nothosaerva brachiata AC100
Aerva javanica AC1181
Allmaniopsis fruticulosa AC197
Digera muricata AC1212
Digera muricata AC1180
Digera muricata AC1219
Pleuropterantha revoilii AC976
Amaranthus viridis AC378
Amaranthus asplundii AC377
Amaranthus praetermissus AC239
Amaranthus greggii AC059
Chamissoa altissima AC676
Lagrezia sp. AC896
Celosia argentea AC1092
Pleuropetalum sprucei AC020
Hermbstaedtia glauca AC041
Deeringia amaranthoides AC044
Celosia polystachia AC1098
Henonia scoparia AC905
Charpentiera ovata AY514856
Charpentiera obovata AY514855
Bosea yervamora AC029
Chenopodium quinoa AC401
Chenopodium album AC602
Chenopodium nutans AC525
Chenopodium vul var. a AC412
Atriplex truncata
Atriplex sagittata AC533
Microgynoecium tibeticum AC656
Chenopodiastrum coronopus AC570
Oxybasis urbica AC576
Oxybasis rubra AC411
Lipandra polysperma AC944
Dysphania ambrosioides AC867
Chenopodium acuminatum
Teloxys aristata AC654
Blitum virgatum AC392
Blitum nuttallianum AC621
Blitum bonus henricus
Spinacia oleracea
Krascheninnikovia ceratoides AC532
Ceratocarpus arenarius AC531
Axyris prostrata AC529
Corispermum ladakhianum
Anthochlamys polygaloides AC1252
Agriophyllum squarrosum
Acroglochin chenopodioides
Salsola sp. AC879
Salsola kali
Camphorosma monspeliaca
Bassia hirsuta
Halocnemum strobilaceum
Allenrolfea vaginata AC017
Bienertia cycloptera
Patellifolia procumbens AC180
Hablitzia tamnoides AC018
Oreobliton thesioides AC0177
Aphanisma blitoides
Beta vulgaris
Polycnemum verrucosum
Polycnemum majus
Nitrophila occidentalis AC089
Phaulothamnus spinescens AC060
Achatocarpus praecox AC073
Silene otites
Scleranthus perennis
Illecebrum verticillatum
Rivina humilis
Rhipsalis floccosa
Frankenia laevis
Drosophyllum lusitanicum
Limonium latifolium
Simmondsia chinensis
Gunnera tinctoria
Cercidiphyllum japonicum
Berberidopsis corallina
Dichroa versicolor
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Chapter 4

Treatment of *Gomphrena* s.str.in Bolivia

4.1. The Genus *Gomphrena* in Bolivia

In this chapter, a first approach for a treatment of the genus *Gomphrena* from Bolivia is presented. However, because of many taxa new to science the descriptions here are more detailed then they will be in the final version in the Flora. The descriptive data will also serve for a later elaboration of a manuscript that will focus on species limits and descriptions of new species.

The Flora of Bolivia at present is a new initiative. It will be the next phase in inventorying and describing the plant diversity of Bolivia, including keys for identification, after the culmination of the catalogue of vascular plants of Bolivia published already some years ago (Jorgensen, Nee & Beck 2014). The catalogue includes twenty six species (Borsch et al. 2014) identified as core C_4 *Gomphrena* (see Chapter 3: phylogenetic results); the other six belong to a different lingeage because *Gomphrena* as circumscribed in the catalogue is polyphyletic. Twenty-three species cited in the catalogue of vascular plants of Bolivia (2014) are included in this chapter (tree species missing), seven species accepted here are probably representing new species and there are two former infraspecific taxa that should be recognized as new species.

4.1.1. Material and methodology

The descriptions are organized corresponding to the clades annotated in the phylogenetic trees of Chapter three. The treatment included in this chapter presents the accepted name, synonymy, citation of publication of protologues as well as type information for the respective names (with type localities, collector and number and herbarium where types are deposited). In addition to printed publications the Biodiversity Heritage Library (BHL; https://www.biodiversitylibrary.org) was consulted, as well as the type of specimens visible through JSTOR Global Plants (https://plants.jstor.org), bibliographic citations and species names reviewed at: IPNI- International Plant Names Index, "Natural Museum of Histoire Naturelle" (MNHN), Tropicos- MOBOT.

Descriptions were made on the basis of a defined terminology (see Chapter 2) and precise measurements taken from selected specimens cited as vouchers under the respective description. For the description of habitat and ecology, label information was used from the database of the revised specimens. For the generation of the distribution maps, specimen metadata were used, data which were checked for correct identification (cited under "Specimens examined for distribution assessment) from herbaria of the Bolivian institutions, including the "Herbario Nacional de Bolivia" (LPB), "Herbario Nacional Forestal" (BOLV), "Herbario del Oriente Boliviano" (USZ), "Herbario del Sur de Bolivia" (HSB), the herbarium of the Instituto Darwinion (SI) in Buenos Aires, Argentina, the herbarium of the BGBM Berlin (B), of the Missouri Botanical Garden(MO), the "University of São Paulo (USP)", the Royal Botanic Gardens, Kew (K), and the Friedrich-Schiller-Universität Jena (JE), and the "State University of the Southwest of Bahia" (HUESB). Specimen information for *Blutaparon* was taken from the African Plant Database (CJB) specimens from West Africa. All coordinates were verified by ArcGIS 10.3 program. Records from Australia were downloaded via GBIF from the Australian Herbarium CSIRO, National Herbarium of New South Wales (NSW) in Sydney, the State Herbarium of South Australia Adelaide (AD), and the Northern Territory Herbarium Darwin (DNA).

All the reviewed specimen information was included in an Excel spreadsheet. In the case where the data sets only had locality information, data were completed through a process of georeferencing using in different tools like digitized maps of regions (with departments, provinces, roads) in ArcGIS 10.3 as well as images available through Google Earth. The georeferenced data was recorded in "DECIMAL DEGREES" format. The georeferenced data were then mapped onto a departmental map for Bolivia (see descriptions below). The georeferenced data of Bolivian species grouped according the phylogenetic section were mapped in the ecoregion's layers (Ibisch et al. 2003) (see Fig. 4-1and Table 4-1). In order to obtain climatic data here the Word Clim layers (http: // www. worldclim.org/) were used for maps with each voucher per species considering annual mean temperature (Tp, BIO1, Fig. 4.3), and the annual mean precipitation (Pp, Bio12, Fig. 4-2). The values were extracted of the ArcGIS 10-3 to an excel sheet. The table 4-3 shows the values for each species, including the average, the minimum and maximum values of Tp and Pp. In some species with few specimens only the Min. and Max. of the Tp And Pp are shown. In some species the ranges display big differences depending of the range of distribution. Also the mean temperature driest quarter is included (Fig. 4-4).

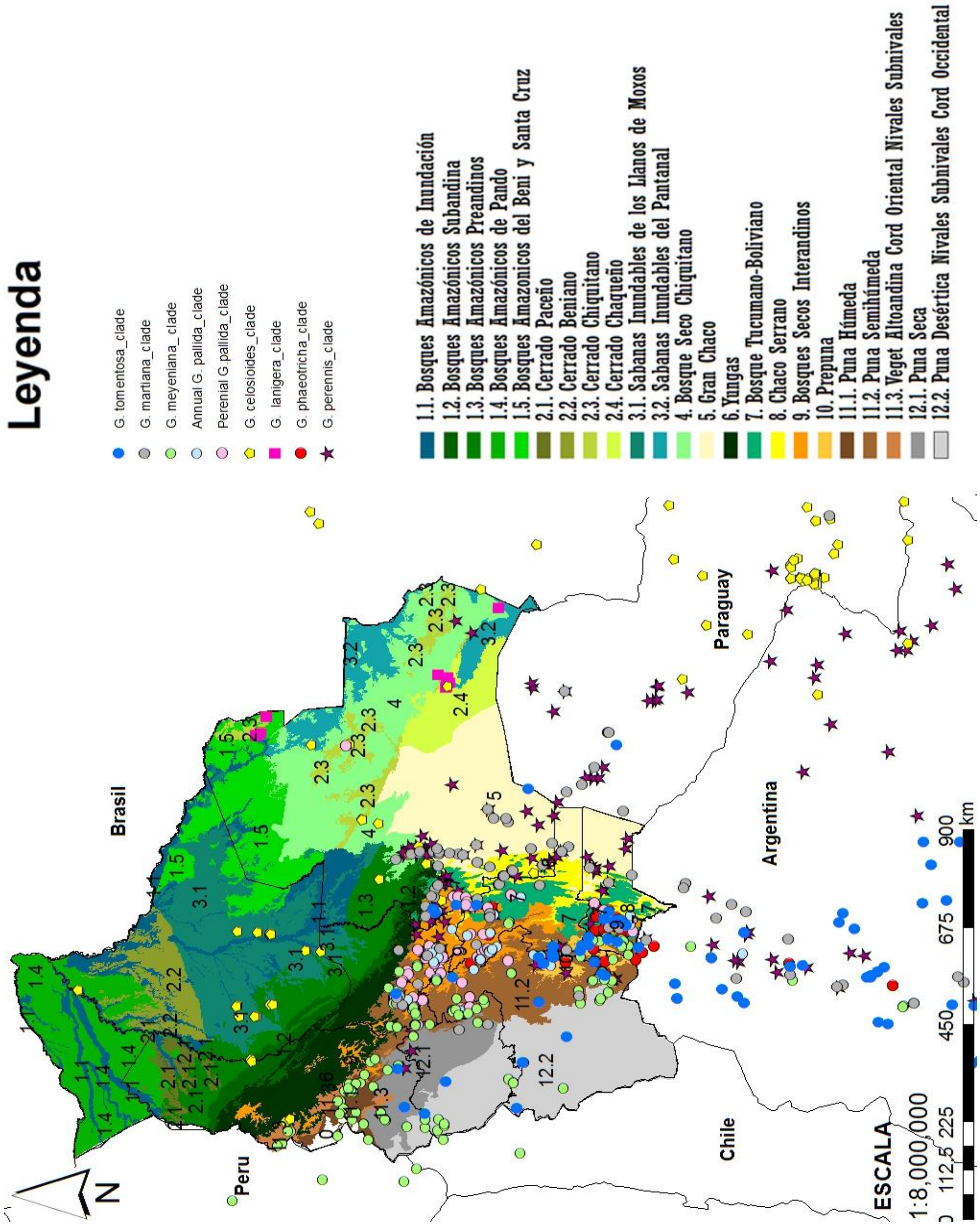


Fig. 4-1. Ecoregion of Bolivia based on Ibisch et al. (2003). From group 1 (see table 4-1), *G. perennis* is rarely found in the pre-Amazonian subecoregions and is common in the Cerrado Chiquitano in the ecoregion Eastern slopes and inter Andean valleys, and sporadically in the subecoregion of the semi humid and dry Puna. While, *G. hankeana* and *G. trollii* are restricted to the ecoregion Eastern slopes and inter-Andean valleys, with some presence of *G. haenkeana* in semi humid and dry Puna. Although, *G. trollii* is common in the Prepuna, climbing to the semihuned Puna. And the from group 3 (see table 4-3), restricted in Bolivia the Cerrado Chaqueño and Chiquitano dry forest subecoregions are *G. agrestis* and *G. cardenasii*, while *G. lanigera* is found in the CerradChiquitano.

4.1.2. *Gomphrena* distribution in Bolivia

Gomphrena species in Bolivia are concentrated in central and southwestern Bolivia, predominately in the ecoregions Semi humid Puna (24 spp.), Inter Andean dry forest (18 spp.),

Prepuna (9 spp.), Dry Puna 6 spp.) along the central Andes reaching the Tucumano Bolivian forest (13 spp.), Gran Chaco in the south and the Chiquitano dry forest in the east. Fig. 4-1 shows the distribution of species grouped in 9 groups and/or clades in 18 subecoregions proposed by Ibisch et al. (2003).

The clade of *G. celosioides* is the only one present in the sub-regions of Lowland, encompassing the pre-Amazonic Forest, through the Cerrado Chiquitano (to the east to the Brazilian Cerrado, Caatinga, Campos rupestres), to the Chaco, this often ruderal species are widely disseminated as ornamental, in the continents of North America, Africa, Europe, Asia and Australia.

The annual species of the group *G. pallida* are distributed throughout the Eastern slopes in inter Andean valleys except in the Yungas (Tables 4-1 and 4-2) and in addition in Semi humid Puna, where *G. sp. nov.* (Spec2) and in dry valleys of the north region of Potosi in Bolivia (*G sp. nov.* Sarijchi) occurs.

The *G. phaeotricha* clade is distributed in the Tucuman Bolivian forest, inter Andean dry forest and Prepuna. On the other hand, new entities (including types of infraspecific taxa '*flexuosa*' and '*calva*') are distributed in the Tucuman Bolivian forest and in the mountain Puna in North Argentina.

The perennial species related to *G. pallida* almost all are present in the semi humid Puna, except the new entity ('*stolonifera*') and *G. stellata* that are in the Chaco serrano and inter Andean dry forest, respectively. *G. fuscipellita* and *G. oligocephala* are found in the southern inter Andean dry forest and in Tucumano Bolivian forest, arriving the second to the closed Chiquitano towards the east.

The clade of *G. meyeniana* is widely distributed in the High mountain Altiplano ascending towards the North West arriving until Peru and Chile, whereas, towards the South it arrives until North Argentina.

From group 8, *G. tomentosa* is widely distributed throughout the Eastern slopes and inter-Andean valleys, except in the Yungas (Tables 4-1 and 4-2) and in the Gran Chaco, while *G. umbellata* grows exceptionally in the semi humid Puna and frequently in Deserted and dry Puna. And the *G. martiana* clade is frequently distributed in Eastern slopes inter Andean valleys in addition to the Chiquitano dry forest and Gran Chaco.

The physiognomy of the vegetation in an altitudinal gradient between 2900 to 4200 m distinguishes the subecoregion inter Andean dry forest. There, *Gomphrena s. str.* (18 ssp.) grows in open places between spinous trees and scrubs such as *Prosopis ferox* Griseb. ("churqui"), *Senegalia visco* (Lorentz ex Griseb.) Seigler & Ebinger and *Prosopis alba* Griseb. (< 2300 m), mixed with the columnar cactus *Neoraimondia herzogiana* (Backeb.) Buxb. (Cactaceae).

4.1.3. Climate and altitudinal range

Most of the inter Andean dry forests are distributed in the center and south of Bolivia. They present a high diversity of endemic species; the formations present valleys more or less dissected and small plains, where the principal vegetation is the deciduous mixed dry forest (10 to 20 m), with trees as of *Schinopsis marginata* Engl. and *Aspidosperma quebracho-blanco* Schltdl., (2300 – 3000 m). Table 4-1 shows the annual average temperature (Tp), for the sub ecoregions is 12 to 16^{a}C with an average precipitation (Pp) of 500 to 600 m (Ibisch et al. 2003).

In the upper part of the scheme, between 3200 and 4200 m a high number of species (24 ssp.) were collected in the SemiHumid Puna. Generally, they grow protected between rocky outcrops close to remnants of forests from different species of *Polylepis* as *P. besseri* Hieron., *P. tomentella* Wedd., scrubs (*Baccharis* ssp, *Parastrephia* ssp.) or small herbs of the family Asteraceae, Rosaceae, Caryophyllaceae, Gentianaceae, Leguminosae, grassland Poaceae, or around an azonal zone of peatlands.

Gomphrena species are common in the dry Puna, between 3500 – 4100 m, the formations present high mountains, and altiplanic plateaus. Vegetation is composed by herbs with resinous shrubs or scrubs (tholares of *Parastrephia* spp., *Fabiana* ssp. *Baccharis* ssp.) mixed with grassland, azonal humid places occurs peatlands usually dominated by Juncaceae. More to the Southwest the desertic Puna is found dominated by prairies or/and shrubs of halophytes and dunes vegetation, where *G. umbellata,* and *G. spissa* grow.

The inferior high Andean vegetation starts from ca. 4000-4100 m between 4500-4600 m, and superior high Andean 4600-5000 m. At this altitude, the formations present valleys with lagoons, slopes, peaks, and rocky peaks. The vegetation grows in fissures in the soil, also there is vegetation of rosette plants such as *G. meyeniana,* and *G. sp. nov.* (*fusci 2*), that are found as herbs in rocky open places, and cushion plants as *Azorella compacta* Phil., and *Pycnophyllum* ssp. The annual mean temperatures are lower than 0-3^{a}C (Ibisch, et al. 2003).

Table 4-1. Ecoregions subecoregions and corresponding, mean annual temperature, precipitations, range altitudinal with the number of the species of *Gomphrena* s. str. The names and the coded for better recognize in the table 4-3 and the document was codified follow Ibisch et al. 2003.

Cod.	Ecoregions	Cod.	Subecoregion	Altitud (m)	Mean Anual Precipitations (mm)	Arid months Per year	Mean annual Temp. °C	Number species
1	Southwest Amazonia	1.1	Bosques Amazónicos de Inundación	1000-4500	100-800-1000	-	2.27	1
		1.3	Pre-andean Amazonian forest	1300->7000	150-500	-	24-28	3
2	Cerrado	2.3	Cerrado Chiquitano	600-2000	120-1000	6-7	21-27	3
		2.4	Cerrado Chaqueño	700-1400	170-1100	6-9	20-26	3
3	Flooded savannas	3.1	Flooded savannas from Llanos de Moxos	1100-5500	100-200	-	22-27	1
		3.2	Flooded savannas from Pantanal	700-1400	100-800	0-5	23-28	1
4	Chiquitano dry forest	4	Chiquitano dry forest	500-2300	100-1400	3-8 (*)	21-28	7
5	Gran Chaco	5	Gran Chaco	400-900	200-600	6-10 (*)	25-26	7
6	Yungas	6	Yungas	1500->2000	3100-3700	3-5	7-24	2
7	Tucuman-Bolivian forest	7	Tucuman-Bolivian forest	700-2000	800-3900	3-5 (*)	5-23	13
8	Chaco Serrano	8	Chaco Serjjj0orano	700-1000	700-1000	6-7 (*)	18-22	7
9	Inter-Andean dry forest	9	Inter-Andean dry forest	500 - 700	2300-3000	6-8	12-16	17
10	Prepuna	10	Prepuna	300-400	2300-3400	8-10	15-17	9
11	North Puna	11.1	Wet (or humid) Puna	500 -1600	3800-4100	5-6	7-9	2
		11.2	Semi humid puna	400-1100	3200-4200	6-7	7-10	24
		11.3	High Andean vegetation from Cordillera Oriental, nival and subnival floors	500 to >1000	4600-5100	2-5	<0-3	2
12	South Puna	12.1	Dry Puna	250-400	3500-4100	6-9	2-7	6
		12.2	Desertic Puna	<50-250	3800-6000	9-10 (12)	0-5	3

(*): Influenced by strong winds from south Influenced by strong winds from south with low Temp

Table 4-2. *Gomphrena* s. str. from Bolivia described in this work with information on the clade groups in which they are classified, including their distribution in ecoregions and sub-ecoregions according to Ibisch, et al. 2003). The ecoregion and sub-ecoregion codes are coded with correspondence to Table 4-2. The abbreviations EN indicates the species to be endemic for Bolivia.

Group	Species	Lowland								East slope InterAndean valleys					High Mountain Altiplano				
		1		2		3		4	5	6	7	8	9	10	11			12	
		1.1	1.3	2.3	2.4	3.1	3.2	4	5	6	7	8	9	10	11.1	11.2	11.3	12.1	12.2
1	*Gomphrena perennis* L.		x	x				x	x		x	x	x	x		x		x	
	Gomphrena haenkeana Mart.							x	x		x	x	x			x		x	
	Gomphrena ferruginea var. *ferruginea* Pedersen										x		x						
	Gomphrena trollii Suess. (EN)													x		x			
2	*Gomphrena phaeotricha* Pedersen										x		x	x		x			
	Gomphrena sp. nov. type b Ortuño & Borsch										x								
	Gomphrena sp. nov. (Spec7) Ortuño & Borsch (EN)												x	x		x			
	Gomphrena nov. comb.(flexuosa=munda) Ortuño & Borsch																		
	Gomphrena nov. comb. (f. calva) Ortuño & Borsch										x								
3	*Gomphrena cardenasii* Standl. ex Holzh. (EN)				x			x											
	Gomphrena agrestis Mart.				x			x											
	Gomphrena lanigera Pohl.			x															
4	*Gomphrena celosioides* Mart.	x	x		x	x	x	x	x	x			x				x		
5	*Gomphrena pallida* (Suess.) Pedersen										x	x	x	x		x			
	Gomphrena mizqueensis Ortuño & Borsch (EN)												x						
	Gomphrena sp. nov. (Spec2a) Ortuño & Borsch (EN)															x			
	Gomphrena sp. nov. (Spec2b) Ortuño & Borsch (EN)															x			
	Gomphrena sp. nov. (Sarijchi) Ortuño & Lluilly (EN)															x			
6	*Gomphrena oligocephala* Remy (EN)			x							x		x			x			
	Gomphrena fuscipellita Ortuño & Borsch (EN)										x		x			x			
	Gomphrena potosiana Suess.et Benl. (EN)												x	x		x			
	Gomphrena bicolor Mart												x			x			
	Gomphrena potosiana (type b) (EN)															x			
	Gomphrena sp. nov. (spec3) Ortuño & Borsch (EN)															x			
	Gomphrena sp. nov. (fusci2) Ortuño & Lliully (EN)															x			
	Gomphrena sp. nov. (stolonifera) Ortuño & Borsch (EN)												x						
	Gomphrena stellata Ortuño & Borsch (EN)											x							
7	*Gomphrena meyeniana* var. *flaccida* Ortuño & Borsch														x	x			x
	Gomphrena meyeniana Walp.														x	x	x	x	x
	Gomphrena meyeniana var. *caulescens* Holzhamm.													x		x			
	Gomphrena *meyeniana* var. *levitepala* Ortuño & Borsch.															x		x	
	Gomphrena meyeniana var. *conwayi* (Rusby). Suess												x			x			
	Gomphrena meyeniana var. *genuina* Stuchlík.																		
8	*Gomphrena tomentosa* (Griseb.) R.E.Fr.								x		x	x	x	x		x			
	Gomphrena umbellata Remy															x		x	x
	Gomphrena radiata Pedersen																		
9	*Gomphrena boliviana* Moq.							x	x		x	x	x						
	Gomphrena boliviana fa. *robusta* (Hicken) Pedersen								x		x			x		x			
	Gomphrena martiana Gillies ex Moq.							x	x		x	x	x	x					
	Gomphrena spissa Pedersen (EN)																	x	

The figure 4-2, 4-3, 4-4 shows the distribution of *Gomphrena* s. str. grouped into nine clades mapped with the layers of the annual mean precipitation (Pp, Fig. 4-2), annual mean temperature (Tp, Fig. 4-3) and precipitation of driest months (BIO14, Fig. 4-4). The table 4-3 shows the minumiun, maximun and average of Tp and Pp. However, the (MDPp) is not included because most of them correspond MDPp data lower than < 100 mm, considering that the values belong to the dry season-winter station (prolonged in some regions more than 6 month, (see table 4-3). The relation within the climate take in count minimum and maximum of the Tp (BIO1) and Pp (BIO12) data and the ecoregions distribution for clade shows that:

The *G. celosioides clade* is found in a wide range of precipitations (591-2850 mm) and temperatures (18-27.1 °C) (see table 4-3), being the only species of *Gomphrena* s. str. in the Amazonian region of Pando, in Bolivia's northern end, at an altitude < 100 m. It occurs also in the Inter-Andean dry forests (2200 m), reaching regions within the semiarid to humid places.

Another species found in a wide altitudinal range (>100-3000 m) is *G. perennis*, where temperatures span from 6.9- 25 °C and precipitations from 400 -1742 mm, being distributed from Chiquitano forest, inter Andean forest, Prepuna up to the Gran Chaco, reach region within the semiarid to humid places. A similar distributional pattern is exhibited by *G. haenkeana, G. martiana y G. boliviana.*

The Gran Chaco, where nine species of *Gomphrena* s. str. were found, has mean annual temperatures spanning from 25 to 30 °C, and maxima may reach 48 °C. In winter there can be freezing temperatures due to the arrival of polar air masses. Most rainfall occurs from October through April, and reaches around 1200 mm. There are important seasonal and daily temperature differences in the Chaco due to its more subtropical location.

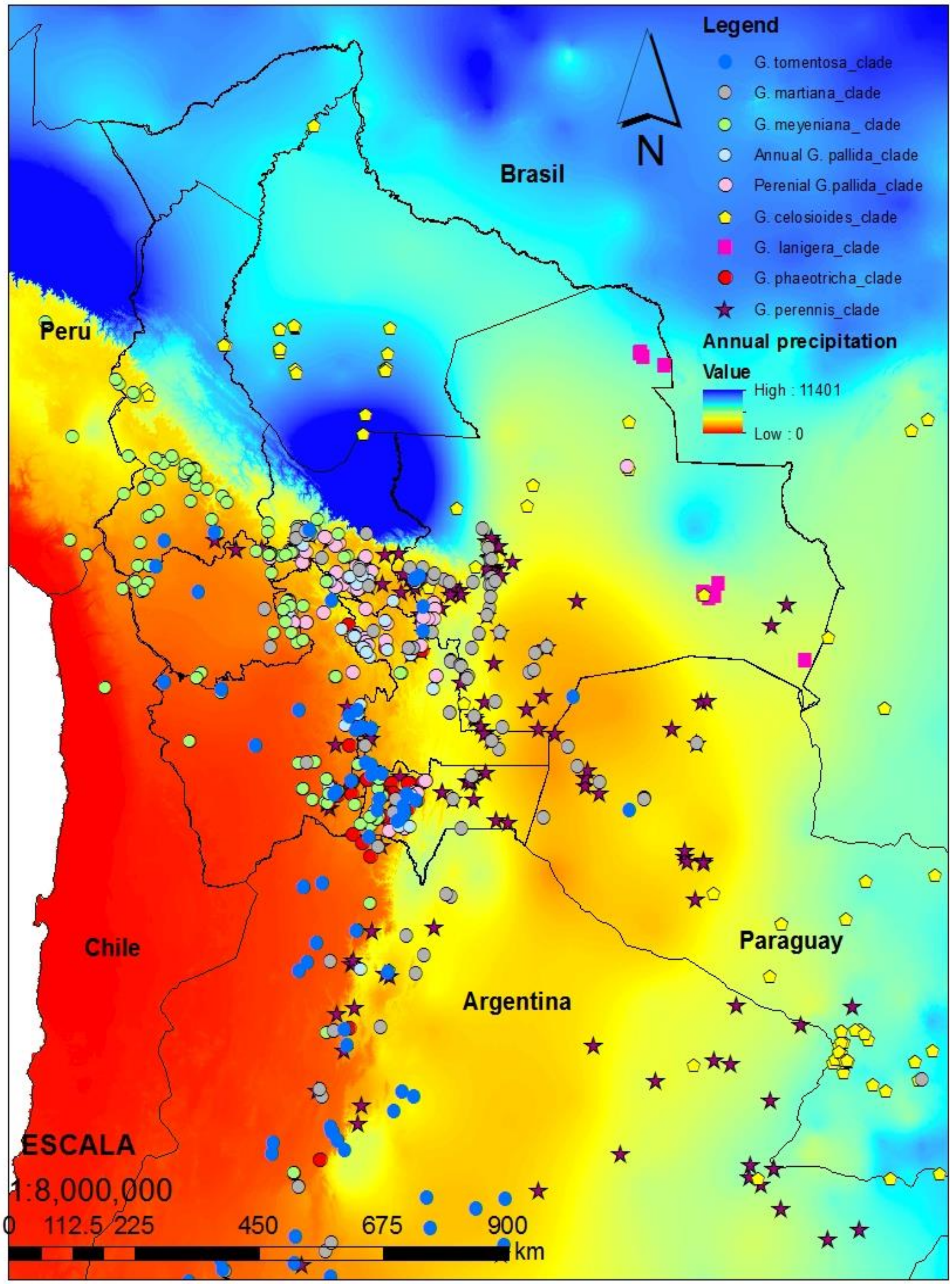


Fig. 4-2. *Gomphrena* distribution superimposed on the map of annual mean precipitation (Pp).

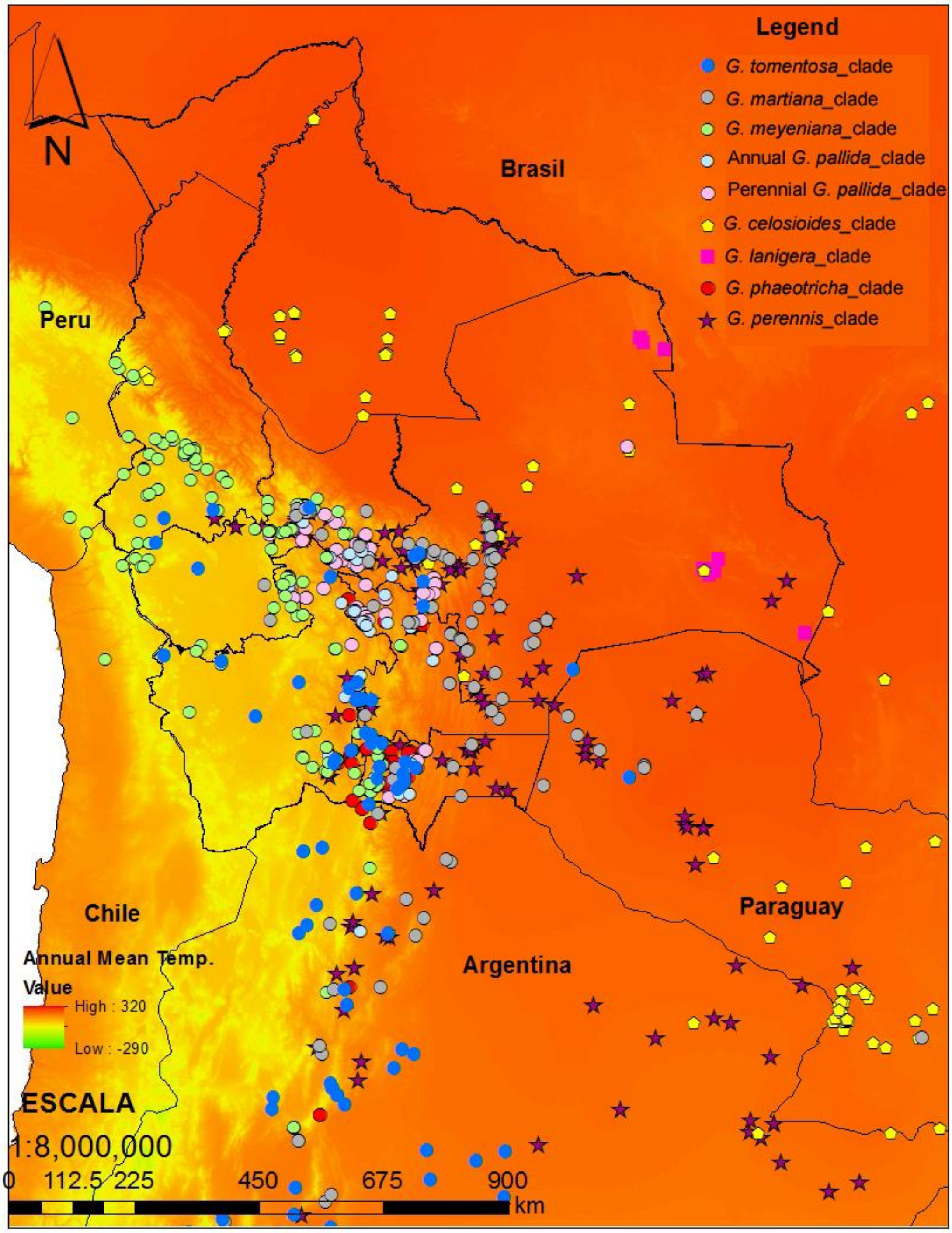


Fig. 4-3. *Gomphrena* distribution superimposed on the map of the annual mean temperature (Tp).

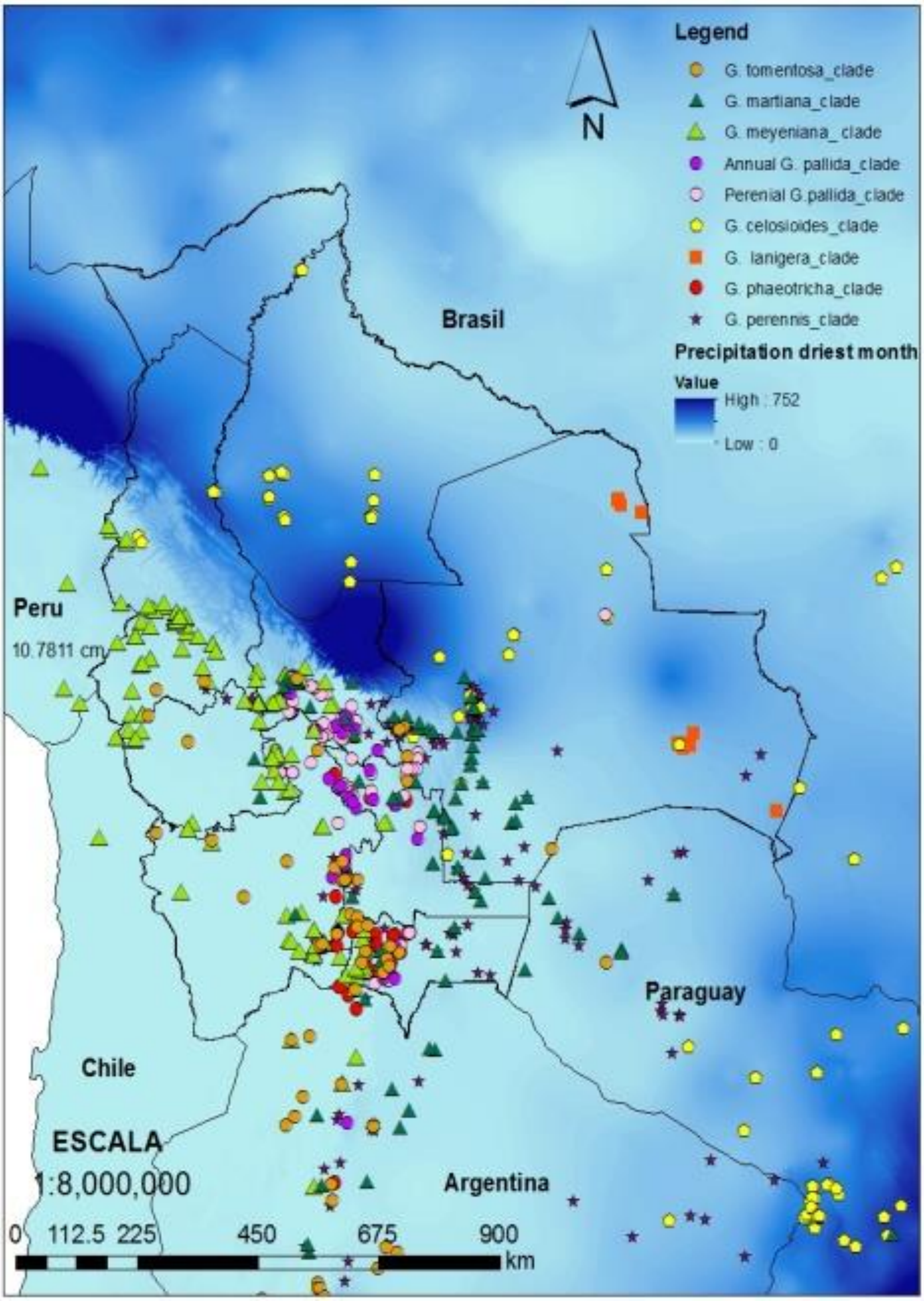


Fig. 4-4. *Gomphrena* distribution superimposed on the map of the precipitación of the driest months.

The species of the *Gomphrena lanigera* clade are restricted to the Chaco Cerrado and the dry Chiquitos forests ecoregions. The minimum and maximum ranges of the mean annual temperatures where the species are collected fluctuate between 16 and 25 °C based on Min and Max Tp (Word Clim data). However, the temperatures in the regions are quite uniform during the year except when polar masses arrive in winter. The rain shows more variability with a greater rainfall in the more septentrional localities. Observing the NE places where *G. lanigera* was found, range varies from Pp Min. 1400 Pp Max. 1500 mm, whereas *G. cardenasii*, collected more to the south, is found in localities where there are wider ranges of Pp Min. 1000 in the dry season and Pp Max.1100 mm in the humid season.

The distributed sections of *Gomphrena* s. str. are in the central part of the Eastern Cordillera, extending south along a continuous corridor in the Andes, where we find the inter-Andean dry forests, the semi-humid Puna, the Tucumano Boliviano forest and the Chaco; and more to the west there is the Dry and Desert Puna. Except the Tucumano Boliviano forest, more of these regions are characterized by having low rainfall (arid- semiarid regions, Fig. 4A, table 4) especially during the driest month of precipitations (Fig. 4C), and several dry months during the year, which are more intense towards the west.

The *G. phaeotricha* clade is frequent between 2000-3600 m. including *G. sp. nov (type b)* and restricted to the Tucumano-Bolivano forests, where yearly rainfall exceeds 1500 mm and mean temperatures span from 14 to 20 degrees Celsius. In winter, polar air masses may cause freezing temperatures during some days. *Gomphrena phaeotricha* has a wider environmental range. It may be found in the semi or wet Puna, with precipitations around 500 700 mm and mean temperatures of (6-9) 12-16 °C depending on altitude and ecoregions, more common in the Semi humed Puna, Tucumano boliviano forest, rarely collected in dryest region as the Prepuna. However the *G. spec. 7 nov.* was frequently collected in the arid ecoregion of Prepuna where the rainfall is around 300 mm (8-10 dry months per year); and in the semiarid Puna with mean temperatures of 7-10 °C and rainfall of 300-400 mm per year (2-5 dry months per year).

In group 5, the *G. pallida* samples and relatives show a similar distribution pattern as that of *G. phaeotricha*. *Gomphrena mizqueensis* is restricted to the Inter-Andean Dry Forest, and was collected in regions with mean temperaturas between 12.3 – 19.7, and precipitationss < 700 mm. Likewise, the *G. sp. 2 nov.* is found mainly in the Semi-humid Puna, between 3400 and 3600, with lower mean temperatures (10.8-12.7 °C).

Table 4-3. Species of *Gomphrena* s.str. and their occurrence at altitudinal ranges, at the minimum and maximum range of the annual mean temperature (Tp), and precipitation (Pp) (+ the mean data). The values were extracted of the WordClim web page.

Group	**Species**	**Altitud (m)**	**Annual mean Temp. (Tp) Min..- average- Max. (ºC)**	**Annual Mean Prec. (Pp) Left Min. - average - Max. (mm)**
1	*Gomphrena perennis* L.	121-2900	6.9 - 20.6 - 25.3	400- 850 -1742
	Gomphrena haenkeana Mart.	320 – 3103	5.9 - 24.4	400 - 650 -1200
	Gomphrena ferruginea Pedersen	1600 – 2650	13.1 - 15 - 17.8	371 - 517 - 661
	Gomphrena trollii Suess.	2700 – 3920	9.9 - 13.3 -14.8	217 - 300 - 440
2	*Gomphrena phaeotricha* Pedersen	2100 - 3600 (4000)	(6.9) 10 -14.5 -17.5	400 - 485 -733
	Gomphrena sp. nov. type b Ortuño & Borsch	2094 – 3200	15 - 17 -19.6	530 - 600 - 750
	Gomphrena sp. nov. (Spec7) Ortuño & Borsch	2400 – 3700	9.9 - 13.2 - 22.4	217 - 360 - 900
	Gomphrena nov. comb.(flexuosa=munda) Ortuño & Borsch	3400 – 3600	10.5	330
	Gomphrena nov. comb. (f. calva) Ortuño & Borsch	2700 – 3200	15	500
3	*Gomphrena cardenasii* Standl. ex Holzh.	300 – 660	22.7 - 24 - 25.4	1000 - 1120 -1170
	Gomphrena agrestis Mart.	140 – 868	16 - 21.4 - 27	1000 - 1100 - 1700
	Gomphrena lanigera Pohl.	300 – 955	16 - 20.7 - 22	1400 - 1450 - 1500
4	*Gomphrena celosioides* Mart.	140 - 2250	18.0 - 22.7 - 27.1	519 - 1356 - 2850
5	*Gomphrena pallida* (Suess.) Pedersen	1207 - 3400	12.3 - 16.2 - 21.5	261 - 560 - 910
	Gomphrena mizqueensis Ortuño & Borsch	2130 - 3200	15.9 - 17.2 - 18.7	509 - 600 - 720
	Gomphrena sp. nov. (Spec2a) Ortuño & Borsch	3400 - 3500	10.8 - 11.4 - 12.6	500 - 555- 600
	Gomphrena sp. nov. (Spec2b) Ortuño & Borsch	3400 - 3600	10.8 - 11.4 - 12.7	500 - 601
	Gomphrena sp. nov. (Sarijchi) Ortuño & Lluilly	2800	-	-
6	*Gomphrena bicolor* Mart	1900 - 3900	6.7 - 12.5 - 19.4	398 - 670 - 989
	Gomphrena oligocephala Remy	400 - 3900	9 - 15.8 - 23.4	450 - 700 -1100
	Gomphrena fuscipellita Ortuño & Borsch	2280 - 3400	11.6 - 15.6 - 18.1	477- 620 - 703
	Gomphrena potosiana Suess.et Benl.	3350 - 3900	9.8 - 11.8 - 15.9	281- 400 - 445
	Gomphrena potosiana type a	3300 - 3450	7.3 - 11.6 - 15.9	301- 667
	Gomphrena sp. nov. (spec3) Ortuño & Borsch	3600 - 3700	10.7	580 - 600
	Gomphrena sp. nov. (fusci2) Ortuño & Lliully	3600 - 4300	7.6 - 13.5 - 17.6	330 - 542 - 672
	Gomphrena sp. nov. (stolonifera) Ortuño & Borsch	2200 - 3000	14 - 16 - 20	500 - 600 - 750
	Gomphrena stellata Ortuño & Borsch	1100 -1400	22 - 21.2 - 22	520 - 620 - 740
7	*Gomphrena meyeniana* var. *flaccida* Ortuño & Borsch	3200 - 4300	5.7 - 12.8	260 - 700
	Gomphrena meyeniana Walp.	3400 - 4700	4.9 - 7.9 - 13.6	96 - 400 - 800
	Gomphrena meyeniana var. *caulescens* Holzh.	3400 - 4000	9.3 - 12.8	163 - 380
	Gomphrena *meyeniana* var. *levitepala* Ortuño & Borsch.	3200 - 4200	6.5 - 13.8	<100 - 500
	Gomphrena meyeniana var. *conwayi* (Rusby). Suess	3800 - 3900	8.6 - 10.3	670 - 700
	Gomphrena meyeniana var. *genuina* Stuchlík.	3500 - 4600	4.1 - 10.8	500 - 800
8	*Gomphrena tomentosa* (Griseb.) R.E.Fr.	250 - 3600	9.9 - 16.6 - 24.9	128 - 470 - 850
	Gomphrena umbellata Remy	2800 – 4000	7.6 - 9.9 - 15.2	150 (300) - 370 - 700
	Gomphrena radiata Pedersen	2850 - 3660	7.7 - 12.8 - 20	126 - 274 - 619
9	*Gomphrena boliviana* Moq.	200 - 2800	15.4 - 21.4 - 24.9	96 - 500 -1108
	Gomphrena boliviana fa. *robusta* (Hicken) Pedersen	2000 - 2100	16.3 - 17.5 - 24.5	808 - 995 -1200
	Gomphrena martiana Gillies ex Moq.	300 - 2800	4.4 - 20 - 25.1	158 - 750 - 1100
	Gomphrena spissa Pedersen	3700-3770	8.3 - 9.3 - 10.3	292 - 300

The species of clade 6, *G. bicolor*, *G. sp. nov.* (‘*stolonifera*’), *G. fuscipellita, G. oligocephala*, are frequent within a temperatura range of 7-23 °C, and rainfall between 300-

700-1000 mm. They are found in the Inter-Andean Forest and the Semi-humid Puna, between 1900-3900 m. *Gomphrena sp. nov. (fusci 2)* grows in the Semi-humid Puna, at greater altitudes than the other species in the clade (3600-4300 m), in fissures among rocks where few species survive. *Gomphrena sp. Spec3 nov.* has been collected few times in rocks in the Chataquila region (Chuquisaca), with mean temperaturas of 10-11 °C and precipitations of 500-600 mm (semiarid regions). *G. stolonifera* is restricted to areas with Sandy soils and/or near *Polylepis* forest remnants in high places of Puna around the Inter-Andean Dry Forest.

The *G. meyeniana* clade, widely distributed in the Altiplano, reaches altitudes of 3200-4600 m, the hitherto only specieswith C4 photosynthesis known as growing in this altitude (Sage et al. 2007). The new data in this thesis show that *sp. nov. (fusci 2)* reaches a similar high altitude. But *G. meyeniana* is the only species frequently found along the Eastern and Western Cordilleras, from semiarid (to arid) places in the southern Desert Puna were the minimum Pp possible precipitation is < 100 mm; around of the Salar Uyuni, to semi-humid localities in the Humid Puna (around Titicaca Lake, Tunicondoriri, and Pampalarama, with 800 mm). Fluctuations of temperature are high extremely high during the day, and temperatures reach less than zero degrees during the night. Some varieties are more restricted to certain environments, such as *G. meyeniana* var. *caulescens*, collected in the Chaco Serrano and the Semi-humid Puna, and *G. meyeniana var. conwayi*, collected only in the inter-Andean valleys.

The Group 8 shows that *G. tomentosa* has a wide distribution in SW Bolivia, Northern Argentina, and Eastern Paraguay, between 250 - 3600 m. It is frequent along the Eastern slopes of the inter-Andean valleys, the Prepuna, reaching to the Gran Chaco, with a Tp Min., average and Max are in the range between 10-16-24 °C respectively, and rainfall between 128 – 400 - 800 mm in arid to semiarid regions. *Gomphrena umbellata*, growing between 2800- 4100 m, is restricted to sandy environments of the dry Puna and Desert Puna, and collected only in the rainy season (annual habit). It lives in places with Tp Min., average and Max between 7.6-9.9- 15.°C, and precipitations between 150- 300- 700 mm. In this study also is included *G. radiata* collected in dry Puna of Argentina close to Bolivia with Pp. 120 -270-600 mm.

Based on the distribution of *Gomphrena* s. str. (Fig. 4 A, B, C y table 4), it is evident that the preference of these species is for environments with low rainfall and high temperatures (such as the Chaco), especially during mid day, but plants can be also exposed to cold related to "surasos" influenced by strong winds from south, and "helada" low temperatures during the night especially in winter. Many of the species are hemicryptophytes or annuals, and flowers appear only in the humid season, as a strategy of survival in arid and semiard environments. It is important to say that in the Inter-Andean Dry Forests located in the north (around La Paz city), *Gomphrena* s.str. is absent, except for *G. meyeniana* (Fig. 4-1).

4.2. Description of the genus *Gomphrena* s. str. as found in Bolivia

Gomphrena L., Sp. Pl. 224 (1753); Gen. Pl. ed. 5:105 (1754).
Lectotype: *G. globosa* L. (fide Hitchcock & Green, Ramsbottom et al., Int. Bot. Congr. Cambridge (England), 1930, Nomenclature, Prop. British Bot. p. 137 (1929). (HMSO: London).
≡ *Coluppa* Adams. Fam. Pl. (Adanson) 2: 268. 1763.
≡ *Gomphraena* Jacq. Select. Am. 88 (1763).
= *Bragantia* Vand. Flora Cochinchinensis 517, 528. 1790. (Sep 1790)
≡ *Wadapus* Rafin. Fl- Tellur. 3:77. 1836.
= *Ninanga* Rafin, Fl. Tellur- 3:76.1836
Lectotype: Illustration in Dillenius, Hortus Elthamensis 24.t.20.f 22, based on a plant from "Bonarea" (Designated by Mears in 1980: 86
≡ *Xeraea* (L.) Kuntze, Rev. Gen. Pl. 2: 545 (1891) nom. illeg.
= *Choanthus* Phil. Anal, Univ. Chile 2:404.1862
Type: Mendoza, Diaz W s.n. (HT: SGO SGO000001667).

Habit annual or perennial herbs or subshrubs. ***Root*** fleshy, fibrous, Taproot stolon, adventicious. ***Stems*** prostrate, decumbent or erect; unbranched or as secondary, tertiary or quaternary branched system, with or without determinate growth stems, the branches firm or voluble and thin consistence; trichomes multicellular, uniseriate, appressed, indumentum villous, lanate, or hirsute or glabrous, colour of trichomes yellow, light to dark brown; indumentum usually denser close to the nodes and inflorescence. ***Basal leaves*** present or absent, lanceolate, linear or ovate – lanceolate, usually sessile or decurrent in the stems, middle nerve prominent, acute or acuminate at apex, glabrous, trichomes usually denser in the abaxial side of leaves, the indumentum and type of trichomes similar than on the stems. ***Cauline leaves*** sessile, opposite, ovolanceolate to elliptic, ovolanceolate to oblong or linear lanceolate in shape, acute and mucronate at apex, cuspitate, acuminate, margin generally entire, dark or pale green, trichomes present or glabrous, indumentum and type of trichomes similar than on stems. ***Small leaves*** usually present in perennials (i.e. a short shoot with two or four small leaves develop in one leaf axil (e.g. in *G. perennis*). ***Apical leaves subtending the paracladia*** (inflorescence) absent or present. If present, 2-4-5 or 6 leaves, usually sessile. Either similar in shape to cauline leaves, or different and then usually stellately arranged, modified to pseudantial leaves arranged in a whorl or two opposite unspecialized, glabrous or with the trichomes, indumentum differentiated between the adaxial and abaxial leave surfaces, trichomes white, light to dark brown, usually denser in the abaxial surface of leaf blade and in the margin. ***Infloresecence*** globose or elongate, terminal or axillar. ***Arrangenent of paracladia*** solitary and terminal on lateral branches (as *G. celosioides*); solitary with paracladia in the axes of the cauline leaves and leaves in terminal parts of major branches of the plant (there can be both elongated and reduced axes bearing paracladia in a single leave axil in *G. tomentosa*); strongly condensed in a way that multiple paracladia appear in a terminal whorl-like structure consisting in 3 - 5 (--6) partial florescences, individual paracladia without visible inflorescence axes (e.g. *G. pallida*, *G. haenkeana*). ***Flowers*** solitary and supported by one bract and two bracteoles. ***Bract*** ovate or linear-lanceolate, elliptic to oblong, ovolanceolate or suborbicular in shape, usually cymbiform, but some appearing like envelopes (e.g. *G. tomentosa* clade), acuminate, acute, rounted, semifornicate at apex; margin entire, dentate or undulate, membranous, fine membranous, texture chartaceous or papyrous, white, light to dark brown (e.g. *G. bicolor*, *G. spec. 2 nov.*) rarely green (*G. umbellata*); trichomes present (*G. tomentosa*) or absent (most the species), a very small crest in some species (e.g. *G. pallida)*. ***Bracteoles*** ovolanceolate, ovate to orbicular or linear, suborbicular, apex acute, apiculate or rounted to spatulate, membranous texture, usually, white opaque or translucent color, only *G. sp. spec3 nov.* with dark brown in the apex. External dorsal crest present, varies in size and shape depending of the species (e.g. short at the apex in *G. potosiana*, or broadly winged in *G. phaeotricha*), generally toothed at the margin. ***Tepals*** always differing in two external, one intermediate, and two smaller ones, becoming coriaceous in middle part at maturity; linear oblong, lanceolate lanceolate narrow in the middle part, spathulate in shapes. Membranous, fine menbranous or chartaceous in texture, apiculate, acute or rounded at apex. White to light yellow, yellow, light brown, or dark pink (*G. haenkeana*), purple (*G. trollii*); glabrous or with all the tepals with trichomes in dorsal part, and at the margin. The external tepals glabrous and the inner with trichomes, or vice versa. ***Androceum** with* filaments united more or less into a tube, at the apex with a free portions of the filament. These free parts are variable and may lack or posess filament appendages. ***Filament appendices*** located terminally in the free part on each side of the filament, variable in size and form depending of the species. ***Anthers*** unicular, oblong, attached in different ways, i) between the filament appendices, ii) sunken between two filament appendices, iii) alternanting with appendices (*G. canescens*). ***Gynoecium*** with two filiform branches, the size of branches varies depending on the species, similar than the style that varies in length depending on the species; the ovary is globose or sometimes elongate but always with only one ovule. ***Fruit*** a dry utricule, in sizes of approximately 1-1.5 mm, brown color.

Micromorphology of trichomes. Always multicellular uniseriate, not dendritic, candelabriform with or without division. On ***sterms and cauline*** leaves with 1-2 strong and conspicuous basal cells, firm to collapsed consistency, usually the first rounded the second straight, cylindrical, flat or with ornamentation, with the ornamentation either spinous, granulate or salicose. The 4-6 upper cells of trichomes with firm consistence, salicose, spinous ornamentation, the cuticle walls striate in ornamentation. ***Interlocking junctions*** conspicuous in the case of firm trichomes, variable in linear projection and overlapping in both extreme border cells from displaying a zero angle in the scars or the linear scars reach > 45° in angle, sometimes the spines are divided in two branches in the apex. On ***apical leaves subtending paracladia*** the trichomes in some species show differences between the adaxial and abaxial surface, usually the abaxial are similar with the stems and cauline leaves, they vary in several species with the colours more dark, and higher in density.

In the first clade, two species show short trichomes with a maximum of two elliptical upper cells; in the second clade short trichomes with two or three straight cells are detected, this character does not belong only to this clade but also *G. perennis* and *G. ferruginea* present it. Other characteristics of the Andean species are adaxial leaves that are glabrous for example in *G. haenkeana* and *G. phaeotricha*. Trichomes on ***tepals*** with 1 or 2 basal cells and firm consistence, the upper collapsed, sinuous, in some species cells twisted and a little more hirsute as in *G. lanigera*.

Anatomy of tepal tissues. Composed of elongate straight, cylindrical fiber cells, arranged in one row, all-fitting perfectly, the fiber cells form a tooted irregular margin. This a pattern first described here and this characters may be a synapomorphy in *Gomphrena* s.str.

Pollen. Always metareticulate, pore number and sizes variable, the apertures with ektexinous bodies arranged concentrically in a mosaic-like pattern. Tectum reduced to a distal band in the mesoporia, tapered, the proportions depend on the species, building hexagons and pentagons most the species have acute (sharp) angle corner. ***Tectum*** with columellae in the lower near the middle of the vertical part, arranged around the pore the number and wide and proportions of columnella are variable. The ornamentation of the tectum usually without microspines, or only very small projections are present at the connecting points of mesoporia.

Comment on the taxon concept used here. The limits of the genus *Gomphrena* as used here are based on the results in Chapter three and constitute a monophyletic genus. However, the description was derived from the species present in Bolivia and therefore the overall variation including coastal and Australian species may be greater.

4.3. Treatment of the taxa within *Gomphrena s.str.* as currently accepted to occur in Bolivia

4.3.1. Key to all taxa

I. Plants decumbent to erect. Bracteoles smaller than the tepals. (1)

I' Plants decumbent, prostrate or erect usually < 40 cm. Bracteoles of the same size than tepals or bigger. (VI)

II. Plants with bracteoles with crest near the dorsal apex (in the exceptions with fleshy dorsal middle nerve (*G. trollii*), tepals chartaceous to membranous); with conspicuous filament appendages. (III)

II' Plants with bracteoles without crest, tepals membranous. (IV and IV')

III. Plants with cauline leaves lanceolate to elliptic lanceolate, between 0.7- 2.5 (--4.5) cm long. Filament appendages conspicuous lanceolate between 0.5 -0.8 or 1.2-1.5 mm.

....***G. perennis and allies***

III' Plants with cauline leaves lanceolate (0.8.-1.7 cm) to linear or ovate lanceolate (1.4-4.5 cm) only (*G. agrestis*), filament appendages smaller, conspicuous, between 0.2-0.3 .... ***G. lanigera* CLADE** (4)

1. Perennial plants, > 30 cm in the range up to 100 cm, taproot fleshy or/and woody. (2)

1'. Annual plants, >14 cm the range up to 50 cm, roots fibrous, cauline leaves elliptic lanceolate (3)

2. Cauline leaves ovolanceolate. Tepals white, membranous in texture, bracteoles with short crest that reaches a quarter of of the dorsal part from the apex on middle nerve.. *G. perennis* (Fig.4-5)

2' Cauline leaves linear lanceolate. Tepals intensely purple, chartaceous in texture, bracteoles without crest, only middle nerve broadened ....*G. trollii* (Fig. 4- 11)

3. Apical leaves subtending paracladia (inflorescence) ovolanceolate 0.5(--1) x 0.4(--0.6) cm, tepals fine membranous in texture, white. ....*G. ferruginea* (Fig. 4-8)

3' Apical leaves subtending paracladia (inflorescence) cordate-lanceolate 0.4-0.7 (--0.9) x 0.4-0.6 (--0.8) cm, chartaceous in texture, pink. .... *G. haenkeana* (Fig. 4-13)

4. Plants erect to < 15 cm, all covered with long hirsute indumentum, inflorescence 3.2-3.3 (--4) cm in diameter, apical leaves subtending the paracladia lanceolate to linear..*G. lanigera* (Fig. 4-29)

4' Plants erect to decumbent > 30 cm until 100 cm, with appressed to villous indumentum, inflorescence 1-1.3 cm in diameter (5)

5 Plants with only basal leaves, ovate lanceolate, 2.5-4 (--12) x 0.6- 2 (--3) cm, apical leaves subtending inflorescences, 2-5 leaves arranged symmetrically, cordate to ovate, 0.5-0,8 (--1) x 0.4
(--0.8) cm, acute at apex ....*G. agrestis* (Fig. 4-33)

5'. Plants with cauline leaves oblong lanceolate, 1.5 (--1.7) x 0.5 (--0.7) cm, acute mucronate at apex, inflorescence subglobose, apical leaves subtending inflorescences, cordate to-ovate, 0.5-0.6 (--1) x 0.3 (--0.5) cm, acuminate apex .... *G. cardenasii* (Fig. 4-31)

IV. Stems with always with secondary or tertiary branches, with basal leaves in rosette or not. (V)

IV'. Plants unbranched, stems decumbent to erect or without stems, always with basal leaves in a rosette. ....**G. *meyeniana* CLADE** (12)

V. Plants with prostrate stems, bracteoles and bract orbicular, spatulate usually with rounded or undulate apex... **G. tomentosa CLADE** (6)

V' Plants decumbent to erect, bracteoles and bract ovolanceolate to oblong lanceolate with acute apex .... **G. martiana and G. boliviana CLADE** (9)

6. Perennial plants with taproot, fleshy. Plants with indeterminate type of growth. (7 and 7')

6'. Annual plants with fibrous root. Plants with determinate type of growth. (8)

7 Flowers 4.8-5 mm long. Bract rounded-ovate and bracteoles ovate- lanceolate, covered with tomentose trichomes at the apex on the dorsal part ....*G. tomentosa* (Fig. 4- 81)

7' Flowers 1.4-2 (--2.4) mm of long. Bract and bracteoles ovate, roundish to spathulate, without trichomes .... *G. radiata* (Fig. 4- 86)

8. Flowers 1.4-2 (--2.4) mm long. Stems prostrate, always with tertiary and quaternary stems, terminating in a radial umbrella-like structure.........................*G. umbellata* (Fig. 4-83, 4-84).

9. Plants with stems decumbent to prostrate, < 20 cm usually 7 to 15 cm... *G. spissa* (Fig. 4-92)

9'. Plants with stems decumbent to erect, ramose > 40 cm to 150 cm (10).

10. Plants with basal leaves, apical leaves subtending the paracladia shorter than the inflorescence, with the bract only extending to less than the middle half of the bracteoles ....*G. martiana* (Fig. 4-83).

10'. Plants without basal leaves, apical leaves subtending the paracladia bigger than the inflorescence. Bract longer than the half of the length of the bracteoles (11 and 11')

11. Flowers with the all tepals with indumentum .... *G. boliviana* (Fig. 4-91)

11'. Flowers with the outer tepals without indumentum, but inner tepals with dense trichomes.

.... *G. boliviana* fa. *robusta*

12. Terminal inflorescence on short stems without cauline leaves. (13)

12'. Terminal inflorescence (paracladium) on stems with cauline leaves. Tepals all with indumentum in the dorsal part in all the tepals or only in the inner (15)

13. Tepals all glabrous .... *G. meyeniana* (Fig. 4- 72)

13'.Tepals with indumentum in the dorsal part (14)

14. All the tepals with lanate indumentum in dorsal part .... G. *meyeniana* var. *genuina*

14'. Only the inner tepals with indumentum in the dorsal part .... G-*meyeniana* var. *conwayi*

15. Stems decumbent to ascendant, stems voluble to flaccid, opposite cauline leaves ovolanceolate (16) .... *G. meyeniana* var. *flaccida* (Fig. 4-72)

15'. Stems erect, consistence firm, cauline leaves lanceolate to linear .... *G- meyeniana caulecens* (Fig. 4-77)

16. Only the inner tepals with indumentum in the dorsal part .... *G. meyeniana* var. *levitepala* (Fig. 4-76)

VI. Plants always annual, teplas without trichomes in the margin, or few in the dorsal part, the inner tepasl smaller than the outer .... **G. *phaeotricha* CLADE (17)**

VI'. Plants annual or perennial, tepals with trichomes at the margin, (exception *G. potosiana*), or few trichomes in the dorsal part, margin deeply dentate (21)

17. Tepals completely glabrous. Bracteoles with widely prominent crest extended on all the dorsal part of the middle nerve. (18)

17' Tepals with trichomes on the inner tepals or in the dorsal part but never in the margin, anther appearing united between filament appendices (19)

18. Anther appearing sunken between two filament appendages. Inner tepals much shorter than the external tepals, glabrous. Trichomes light brown to dark brown... *G. phaeotricha* (Fig. 4-17)

18'. Anther united between filament appendages, crest extended narrowly along all the bracteole ....*G. sp. nov.* *(*Fig.4- 26*)*

19. All the tepals with trichomes in the dorsal part, dentate on the bract at apex (20)

19'. Inner tepals with trichomes in dorsal part. The apical leaves subtending the paracladia ovolanceolate to cordate, acute at apex, smaller than the inflorescence and glabrous. ....*G. sp. nov (type b)* (Fig., 4-19)

20. Voluble and thinly branched stems. The apical leaves subtending the paracladia with trichomes in the adaxial part with two ovate to elliptic and broad interlocking junctions... *G. sp. nov. (flexuosa)* (Fig. 4- 24)

20'. Stems with firm consistence. The apical leaves subtending the paracladia on the adaxial surface covered with short trichomes ovate to elliptic in outline, and narrow interlocking junctions .... *G. sp. nov (spec7)* (Fig., 4-21)

21 Plants annual ....**annual *G. pallida* CLADE** (22)

21' Plants perennial with stolons or taproots.......................... **perennial *G. pallida* CLADE** (26)

22. Plants 5 - 20 (--40) cm tall, stems decumbent to ascendant or erect, with firm consistence, and secondary or tertiary branches. Terminal inflorescence usually more than >1.5 cm (but in the range of 0.7-2.5 cm) in diameter. (23)

22'. Plants usually not more than 15 cm tall, mostly <10 cm, decumbent to erect, with secondary or tertiary stems branched. Terminal inflorescence usually more than <1.1 cm in the range of 0.7-1.1 cm in diameter (24)

23. Tepals lanceolate narrowly at middle part (unguiculate), dentate in the margin, trichomes of the stems and cauline leaves with or light yellow. Anther inserted between the filament appendages………………………………………………………….… *G. pallida* (Fig.4- 39, 4-40)

23'. Tepals lanceolate to spathulate, deeply dentate especially at the apex, trichomes of the stems and cauline leaves with light to dark brown, darker especially near the inflorescence. Anther appears sunken between the filament appendages..…..………*G. mizqueensis* (Fig.4- 42)

24. Cauline leaves lanceolate to cordate, light to dark green marmorated color, acute at apex, all the leaves with scarce villous indumentum, usually glabrous, bract semiforcate (more broad at the apex). Anther appears sunken between two filament appendages. (25)

24'. Cauline leaves ovolanceolate, light green in colour, apiculate and mucronate at apex, covered with homogeneous indumentum, the apical leaves with short trichomes (2-3 cells) hirsute. Anther united between the filament appendages ……..………… *G. sp. nov. (sarijchi)* (Fig.4- 48)

25. Stems decumbent to erect, trichomes light to dark brown to black, (Toro Toro) ………………………………………………………………… *G. sp. nov (spec2 a)* (Fig.4-44)

25' Stems decumbent to ascendent, trichomes white (Chataquila)...*G. sp. nov. (spec2 b)* (Fig. 4-46)

26. Plants connected to the main stolon, root woody, basal leaves in a loose rosette, erect, stems unbranched ………………………………………………*G. spec. nov. stolonifera type* (Fig. 4-62)

26'. Plants with fleshy or/and woody taproot. (27)

27. Tepals ovolanceolate without trichomes at the margin and the dorsal part, bracteoles crested for 15% near the apex of the dorsal part or without crest ………….. *G. potosiana* (Fig. 4-55)

27'. Tepals with trichomes at the margin and with or without crest in the dorsal part. (28)

28. Anther attached between the filament appendages. (32)

28' Anther attached between two filament appendices, sunken. (31)

29. Trichomes on the cauline leaves light yellow or white. (30)

29' Trichomes on stems close to the inflorescence and in the cauline leaves white to light brown, brown or dark brown. (31)

30. Bracteoles with toothed crest for about 20%, bract membranous ovate, acuminate at apex, white and white membranous…………………………………...*G. oligocephala* (Fig.4- 53)

30'. Bracteoles with crest for the half, crest abruptly widened to the apex of bracteole and dentate, bract ovate, membranous, acute at apex. . …………………… *G. stellata* (Fig. 4-64)

31. Bract ovate, texture membranous, acuminate at apex, cream at the base dark and brown at the apex, sometimes with trichomes near the apex. Trichomes in the stems, and in the margin and nerve of the cauline leaves appressed to villous. ………………………… *G. bicolor* (Fig.4-51)

31' Bract ovate lanceolate, membranous, acute apex, white, trichomes in the stems, and in the margin and nerve of the cauline leaves hirsute indumentum.........G. sp. nov. (fusci2) (Fig.4-68)

32. Trichomes white, cauline leaves ovolanceolate with appressed trichomes, tepals ovolanceolates
....*G. potosiana* (a)

32' Trichomes with color indumentum of the stems hirsute and margin cauline leaves hirsute, Apical leaves subtending the paracladia hirsute. (33)

33. Colour of the trichomes light brown (fusco), leaves ovolancolates, stems with hirsute trichomes
.... *G. fuscipellita* (Fig. 4-67).

33' Colour of the trichomes light brown to dark brown, especially close the inflorescensce. Bract and bracteoles light brown at the base and dark brown to black further along, tepals yellow to light brown at the base and becoming dark brown at the tip, filament tube dark yellow .... *G. sp. nov.* (*spec3*) (Fig.4- 57)

4.3.2. *Gomphrena perennis* and allies within the Mostly Andean Clade A

The nuclear marker (ITS) showed that most samples of *G. trollii*, *G. haenkeana* and *G. perennis* are included in a weekly supported clade (0.662 PP, 54 JK). Most closely related to this clade is the Mexican *G. cf. nitida* (sample AC496). Two accessions of *G. ferruginea* var. *ferruginea* (0.99 PP, 71 JK) are depicted as sister to this clade (0.58 PP), whereas the accession of *G. ferruginea* var. *rustica* (with trichomes on the internal tepals) is included in the actual lineage of *G. perennis* and allies.

The chloroplast data (*matK-trnK*) show that the species *G. perennis*, *G. ferruginea*, *G. haenkeana*, *G. trollii* form a medium supported clade (0.86 PP, 100 BS, 69 JK). This clade is annotated as "Mostly Andean Clade A" in the trees showing the overall relationships within *Gomphrena* (see Chapter 3), which also includes the lineage of *G. phaeotrichia* and allies. The chloroplast tree depicts the sample of *G. nitida* from Mexico outside of the "Mostly Andean Clade A", in contrast to the ITS trees.

The four species *Gomphrena perennis*, *G. trollii*, *G. haenkeana*, and *G. ferruginea* have some morphological characters in common. The most evident of these are the very short bracteoles in relation to the tepals. Also, the stems are erect to decumbent and bear most of the cauline leaves in the lower parts of the stems. Usually, several paracladia (= partial florescences) appear around a central paracladium. However, this character is different in *G. nitida*, which has only one partial inflorescence (a simple inflorescence head like in *G. celosioides*). But the four species also have clear differences in the morphology of the bracteoles with the laterally compressed crest located close to the apex. Whereas in *G. perennis* the apex of the bracteole is acute and the crest is only a little wing, in *G. haenkeana* the apex is acuminated with the crest deeply toothed; and in *G. ferruginea* the crest is wider. The tepals vary in texture and in color. Tepals of *G. ferruginea* and *G. perennis* are white, but in *G. ferruginea* they have a thinner texture. In *G. haenkeana* and *G. trollii* the tepals are chartaceous and pink or purple, respectively.

Some species such as *G. perennis* are widely distributed. To the contrary, *G. trollii* is endemic to the prepuna of Bolivia, and resistant to extreme environmental conditions such as high temperatures and scarce water supply. *Gomphrena ferrruginea* is restricted to the Tucuman forest and the Dry Valleys of Argentina and Bolivia, whereas *G. haenkeana* grows in the Chaco and dry valleys of Bolivia, Argentina and Paraguay.

Key to *Gomphrena perennis* and close relatives

1. Perennial plants, > 30 cm up to 100 cm, taproot fleshy, or woody. (2)

2. Cauline leaves ovolanceolate, inflorescence 1.2-1.5 (--2) cm in diameter, tepals white, membranous texture, bracteoles with short crest extending about one quarter from the apex of the dorsal part on middle nerve…………………………………………… *G. perennis* (Fig. 4-5)

2’ Cauline leaves linear lanceolate, Inflorescence 1.5. 2 (--3) cm in diameter, tepals strong purple, chartaceous in texture, bracteoles without crest only middle nerve thickened ……………………………………………………………………………….. *G. trollii* (Fig. 11).

1’. Annual plants, >14 cm, up to 50 cm, roots fibrous, cauline leaves elliptic lanceolate. (3)

3. Apical leaves subtending inflorescence ovolanceolate 0.5(--1) x 0.4(--0.6) cm, tepals fine membranous texture white. ……………………………………………………… *G. ferruginea* (Fig. 8)

3’ Apical leaves subtending inflorescence cordate-lanceolate 0.4-0.7 (--0.9) x 0.4-0.6 (--0.8) cm, chartaceous texture, pink strong colour……………………………………*G. haenkeana* (Fig. 13).

4.3.2.1. ***Gomphrena perennis*** L., Sp. Pl: 224 (1753).

Lectotype: Illustration in Dillenius, Hortus Elthamensis 24.t.20.f 22, based on a plant from "Bonarea"

(Designated by Mears in Taxon 29(1): 86 (1980) (see Fig. 4-5).

≡ *Gomphrena aggregata* Hort. Monsp. (1828) ex Moq., Prodr. DC. 13(2) : 414 (1849). nom. nud. et nom. Illeg., non Willd. (1809).

≡ *Xeraea perennis* (L.) Kuntze, Revis. Gen. Pl. 2: 545 (1891).

≡ *Gomphrena exaltata* Hort. Tolos. ex Moq. , Prodr. DC. 13(2): 414 (1849), nom. nud.

= *Gomphrena villosa* Mart., Beitr. Amarant. Nova Acta Acad. Caes. Leop. Carol. Nat. Cur.13: 303 (1826).

Type: Uruguay, Montevideo, *Sellow* (HT: B).

≡ *Xeraea villosa* (Mart.) Kuntze, Rev. Gen. Plant.2:545 (1891).

= *Ninanga bicolor* Raf., Fl. Tellur. 3:76 (1836).

Type: based on illustration in Curtis Bot. Mag. 2614.

= G. *silenoides* Chodat, Bull. Herb. Boissier, ser. 2, 3: 388 (1903).

Type: Paraguay, *E. Hassler* 7491 (HT: G G00103696, IS: P P00623708, C C10005407, MPU 016000).

= *Gomphrena perennis* var. *subalpina* (Herzog*) Suess.*, Fedde. Repert. Spec. Nov. 35: 315 (1934).

Type: Bolivia, Cuesta de los Monos, *Herzog* 1699 (IT: M M0241770).

≡ *Gomphrena perennis f. subalpina* Herzog, Meded. Rijks- Herb. Leiden 46: 7 (1922).

= *Gomphrena perennis* var. *brunnea* Stuchlik, Fedde Rep. *G.* Sp. Nov. 11: 153 (1912/1913) et 12: 520 (1913).

Type: Argentina, *Lorentz* 17(B), 171(B), (HT: B, ST: Uruguay Montevideo, *Gaudich.* (B), Brasil, *Martius* (ST: M M0241773), sin loc. ex Herb. Ledebour (LE)).

= *Gomphrena perennis* var. *matogrossensis* R.E.Fries, Ark. Bot. 16(12): 40 (1920).

Type: Brasilia, Matto Grosso, *Malme* s.n. (HT: S S07-12667)

= *Gomphrena perennis* var. *saxatilis* R.E.Fries, Ark. Bot. 16(12): 40 (1920).

Lectotype: Bolivia, Tarija, in declivilus montis apricis siccis in fisuris. Exped. Suec in reg. Chaco Andinis. *R.E. Fries* 1218 (LT: S R-2449, P 00623709). Designated by Bena Phytotaxa 296(2):141 (2017).

= *Gomphrena perennis* var. *divergens* Suess., Fedde. Rep. *G.* Sp. Nov. 42: 57 (1937).

Type: Ecuador province Guayas. Guayaquil, alt. 0-50 m, june 18-20, 26, 1923. *Hitchcock*, A.S. 19971 (HT: G, H, IS: US 00902462).

= *Gomphrena perennis* var. *silenoides* (Chodat) Suess. ex. E. Holzh., Mitt. Bot. Staatssamml. München 14-15: 185 (1956).

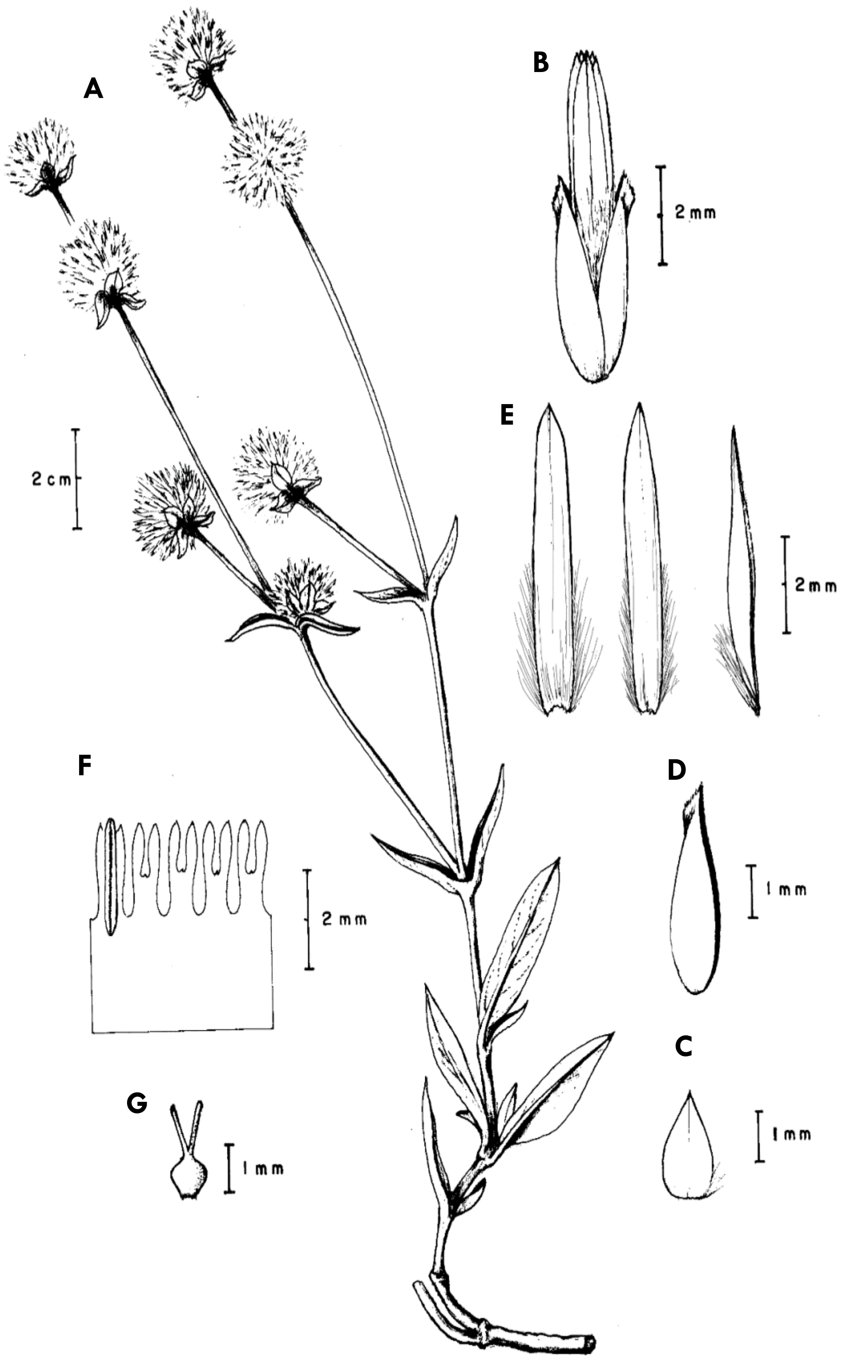
Type: Argentinien: Córdoba, Unquillo, Bruch N°1002 (HT: M, IS: P00623708).

Perennial herb, 30-70 (--100) cm. ***Root*** a fleshy tapoot with many nodes. ***Stems*** erect to ascendant, up to 1 meter tall, always with secondary and often with tertiary stems with dense indumentum appressed, white, 1-1.3(--3) mm long trichomes. ***Cauline leaves*** sessile, ovolanceolate to elliptic, 1.5-2.5 (--4.5) x 0.5-1 (--2) cm, acute and mucronate (0.5 cm) apex (midrib excurrent for 5.0 mm), margin entire, green, with densely arranged trichomes, on lower and upper surface and at the margin, 1-1.4 (--3) mm long, white to yellow. Sometimes short lateral branched in the axils of cauline leaves, these with small leaves 0.5 (--0.8) x 0.2 (--0.5) cm. ***Apical leaves substendig paracladia*** 2-5 leaves arranged symmetrically, cordate to ovate, 0.5-0.8 (--1.1) x 0.3-0.5 (--0.6) cm, acute and mucronate (0.5 cm) apex, with dense appressed, white to yellow trichomes in both sides (upper and lower surface). ***Infloresecence*** globose, terminal and axillar, 1.2-1.5 (--2.0) cm in diameter, consisting 3-6 groups of partial florescences, that appear in a terminal whorl-like structure without visible axes. ***Flowers*** 4-6.4 (--7) mm long. ***Bract*** ovate-lanceolate, cymbiform, 1-1.6 (--2) x 0.7-1 mm, chartaceo texture, white opaque, apiculate apex, the margin entire with a few teeth. ***Bracteoles*** ovolanceolate, 2.8-3 (4) x 1.5 mm, membranous texture, white opaque color, with toothed margin, crest extending dorsally on the apical quarter, shorter than tepals ***Tepals*** linear to lanceolate, membranous texture, white to light yellow, trichomes present at the base and on the margin, margin with teeth, size unequal bigger than the bracteoles, external and intermediate tepal, 4.4- 5.5 (--6.6) x 0.8 mm, inner tepals, 4.2-5.4 (--6.4) x 0.6 mm. ***Filament*** 5.4- 6.4 (--7) mm of long, fused into for a tube 3.4-4.4 (--5) free part 2.0-2.2 mm . ***Filament appendices*** conspicuous, 1.3-14 mm long ligulated shape lobes (base unites 0.6-0.8 mm) arising at the tip of the filament. ***Anthers*** oblong, 1.6-1.8 (--2) mm long, inserting between the two filament appendices. ***Gynoecium*** with two filiform stigma branches of 1-1.4 mm, the style is 0.2 mm long, the ovary is globose, 0.6-1.2 mm long [voucher: Borsch & Ortuño, 3664 = AC257].

Micromorphology of trichomes. Multicellular uniseriate on stems and cauline leaves, with 1-2 conspicuous basal cells, the first globose, the second straight, the border with large spinous and salicose ornamentation. The 4-6 upper cells with firm consistence, salicose, spinous ornamentation, striated texture walls cuticle. ***Interlocking junctions*** conspicuous, vary in: i) linear scars arranged in > 45° with the spines divided as "T" in the apex (the first cells), or ii) scar arranged in >45° with straight spines (the uppers cells). ***Trichomes on apical leaves subtending paracladia*** on the abaxial surface with 1-2 rounded basal cells, the 4 to 6 upper cells with firm consistence, spinous ornamentations, the interlocking junctions conspicuous, linear scar arranged in >forty five degree as strait spines; on the adaxial side leaf with trichomes short, with 1,2 basal cells, 2 upper cells with straight, firm consistence, spinous ornamentations. Trichomes on tepals with 1, 2 basal cells firm consistence, the upper with collapsed, sinuous, twisted cells. ***Anatomy of tepals.*** Tissues are composed by elongate straight, cylindrical cells, arranged in one row, all fitting perfectly, in the margin the cells form a tooted irregular outline [voucher: Borsch & Ortuño, 3626] (Fig. 4-6 D). ***Pollen.*** Size c. 18, 75 µm. Pore number 44- 46. Pore 3.2 µm of diameter, pore membrane with ektexinous bodies arranged circularly in a mosaic-like pattern. Tectum reduced to a distal band in the mesoporia, tapered, building hexagons and pentagons, acute (sharp) angle corner. Tectum, with columellae in the lower near middle of the vertical part, arranged around the pore (Fig. 4-6 G y H).

Taxonomic remarks. The different populations of *Gomphrena perennis* vary in particular in the complexity of the branching of the stems (and synflorescences), the density of the indumentum and the woodiness at the base of the stems. The infraspecific taxa described seem to represent this variation. They are currently treated as synonyms, but further research is needed to evaluate the species limits of *G. perennis* using both molecular and morphological characters and to analyse phylogeographic patterns within the species. The history of classification and nomenclature of *Gomphrena perennis* is long since it was one of the first species of the Amaranthaceae that was carried from South America to European gardens, where it was cultivated by James and William Sherar in the garden of Eltham. Dillenius made the first drawings of this species in "Hortus Elthamensis" (1732), which contains both figures and descriptions. Carl von Linnaeus then described this species based on a drawing. However, in the Oxford University herbarium, one of the specimens in the “Dillenian herbarium (OXF)” collection belonged to Eltham, 1264 (Fig4-7). The label of the mentioned specimen says “*Amarantoides perenne, bonariense*”. A part of it coincides with the drawing currently used as lectotype, suggesting that this specimen was used as a model for the drawing. The designation of the illustration as lectotype by Mears (1980) may therefore not have been ideal.

Habitat and ecology. Growing in open areas, in flat, some stabilized old sand dunes, grassy places, As associated species were reported : *Bromelia serra* Griseb, *Ceiba speciosa* (A. St.-Hil.), *Acrocomia aculeataex* (Jacq.) Lodd. ex. Mart., *Attalea phalerata* Mart. ex Spreng., *Anadenanthera colubrina* (Vell.), *Crotalaria micans* Link., *Neoraimondia herzogiana* (Backeb.) Buxb., *Podocarpus parlatorei* Pilg.



Flig. 4-5. *Gomphena perennis* L. A) Habit. B) Flowers. C) Bract. D) Bracteoles. E) Tepals. F) Detail of the androecium. G) Gynoecium [voucher: Borsch & Ortuño, 3664].

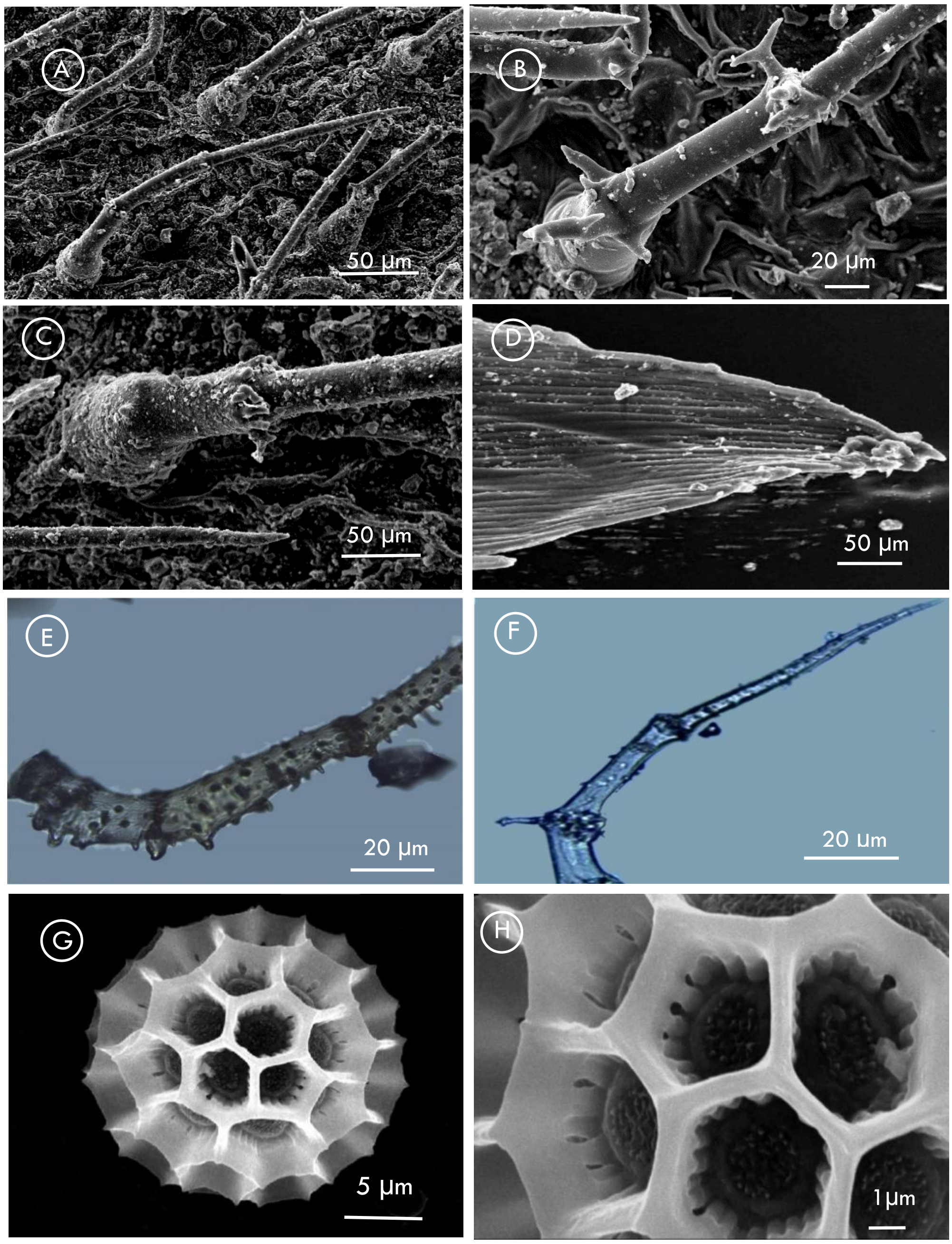


Fig. 4-6. Indumentum and tepals of *Gomphrena perennis* L.: Appressed trichomes with firm cells on abaxial surface of cauline leaves. A) General view of the trichomes, B) detail of the spinous ornamentation at the interlocking junction of cells, either simple or divided and T-shaped. C) Trichomes on the adaxial surface, detail of the rounded basal cells and the salicose ornamentation. D) Tepals with tissues composed of elongate straight, fibrous dermal cells and an acute apex [voucher: Borsch & Ortuño 3626]. Indumentum on apical leaves subtending paracladia. E) Trichomes on abaxial side, similar to those on cauline leaves and stems, basal and cells with spinous ornamentation. F) Trichomes on adaxial surface, which are sligtly shorter with 2-4 cells [voucher: Borsch & Ortuño 3664]. Pollen. G) Overview of metareticulate pollen, tectum reduced to a distal band in the mesoporia. H) Detail of the penta and hexagonal arrangement of mesoporia [voucher: Borsch & Ortuño 3626].

Fig. 4-7. *Gomphena perennis* L. historical material: A) Specimens collected by Elthan (under no, 1264, in OXF). A) [voucher: Elthan, 1264] (OXF). B) Illustration in Dillenius, Hortus Elthamensis 24.t.20.f 22.

The species has a wide ecological amplitude and occurs in Inter Andean dry forest, Semi humid Puna, Yungas, Dry Puna, Prepuna, Gran Chaco, Chiquitano dry forest, Tucuman-Bolivian forest, Chaco Serrano, Pre-andean Amazonian forest, Cerrado Chiquitano ecoregions. Altitudinal range of collections (60)121-2900 m.

Distribution. Widely distributed in the North east of Argentina, province Chaco, Corrientes, Cordoba, Santiago del Estero, (Buenos Aires) and province San Luis, Tucuman in Misiones. North west of Paraguay in provinces, Alto Paraguay, Boquerón, Formosa, Nueva Asunción, Presiden Hayes. In Uruguay provinces Florida, Salto, Rocha, Soriano. South eastern part of Bolivia, provinces Belisario Boeto, Jaime Zudañez, Nor Cinti (Dept. Chuquisaca), province, Narciso Campero, Capinota, Mizque, Quillacollo, José Carrasco Torrico (Dept. Cochabamba), province, Andres Ibañez, Chiquitos, Cordillera, Florida, Germán Busch Becerra, Manuel María Caballero, Ignacio Warnes, Valle Grande (department Santa Cruz), province, Cercado, Eustaquio Méndez, Gran Chaco, Sud Cinti, José María Aviléz, Burnet O'Connor (Dept. Tarija), province Larecaja. (Dept. La Paz) (see Fig. 4-6).

Speciemens examined for distribution assessment. ***ARGENTINA*****, Buenos Aires**, Tandil, [-59,1297220, -37,3722], 278 m, 18, 11, 2009, Zuloaga, F.O., 11362, (SI). **Corrientes**, 36 Km. al NE de Corrientes, Paso de la Patria a la orilla del río Paraná, [-58,5833280, -27,3165711], 53 m, 9, 10, 1983, Beck, S.G., 9475, (LPB). Concepción, Estancia El Transito, [-57,70, -

28,41669], 59 m, 4, 2, 1987, Pedersen, T.M., 14838, (CTES, SI). Dep. Capital, Riachuelo, [-58,797187, -27,550535], 50 m, 10, 1, 1976, Schinini, A., 12379, (CTES, LPB). Paso de los Libres, Ruta 23, 2 Km E del Rio Miriñay, [-57,611, -30,1688], 40 m, 21, 9, 1973, Schinini, A., 7265, (LPB, CTES). San Miguel, Estancia San Juan Poriahú, [-57,191549, -28,26565], 65 m, 19, 12, 1979, Pedersen, T.M., 12745, (CTES, SI). ***BOLIVIA*, Chuquisaca, Belisario Boeto**, Bajando de Nuevo hacia Santa Rosa, en direccion al Río Grande, [-64,2852780, -18,926944], 1379 m, 2, 3, 2006, Wood, J.R.I., 22335, (BOLV, LPB). Camino de Nuevo Mundo.***Nor Cinti***, Municipio de Camargo, saliendo por el camino Camargo-Culpina, [-65,208332, -20,639167], 2417 m, 14, 4, 2009, *Lliully, A., 1656*, (HSB, MO). Saliendo de Camargo, [-65,1346, -20,4343], 2426 m, 14, 4, 2010, *Ortuño, T., 1236*, (LPB). Sud Cinti, [-65,231284, -20,94021], 2289 m, 24, 4, 2009, *Fuentes Bazan, S., 157*, (LPB, B). ***Cochabamba*, *Cercado***, Saliendo de Cochabamba hacia La Paz, en el Km. 46 [-66.3349166667, -17.5091666667], 2465 m, 12, 3, 2009, *Borsch, T., 3962*, (LPB, B). In the foothills of Cordillera Tunari NE of Cochabamba, [-66.13444, -17.3602777778], 2800 m, 3, 2, 1995, *Wood, J.R.I., 9269*, (LPB). 2690 m, 30, 4, 1996, *De la Barra, N., 243*, (LPB). ***Capinota***, Comunidad de Apillapampa, [-66,233, -17,833], 2910 m, 19, 2, 2003, *Thomas, E., 241*, (LPB). Comunidad de Apillapampa, [-66,20, -17,80], 2850 m, 1, 3, 2003, *Thomas, E., 276*, (LPB). ***José Carrasco***, Diampampa, en valle interno del rio San Mateo, [-64,68277, -17,69694], 1640 m, 4, 9, 2003, *Fernández Terrázas, E., 2269*, (BOLV). 5 km (by air) NW of Pojo, 1 km W of bridge over Rio Pojo, [-64,9, -17,716667], 2100 m, 11, 2, 1987, *Nee, M., 34081*, (LPB, NY). Comunidad Hoyadas, [-65,1653249, -17,933], 2380 m, 17, 3, 1992, *Caballero, R., 54*, (LPB). ***Mizque***, Camino de Mizque a Raykampampa, cerca de Tintin, [-65,4388, -18,0039], 2234 m, 3, 4, 2003, *Borsch, T., 3590*, (LPB, B). Raqaypampa, localidad Qollpana, [-65,382581, -18,189083], 2860 m, 10, 4, 1992, *Gutiérrez, E., 57*, (BOLV). On road from Tintin to Raqaypampa c. 0,5 km north of road junction to La Mina, [-63.5131388889, -21.2606666667], 2480 m, 13, 2, 2007, *Wood, J.R.I., 27592*, (LPB). On road from Tintin to Raqaypampa c. 0.5Km north of road junction to La Mina, [-65,46388, -18,061111], 2454 m, 13, 2, 2007, *Wood, J.R.I., 22726*, (BOLV, LPB). ***Narciso Campero***, Aiquile, Camino de Aiquile a Pasorapa, 16 km de Aiquile, [-65,083, -18,189], 2448 m, 5, 4, 2003, *Borsch, T., 3618*, (LPB, B). Camino de Aiquile a Santa Cruz. 6 km de Perez, [-64,8485, -18,15], 1544 m, 6, 4, 2003, *Borsch, T., 3626*, (LPB, B). Pasorapa, 5 Km de Pasorapa, sobre el camino a Pasorapilla, [-64,63333, -18,300], 2153 m, 21, 2, 2003, *Wood, J.R.I., 19160*, (LPB, USZ). ***Quillacollo***, Carretera Cochabamba-Oruro, a la altura de aguas termales la cascada, [-66,3333329, -17,533332], 2446 m, 11, 3, 2003, *Mercado, M., 2591*, (BOLV,LPB). Parotani, 1-2 Km E. of Parotani along railway to Cochabamba near La Cabaña on south side of river, [-66,335, -17,5302778], 2400 m, 7, 2, 2004, *Wood, J.R.I., 20185*, (LPB). ***La Paz*, *Larecaja***, Consata 20 Km hacia Sorata, [-63,20, -17,74166], 1786 m, 16, 12, 1981, *Beck, S.G., 40515*, (LPB). ***Santa Cruz*, *Andres Ibañez***, ca. 16 Km hacia el N de Santa Cruz, por el nuevo Aeropuerto Viru-Viru, [-63,155183, -17,634868], 376 m, 19, 3, 1981, *Beck, S.G., 6673*, (LPB). Camino de Santa Cruz a Terevinto, [-63,3, -17,75], 400 m, 20, 9, 2002, *Borsch, T., 3523*, (LPB, B). Cotoca, Hacienda

Las Bolas, [-62,8833,-17,8], 400 m, 22, 9, 2002, *Borsch, T., 3529*, (LPB, B). 10 km of center of Santa Cruz, on dirt road to Monte Cristo, [-63,0833, -17,75], 390 m, 20, 12, 1991, *Nee, M., 42161*, (LPB, NY). 5 Km SE of Comunidad Don Lorenzo, [-62,833, -17,8249], 320 m, 17, 11, 1990, *Nee, M., 39949*, (LPB, NY). 7 km SE of Naranjillos on road from Santa Cruz to Abapo, at junction with rail road, [--63.2,-18.0416666667], 480 m, 30, 9, 1990, *Nee, M., 38936*, (NY, LPB). Along Río Pantano, 7 km. SE of Palmar del Oratorio and 18 km, SE of center of Santa Cruz, [-63,10, -17,93], 391 m, 9, 12, 1988, *Nee, M., 37111*, (NY, LPB). NW side of "Valle Sanchez", 4 Km W of Aeropuerto Internacional Viru-Viru, 15 Km N of Santa Cruz, [-63,166, -17,633], 375 m, 26, 1, 1989, *Nee, M., 37717*, (LPB, NY). West of Santa Cruz to Montero highway, just S of turnoff to Viru-Viru Airport, [-63,166, -17,65833299], 375 m, 26, 2, 1988, *Nee, M., 36384*, (LPB, NY). 3 Km NW of lomas de arena, [-63,166, -17,916], 420 m, 22, 5, 1991, *Nee, M., 40515*, (LPB, NY). North edge of grassland of Viru-Viru International Airport, with pasture on the other side, 3 km E of highway from Santa Cruz to Warnes, [-63,133333, -17,616667], 360 m, 22, 12, 1997, *Nee, M., 47453*, (LPB, NY). 12.5 Km. of center of Santa Cruz, 3 Km N of Jardin Botanico de Santa Cruz, [-63,077778, -17,73750], 380 m, 23, 12, 1994, *Nee, M., 46108*, (LPB, NY). 3 Km N of Pedro Lorenzo, on old road from Santa Cruz to Ibapo, [-63,25, -17,933], 475 m, 22, 12, 1994, *Nee, M., 46073*, (LPB, NY). Along Quebrada Peji, vicinity bridge on new highway from Santa Cruz to Camiri and railroad bridge, [-63,1833329, -17,95833], 440 m, 11, 12, 1994, *Nee, M., 45834*, (LPB, NY). Viru-Viru International Airport, SW of the buildings, [-63,133, -17,666], 375 m, 5, 1, 1994, *Nee, M., 44331*, (LPB, NY). ***Chiquitos***, Parque National Kaa-Iya, ANMI Norte, gasoducto, progresivas 237-239, [-61,7794439, -18,429444], 300 m, 30, 6, 2001, *Fuentes, A., 3068*, (USZ, LPB). ***Cordillera,*** Aguarati Izozog. Comunidad de Aguarati, [-62.4747222, -19,25148889], 300 m, 25, 5, 1999, *Michel, R. de, 2774*, (LPB). Ca. 200 Km hacia el sur, Proyecto Abapo Izozog, cerca del Rio Grande, [-63,0338, -18,924166], 12, 3, 1981, *Beck, S.G., 6447*, (LPB). Aguarati Izozog, al sureste de la comunidad de Aguaratimi, al limite de esta comunidad, [-62.4747222, -19,42805556], 1000 m, 6, 11, 1998, *Bourdy, G., 1952*, (LPB, NY). Estancia Rancho Chico (puesto nuevo) y alrededores, [-62,603879, -20,12777], 400 m, 22, 5, 1998, *Fuentes, A., 2355*, (MO, USZ). Paja Colorada, 28 Km S de Camiri, camino a Boyuibe, [-63,4500, -20,28333], 900 m, 14, 4, 1977, *Krapovickas, A., 31333*, (LPB, CTES). Ibasiriri Izozog. Del cruce del Espino, hacia La Brecha, Brecha mini, a 30 Km del gasoducto, [-62.7858333, -19,42805556], 400 m, 18, 5, 1999, *Michel, R. de, 2508*, (LPB). Ca. 21 Km. SE of Palmar del Oratorio, ca. 14 Km, SE of Rio Chore-Chore [=Rio Pantano], [-63,0166, -18,033], 365 m, 22, 1, 1989, *Nee, M., 37653*, (LPB, NY). Camino a Camiri, desde Santa Cruz, antes de llegar a Rio Seco, desvio que va a los rieles del tren, Cerca Rio Grande-Rio Seco, [-63,244722, -18,660556], 475 m, 25, 4, 2007, *Ortuño, T., 733*, (LPB). Ruta Boyuibe-Hito Villazon, transchaco, 93 Km E de Boyuibe, en borde de ruta, [-62,416, -20,433], 540 m, 12, 4, 1993, *Saravia Toledo, C., 11748*, (LPB, CTES). Camino Santa Cruz-Camiri, [-63,25, -17,933], 510 m, 22, 11, 2003, *Wood, J.R.I., 20075*, (LPB, HSB, USZ). ***Florida,*** Bella Vista, salida del sendero ecologico el Cañadon, [-63,691194, -18,252549], 1437 m, 14, 12, 2007, *Villarroel, D., 1816*, (LPB, USZ, MO). Comunidad Bella Vista, sobre el camino principal entre la abra hasta la casa de Don Pastor, [-63,676389, -18,331944], 1275 m, 8, 4, 2006, *Villarroel, D., 500*, (LPB, USZ, MO). Comunidad de Bella Vista, salida del sendero el Cañadon, [-63,8057110, -18,196842], 1461 m, 13, 4, 2006, *Villarroel, D., 557*, (LPB, USZ). ***Germán Busch Becerra***, Entre el Carmen Rivero Torrez y el Carmen viejo, llanura con suelo muy arenoso con barbecho o limpiado de vegetacióјn con restos de bosque seco, [-58,618333, -18,818055], 134 m, 28, 4, 2008, *Wood, J.R.I., 24591*, (USZ, LPB). Camino Rivero Torrez y el Carmen Viejo, [-58,371450, -18,4922], 162 m, 17, 5, 2008, *Parada, A., 964*, (USZ,MO). ***Ignacio Warnes***, Near future "Urbanizacion Belgica Chica", 11 Km. by dirt road E of main highway from Santa Cruz to Warnes, 10 Km (by air) SE of Warnes, [-63,06666700, -17,583333], 340 m, 31, 10, 2000, *Nee, M., 51077*, (LPB, NY). Near future "Urbanizacion Belgica Chica", 11 Km. by dirt road E of main highway from Santa Cruz to Warnes, 10 Km (by air) SE of Warnes, [-63,066, -17,583333], 340 m, 31, 10, 2000, *Nee, M., 51078*, (LPB, NY). ***Manuel María Caballero***, On highway from Comarapa to Mairana, 2.4 Km SE of turnoff to Saipina, [-64,400, -18,06], 1575 m, 17, 4, 2002, *Nee, M., 52186*, (LPB, NY). 1 Km al NO de San Isidro, [-64,433, -18,03333], 1600 m, 9, 3, 1988, *Solomon, J.C., 17950*, (LPB, MO). ***Sara***, 8,5 Km (by air) NW of La Belgica. 5,75 Km (by air) NW of bridge over Rio Piraí, [-63,2425, -17,4916667], 320 m, 26, 12, 2010, *Nee, M., 57394*, (LPB, USZ). ***Valle Grande***, 10 km E of Guadalupe, valley of Rio Piraymiri, 1 km. Upstream from "Chorrillos", [-63,991667, -18,55], 1800 m 5, 2, 1988, *Nee, M., 36202*, (LPB,NY). Camino entre la comunidad el Enpinao y La chacra, [-63,8330, -18,337778], 1789 m, 21, 9, 2009, *Arroyo, L., 4611*, (MO, USZ). ***Tarija***, ***Cercado***, Cerca ladera norte, [-64,5742, -21,6543], 2100, 15, 5, 1986, *Bastian, E., 1298*, (LPB). ***Eustaquio Méndez***, Camino entre El Puente y Tomayapa, cerca de Chinchilla, [-65,183, -21,23], 2500 m, 5, 7, 1996, *Lopez, R., 459*, (LPB). ***José María Avilés***, cerca Angostura, [-64,6173940, -21,659244], 1750 m, 4, 3, 1986, *Bastian, E., 950*, (LPB,B, CTES, NY). Ruta Bermejo-Tarija, rio Tarija 27 Km de Tarija, [-64,6117830, -21,71926], 1726 m, 14, 5, 1971, *Krapovickas, A., 18805*, (LPB). Ruta Tarija - Villamontes, Bajada de Chimeo, [-62.785833, -21,406944], 1050, 25, 5, 1971, *Krapovickas, A., 19230*, (LPB, CTES). Cerca Concepcion, S-Exp. 20°, [-64,6833, -21,683299], 1800 m, 22, 5, 1986, *Bastian, E., 1320*, (LPB). ***Burnet O´Connor***, 15 a 20 Km del pueblo de Entre Ríos sobre el camino a Caraparí, [-63,9688, -21,414999], 8, 5, 2005, *Mendoza, M., 1618*, (USZ, LPB). Along road from Entre Ríos to Villa Montes, Cañadas, 40,5 km of Entre Ríos, [--64.1396666667, -21,421], 935 m, 12, 5, 2005, *Nee, M., 52983*, (LPB, MO, NY, USZ). ***Gran Chaco***, camino de Camiri a Villamontes. 33 Km de Camiri, [--63.448, -20.2676666667], 892 m, 9, 4, 2003, *Borsch,T., 3638*, (LPB, B). Camino de Villamontes a Tarija, [-63,9695, -21,4175], 940 m, 9, 4, 2003, *Borsch,T., 3644*, (LPB, B). 4.4 Km W of center of Villa Montes, on road on slope above Río Pilcomayo to Entre Ríos, and Tarija, [-63,506943, -21,2575], 426 m, 19, 3, 2007, *Nee, M., 54784*, (MO, NY, USZ, LPB). 5 Km W de Villamontes, en faldeos de la Boca del Angosto del rio Pilcomayo, [-63,524963, -21,263013], 400 m, 6, 4, 1993, *Saravia Toledo, C., 11352*, (LPB, CTES). Yacuiba. Chaco, Canto del Monte, [-63,10, -

21,86670], 337 m, *Fries, R. E., 1580*, (MO_FC). Yacuiba. Chaco: Fortin Crevaux, [-62,899, -21,89], 295 m, 0, 0, 0, *Fries, R. E., 1584*, (MO_FC). ***Chuquisaca, Sud Cinti***, Camino de Tarija a Potosi, Cerca de Villa Abecia, [--65.2298333333,-20,96416667], 2287 m, 12, 0, 2003, *Borsch, T., 3664*, (LPB, B).

4.3.2.2. *Gomphrena ferruginea* Pedersen, Darwiniana 20(1–2): 273, f. 1. 1976

Type: Argentina, province Salta, department Santa Victoria, and San Felipe, by Rio Lizote. In dry soil by path on hillside, Lat. 22°16'S, Long. 64°58'W, Atl. 2300 m. 14. III. 1966, J. G. Hawkes, J.P. Hjerting & K. Rahn sub, n° 3847 (HT: C C10005390).

Annual plant 14-25 (--43) cm. ***Root*** simple. ***Stems*** erect, with secondary stems, striate, with a dense indumentum of appresed to villous, golden or light brown, 1.2-2(--3.5) mm long trichomes. ***Cauline leaves*** sessile elliptic-lanceolate, 0.7-2.5(--4) x 0.7-0.9(--1.2) cm, acute, mucronulate (midrib excurrent for 0.2-0.4 mm) at apex, green. Sometimes, more than two pairs of small leaves develop on short branches in the nodes, 0.8-1(1.2) x 0.2-0.3(--0.5) cm, with a dense villous indumentum on both sides and the margin, trichomes yellow to dark golden. ***Apical leaves subtending paracladia*** 2-5, arranged symmetrically, ovolanceolate, 0.5(--1) x 0.4(--0.6) cm, acute and mucronate at apex, with appresed trichomes, these denser at the base and the margin, less so on the upper surface. ***Inflorescences*** globose, terminal, and axillar, 1.2(--1.5) cm diameter, consisting of 3-6 paracladia, without visible axis, yellow to light brown. ***Flowers*** 3.6-3.8 (--4) mm long. ***Bract*** elliptic-ovolanceolate, cimbiform, 1.6-2 x 1-1.5 mm, membranous, white translucent, toothed at margin. ***Bracteoles*** ovolanceolate, acuminate, 3.6-3.8(--4.2) x 1.5 mm, membranous translucent, white, toothed at margin, widely crested for about half of the dorsal part, shorter than the tepals. ***Tepals*** navicular to lanceolate, finely membranaceous, white, toothed and apiculate at apex, without trichomes, size unequal; external tepals 3.6-4.3 (5) x 0.7 mm; intermediate tepal 3.4-4.2(--4.9) x 0.7 mm, and inner tepal 3.2-3.3(--4.8) x 0.4 mm. ***Filaments*** 4,2- 4,4 (--5) mm long, fused into a tube for 2.9-3.1(--3.7) mm, free part 1.3 mm. ***Filament appendages*** conspicuous, 0,5-0,8 mm, lanceolate (united part 0.7), arisisng at the tip of the filament. ***Anthers*** oblong, 1.2 (--1.4) mm (Fig. 4-8E). ***Gynoeceum*** with 2 filiform stigma branches, 0.8-1.2 mm in length, style 0.4 mm, ovary 0.6 -1 mm [voucher: Borsch, Ortuño & López 3751 = AC446] (see Fig. 4-8).

Micromorphology of trichomes. Multicellular uniseriate on stems and cauline leaves, the basal cells widened at base and smooth (Fig. 4-9 C). The 4-6 upper cells cylindrical with firm to flexible consistence, salicose, and spinous to granulose ornamentation. ***I****nterlocking junctions* conspicuous with short spines, scars arranged in a zero to forty five degrees angle (Fig 4-9 D). ***Trichomes on apical leaves subtending paracladia***. The adaxial surface leaves shortly trichomes, (Fig 4-9 H). F) abaxial side leaf similar trichones than caulinar leaves (Fig 4-9 G). Sometimes a few trichomes arising on the tepals, consisting only of long elongate cells, cuticle with a finely spinous ornamentation. ***Anatomy of tepals***. Tissues are compose with elongate straight, cylindrical dermal cells, arranged in one row, all fitting perfectly, in the margin the cells form a tooted irregular margin, protrude like fibers [voucher: Borsch, Ortuño & López 3751(B.LPB)].

Taxonomic remarks. Based on morphological differences and indumentum characters, Pedersen (1976) recognized two varieties *Gomphrena ferruginea* var. *adusta*, and *G. ferruginea* var. *rustica*. The first comprises small plants with dark brown colored bracts and bracteoles, and according to Pedersen reported as endemic to the high altitude mountains of Jujuy. Based on the ITS tree, the three samples of *G. ferruginea* included are not depicted as monophyletic but the plastid data do not provide yet enough resolution. It is possible that the species is represented in Bolivia only by var. *rustica*. However, the delimitation of the species requires further study.

Habitat and ecology. Open soil that is often loose and crumbly on sandstone outcrops or hill slopes, also on open areas near rivers. Vegetation with scattered trees such as *Podocarpus sp*., *Vachellia caven* (Molina) Seigler & Ebinger, *Zanthoxylum* coco Gillies ex Hook. f. & Arn., or shrubs such as *Jatropa* **sp.**, *Baccharis dracunculifolia* DC., *Acanthostyles buniifolius* (Hook.ex Arn.) R.M. King & H. Rob., and grasses. In the Inter-Andean dry forest and Tucuman-Bolivian forest ecoregions. Altitudinal range of collections between 1600-2650 m.

Distribution. Northeast of Argentina, province Jujuy and Salta. South of Bolivia, province Tomina (Dept. Chuquisaca), province José Carrasco Torrico, (Dept. Cochabamba), and province Aniceto Arce, Cercado, Eustaquio Mendez, José Maria Aviléz (Dept. Tarija) (Fig. 4-10).

Specimens examined for distribution assessment. ***ARGENTINA*** , ***Jujuy***, Subiendo hacia las lagunas de Yala, [-65,4666670, -24,116667], 1660 m, 9, 4, 2004, *Borsch, T.*, 3751, (=AC446, LPB, B). Valle Grande, Abra del Potrero, [-65,107, -23,5922], 2650 m. *Zuloaga, F.O.*, 11651, (SI). ***Salta***, Camino de Salta a San Antonio de los cobres. 5 km de campo Quijano, [-65,6833330, -24,883333], 1648 m, 8, 4, 2004, *Borsch, T.*, 3743, (= AC444, LPB, B). ***BOLIVIA, Chuquisaca, Tomina***, El Villar saliendo de la comunidad El Villar camino a Alcala, [-64,316, -19,216], 2100 m, 7, 1, 2004, *Carretero, A.*, 1136, (HSB). ***Tarija, Aniceto Arce***, Padcaya, 3 km hacia Tarija, [-64,7, -21,85], 2100 m, 16, 3, 1998, *Beck, S.G.*, 26158, (LPB). Camino de Padcaya a Bermejo asfaltado. Unos 45 minutos de Padcaya, [-64,666667, -21,166], 1905 m, 10, 4, 2003, *Borsch, T.*, 3650, (LPB, B). Cerca de Padcaya, entrando a mano izquierda de la quebrada Wayco, [-64,706597, -21,880610], 2220 m, 28, 1, 1988, *Liberman, M.*, 1830, (LPB). ***Cercado***, Piedra plana ca. 40 km de Tarija sobre la carretera entre rios, entrando en la quebrada de Piedra plana, [-64,45, -21,416667], 2100 m, 10, 3, 2005, *Mendoza, M., 1413*, (USZ). ***Eustaquio Méndez***. Al norte de Sella, [-64,693, -21,693], 1819 m, 24, 4, 1991, *Coro, M., 127*, (LPB, NY). Cuesta de Sama, 10 km de reten de Santa Barra Chica, [-64,799, -21,446], 2246 m, 13, 3, 2005, *Mendoza, M., 1459*, (USZ). ***José María Avilés***, Bajando de Chocloca 2 Km hacia juntas, [-64,7833, -21,766], 2000 m, 12, 3, 1998, *Beck, S.G., 23850*, (LPB).

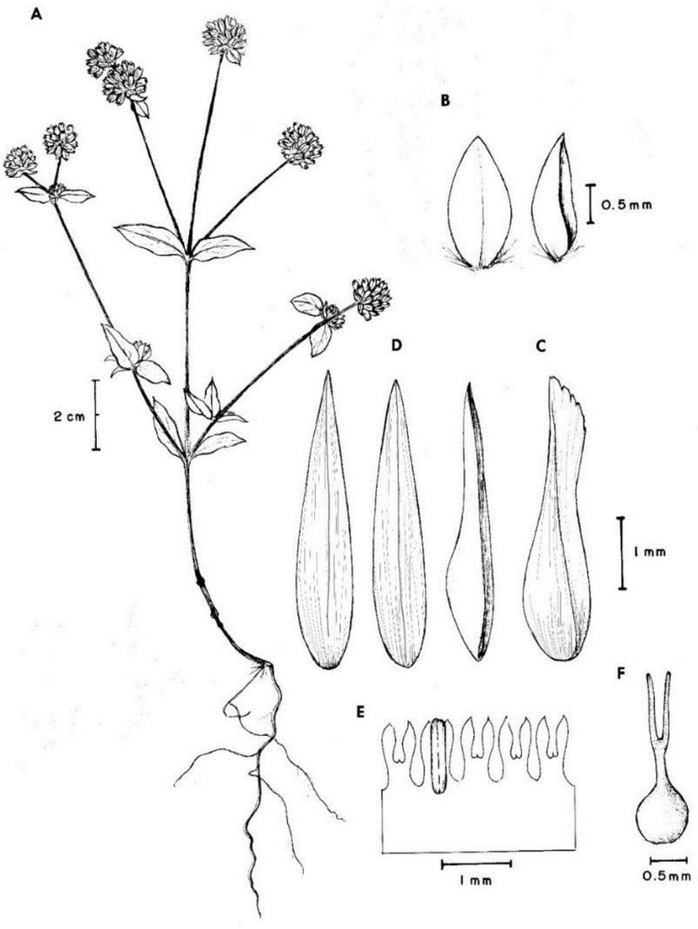


Fig. 4-8. *Gomphena ferruginea Pedersen*. A) Habit. B) Bract. C) Bracteoles. D) Tepals. E) Detail of the androecium. F) Gynoecium [voucher: Borsch, Ortuño & López, 3751(B, LPB)].

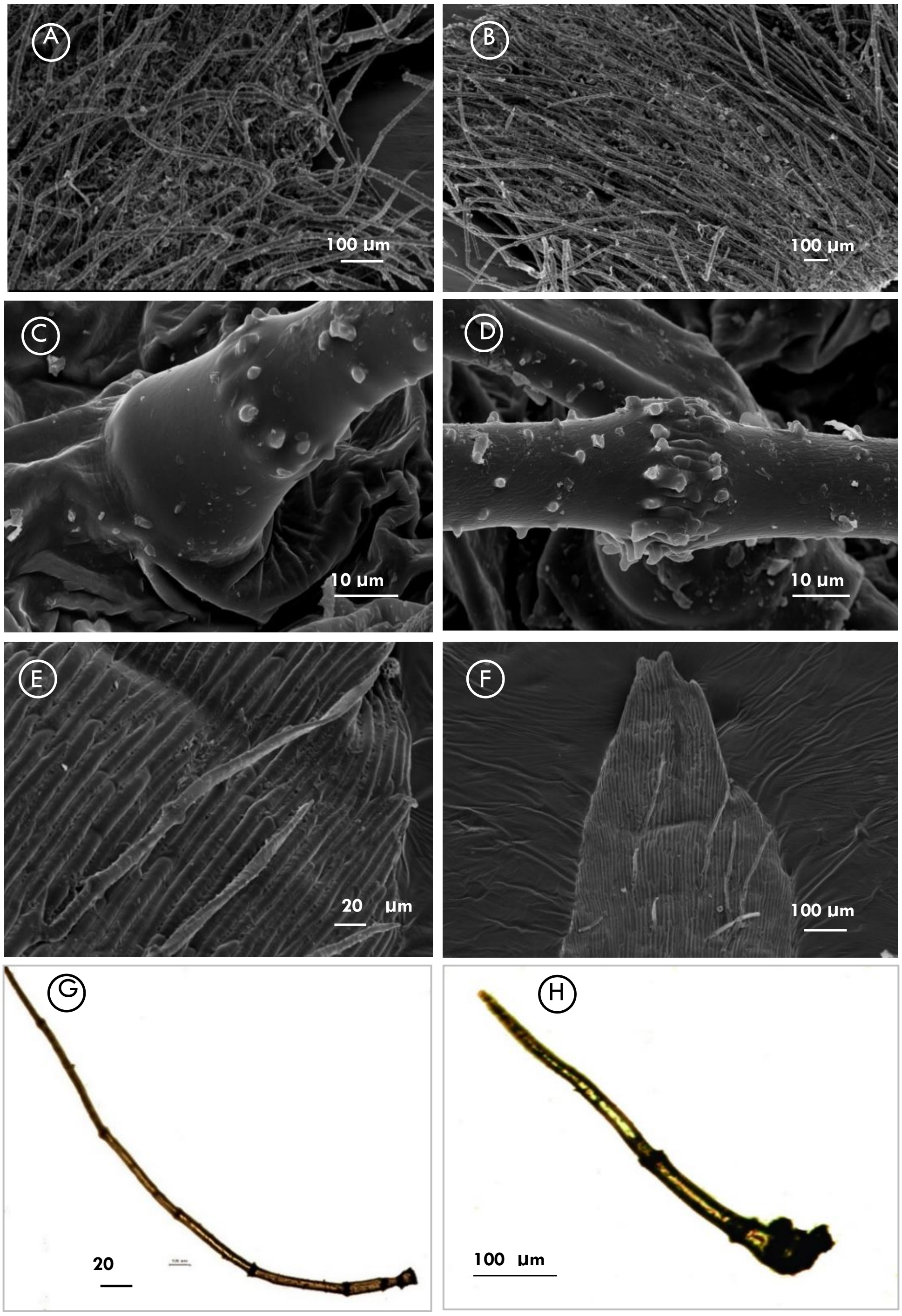


Fig. 4-9. *Gomphrena ferruginea Pedersen*. Indumentum on cauline leaves. A) Upper (Adaxial) surface with appresed to villous trichomes. B) Lower (Abaxial) face of leaves of dense villous to firm trichomes C) the basal cells of trichomes. D) Detail of the interlocking junction. Tepals: E y F) Tissue show the scares trichomes dorsal part of the tepal. Apical leaves subtending paracladia. G) Trichomes of the abaxial surface and margin. H) Trichomes of the adaxial surface [voucher: Borsch, Ortuño & López, 3751(B, LPB)].

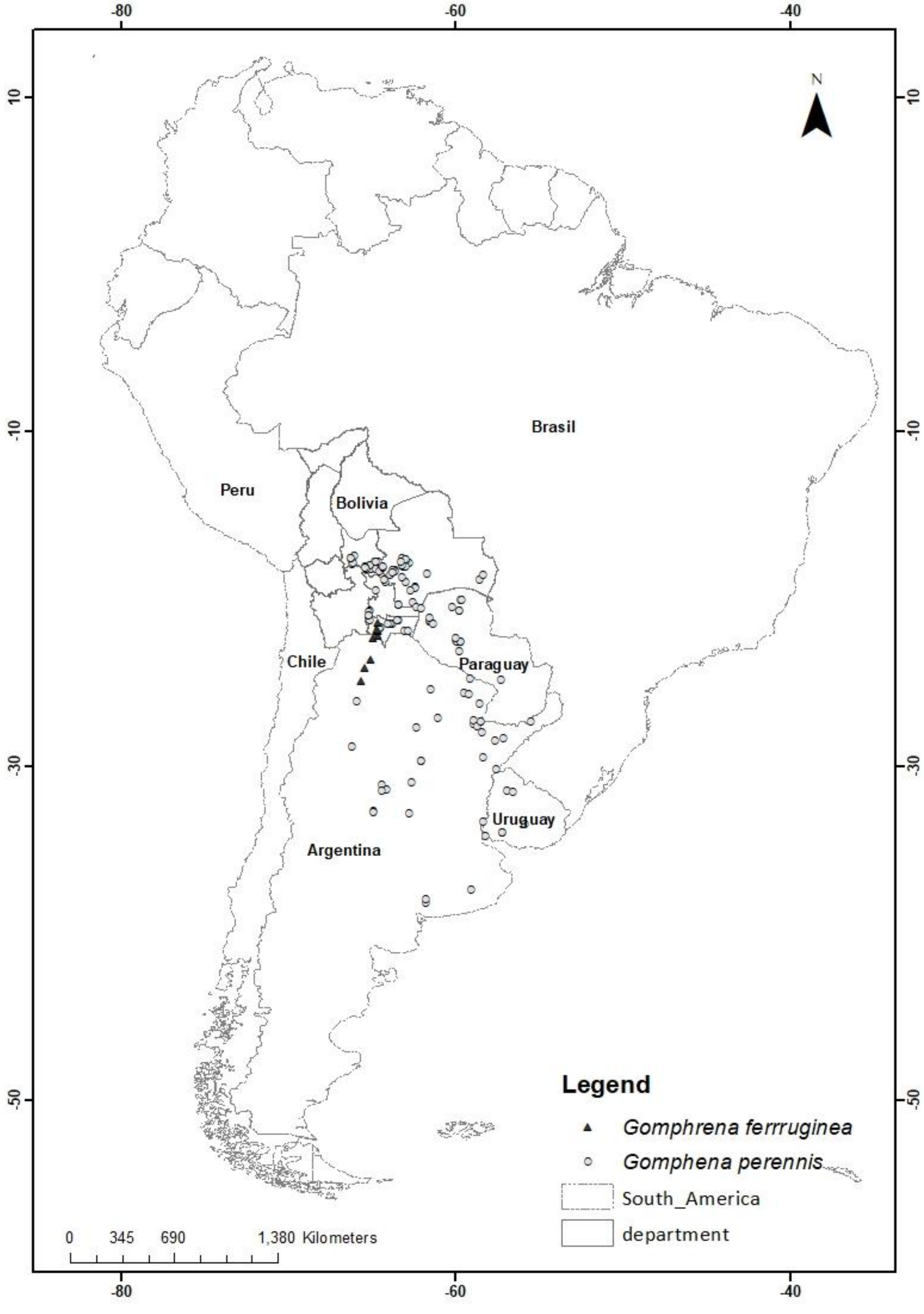


Fig. 4-10. Distribution of the species *Gomphrena perennis* and *G. ferruginea*.

4.3.2.3. ***Gomphrena trollii*** Suess., Repert. Spec. Nov. Regni Veg. 35: 315. 1934.

Type: Bolivia, Dept. Potosí, Cotagaita-Escara, "Trockenbusch", 15. May 1927, 2700 m, C. *Troll 3355* (HT: B 100242294, IT: M).

Perennial herb, 20-30 (--50) cm. ***Root*** a woody taproot, with nodes. ***Stems*** erect, with unbranched principal stems, striated with dense appressed, white to yellowish trichomes. **Cauline *leaves*** on basal parts of the stems sessile, lanceolate, blades 3.2-5.6 (--7.1) x 0.5-0.8 (--1.5) cm, acute and mucronate (midvein excurrent for 0.3 cm), apart from the midvein with two prominent secondary veins, on both surfaces with dense appressed trichomes, 1.6-3.5 mm in length, on remaining parts of stems sessile, lanceolate, 2.0-3.5 (--4.5) x 0.8-0.9 (--1.2) cm, acute and mucronate (midvein excurrent for 0.5-0.6 cm) apex. Sometimes short lateral branches in the axils of cauline leaves, these with small leaves 0.8-1 (--2) x 0.2-0.3 (--0.9) cm. ***Apical leaves subtending paracladia (inflorescences)*** 3-5 leaves arranged symmetrically, cordate to lanceolate 0.6-0-9 (--1.5) x 0.3 (--0.5) cm, acuminate and mucronate at apex, green, with a dense indumentum of appressed trichomes in the lower part, becoming glabrous in the upper part, trichomes white-yellow. ***Inflorescences*** globose, terminal, 1.5-2 (--3) cm in diameter, consisting of 3-6 paracladia that appear in a terminal whorl-like structure without visible axis. ***Flowers*** 10.5 (--12) mm long. ***Bracts*** ovolanceolate, cimbiform 1-2.8 (--3) x 1.5-1.6(--2) mm, chartaceo texture, white opaque colour, acuminate at apex and midvein excurrent, toothed at margin. ***Bracteoles*** ovolanceolate, 2.4-4 (--5) x 1.4-1.5 mm, membranous texture, white to yellowish, near the apex fleshy in dorsal part colour, margin toothed, midvein in the lower part extended into a narrow non-toothed crest; shorter than tepals. ***Tepals*** linear-lanceolate, chartaceos, intensely purple, acute at apex, finely toothed at the margin and close to the apex. With trichomes at the base of the dorsally and at the margin, sizes unequal, external tepals 9 (--9.5) x 0.5-0.9 mm, intermediate 8.9 (--9.4) x 0.5-0.9 mm and inner 8.8 (--9.3) x 0.5 mm. ***Filaments*** 10 (--12) mm long, fused into a tube for 8.2 (--9.5), free part 1mm long. ***Filament appendages*** conspicuous, 1.5 (--2.5) mm long, elliptic lanceolate in shape, arising at the tip. ***Anthers*** oblong, 1.8 mm long, inserted between the two filament appendages. ***Gynoecium*** *with* two filiform stigma branches, of 1.8-2 mm in length, style 0.6 mm, ovary 0.6 -1 mm. [voucher: Ortuño, 1255 (LPB, B)] (Fig. 4-11F).

Micromorphology of trichomes. Multicellular, uniseriate; on ***stems and cauline leaves***, with 1(-3) wider basal cells (Fig. 4-12 D), the basal cell rounded the others more elongate, the juctions with granulose and salicose ornamentations. The 4-6 upper cells with firm consistence, salicose, spinous to granulose ornamentation, striated surface sculture of the cuticule (Fig. 4-12 C). Interlocking junctions conspicuous linear, scars arranged in parallel to the axis of the trichomes (angle zero or shifted forty five degrees). ***Trichomes on apical leaves subtending paracladia*** with the lower surface similar than trichomes on stems and cauline leaves, on the upper surface thin, white, or glabrous. ***Trichomes on tepals*** trichomes have a basal elongate long-cylindrical cells, the uppers collapsed cells, sinuous or twisting. ***Anatomy of tepals.*** Tissue composed by elongate strait, cylindrical dermal cells, arranged in one row (Fig. 4-12E). [voucher: Ortuño, 1255 (B, LPB)].

Taxonomic remarks. The main morphological differences between *G. trollii* and the other species of the clade are the purple color and the chartaceous texture of the tepals. A similar pinkish color of the tepals occurs otherwise also in *G. haenkeana* but they are membranous in texture. Furthermore, *G. haenkeana* is an annual while *G. trollii* has a tough woody taproot. Other differences are the absence of a crest in bracteoles of *G. haenkeana*. In 1927, Carl Troll (1899-1975) a German geographer, botanist and ecologist collected *Gomphrena trollii* during his scientific expedition to the Andean countries (1926-1929): This species was collected near Cotagaita, and was analyzed and studied in the Botanical State Collection of Munich by the German botanist Karl Suessenguth (1893-1955) who gave the name in honor of Carl Troll.

Habitat and ecology. It grows preferably on rocky slopes, in open areas between trees and shrubs as *Prosopis flexuosa* DC., *Schinus areira* L., *Bougainvillea spinosa* (Cav.) Heimerl and *Senegalia feddeana* (Harms) Seigler & Ebinger. Plants were so far all collected in the Red Cordillera of Tupiza, which consists of a thick layer of marine sediments deposited about 400 million years ago in the Devonian period. This hardened reddish substrate called shale is easily affected by imbricated erosion. These landscapes belong to the Semi humid Puna, Prepuna ecoregion. Altitudinal range of the collections is between 2700 – 3920 m. The flowers exude a strong and sweet smell mostly in the evening and at night (pers. obs.).

Distribution. Endemic in Bolivia, distributed in the department Potosi, province Nord Chichas (around the towns of Vitichi and Cotagaita), and in the province of Sud Chichas (near the town of Espicaya) (Fig. 4-16).

Specimens examined for distribution assessment. ***BOLIVIA, Potosí, Nor Chichas***, Vitichi, [-65,355, -20,2718], 3119 m, 18, 4, 2010, *Ortuño, T.,* ***1255***, (B, LPB). Cotagaita-Escara, [-65,597222, -20,455], 2700 m, 15, 5, 1927, *Troll,* C., 3355, (B, M). 7 km al Norte de Cotagaita, [-65,519791, -20,081261], 3030 m, 2, 4, 2004, *Borsch, Th.,* ***3723***, (LPB, B). **Sud Chichas**, Ladera Oeste del Cerro Cieneguillas 4 Km al NE de Tupiza. [-65,68333, -21,416666755]3400 m, 17, 2, 2002, *Müller, J., 9053*, (LPB). Al oeste-sur-oeste en línea recta de la comunidad de Espicava aprox. 5.78 km, [-65,845278, -21,596667], 3412 m, 29, 2, 2012, *Zenteno, R.F., 11635*, (LPB). 0,5 km above la angostura, [-65,700444, -21,50416667] 2900 m, 29, 3, 1997, *Wood, J.R.I., 11925*, (USZ, HSB, K, B). Al oeste en línea recta de la comunidad de Espicaya aprox. 7.92 km, [-65,868056, -21,588056], 3820 m, 29, 2, 2012, *Beck, St.G., 33846*, (LPB). Talina, San José de Pampa Grande, Colina de Pizarra Negra, Casa del Diablo, trayecto a Tupiza. 3100 m, 20, 3, 1977, *Lara Rico, R, 1556A*, (LPB).

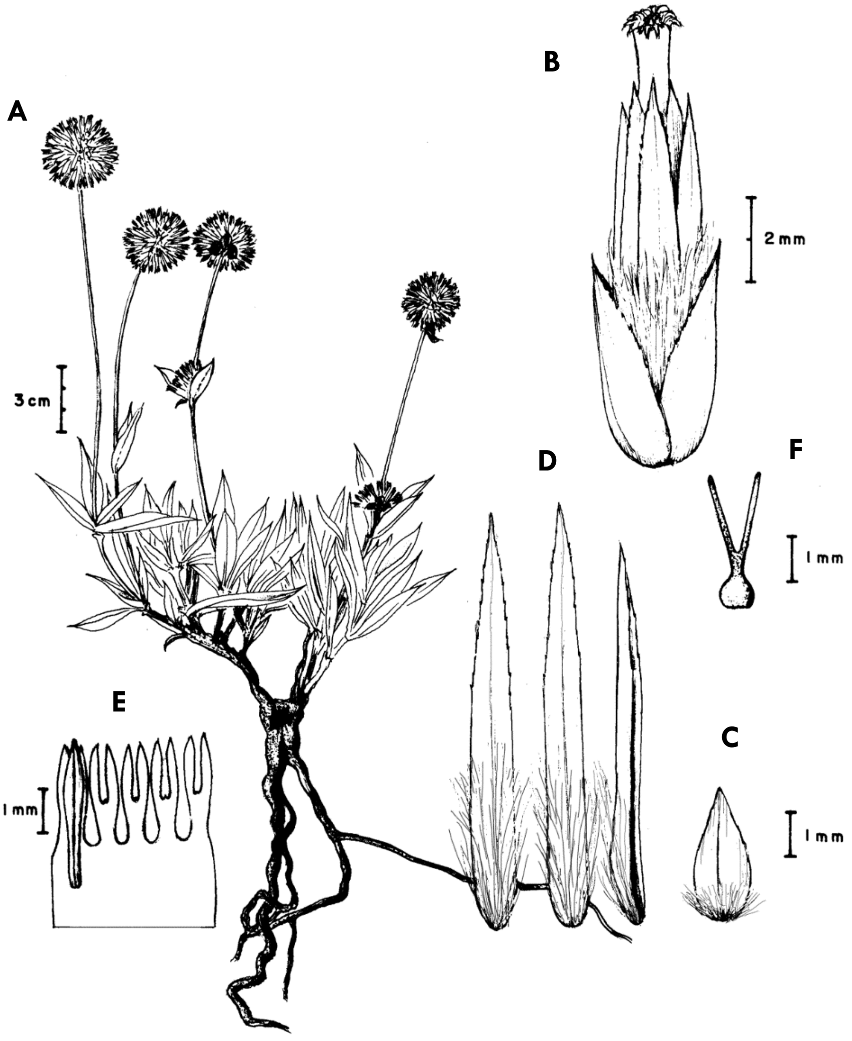


Fig. 4-11. *Gomphrena trollii* Suess. A) Habit. B) Detail of the flower with the two bracteoles. C) Bract. D) Tepals. E) Detail of the filament appendices of the androecium. F) *Gynoecium*. [voucher: Borsch, Ortuño & López 3723 (B, LPB)].

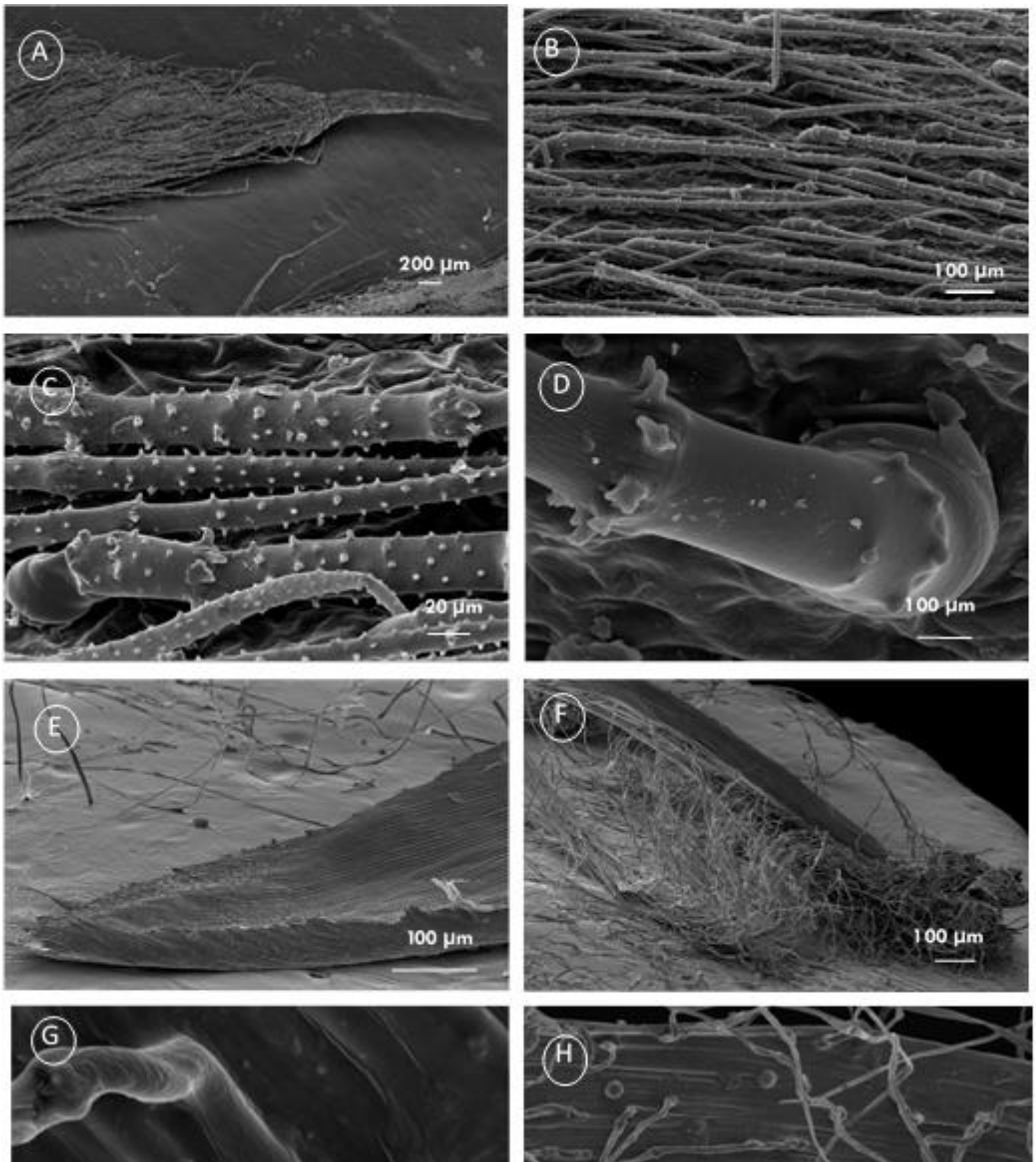


Fig. 4-12. *Gomphrena trollii* Suess. Cauline leaf. A) Upper leaves with mucronulate apex. B) Lower part dense adressed trichomes. C) Detail of salicose, spinous to granulose ornamentations of cells. D) Base and interlocking junction not conspicuous. Tepals. E) Toothed apex. F) Lanate trichomes dorsal part. G) and H) Detail of lanate Interlocks junction not conspicuous trichomes [voucher: Ortuño 1255 (B, LPB)].

4.3.2.4. *Gomphrena haenkeana* Mart., Nov. Act. Nat. Cur. 13: 299. 1826.

Lectotype: Bolivia. Haenke s.n. (LT: M 0241736!, LT designated by Bena Phytotaxa 296(2):136 (2017)

≡ *Xeraea haenkeana* (Mart.) Kuntze, Revis. Gen. Pl. 2: 545.1891.

≡ *Gonphrena pulchella* var. *haenkeana* (Mart.) Suessenguth., Repert. Spec. Nov. Regni Veg. 35: 311(1934: 311).

= *Gomphrena ligulata* Griseb, Abh. Königl. Ges. Wiss. Göttingen 19: 80-81. 1874.

Type: Argentina, Córdoba: frecuens prope urbem, Lorentz, P.G. s.n. (HT: GOET GOET 000081).

Annual herb of 16-22 (--45) cm. ***Root*** simple, fibrous. ***Stems*** erect, with secondary and tertiary stems, green, striated, with dense appressed 1-2.2 (--3) mm long, white-light brown trichomes. ***Cauline leaves*** sessile, elliptic-lanceolate, 1.1-2.4 (--3.9) x 0.6-0.9 (--1.2) cm, acute and mucronate (midvein excurrent for 0.6 cm) (Fig. 4-13A) apex, middle nerve and first pair of lateral veins conspicuous, with a dense appressed indumentum, denser in the abaxial side of the blade and in the margin than on the adaxial surface, trichomes 1 (--1.4) mm long. Sometimes short lateral branches in the axils of cauline leaves, these with usually two small leaves 0.8 x 1 cm. ***Apical leaves subtending paracladia*** *(inflorescences)* 2-5 leaves arranged symmetrically, cordate-lanceolate 0.4-0.7 (--0.9) x 0.4-0.6 (--0.8) cm, acute and mucronate at apex, olive green, with a dense indumentum of appressed trichomes in the abaxial surface and the margin, glabrous in the adaxial, white to light brown. ***Inflorescence*** globose, terminal 1.5-2.5 (--3.4) cm in diameter, consisting of 1-5 paracladia, that appear in a terminal whorl-like structure without visible axis. ***Flowers*** 8-11 (--13) mm of long. ***Bracts*** ovolanceolate, cimbiform, 3-3.5 (--4.5) x 0.8-1.5 mm, chartaceos texture, white/ light yellow colour, acute in the apex, toothed at margin. ***Bracteoles*** ovate lanceolate, 6-6.5 (--7) x 1.1-1.5 mm, chartaceous texture, white-yellow or light brown colour, acuminate apex, with a dorsal crest on the upper quarter, shortly toothed, apex acuminate, shorter than tepals. ***Tepals*** linear-lanceolate, chartaceous, strong pink-fuchsia, apex apiculate, toothed with dense lanate trichomes in the dorsal part, size unequal, external tepals 9.4-10 x 0.7 mm, intermediate tepal 9.2-9.8 x 0.5 mm, inner tepals 9.1- 9.5 x 0.4 mm. ***Filaments*** 10-11 (--11.5) mm long, fused into a tube for 8.4-9.4 mm long, white-light yellow colour, free part 1.6 mm long. ***Filament appendages*** conspicuous, 1.2 mm long elliptic lanceolate (united part 0.6 mm) arising at the tip (Fig. 4-10 F). ***Anthers*** 2.5-2.8 mm long, inserted between the filament appendages. ***Gynocecium*** with 2 filiform stigma branches of 1.5-1.8 mm in length, style 0.3-0.4-mm, ovary subglobose 1.5-1.8, one ovule. [voucher: Borsch & Ortuño, 3572 (B, LPB) = AC141].

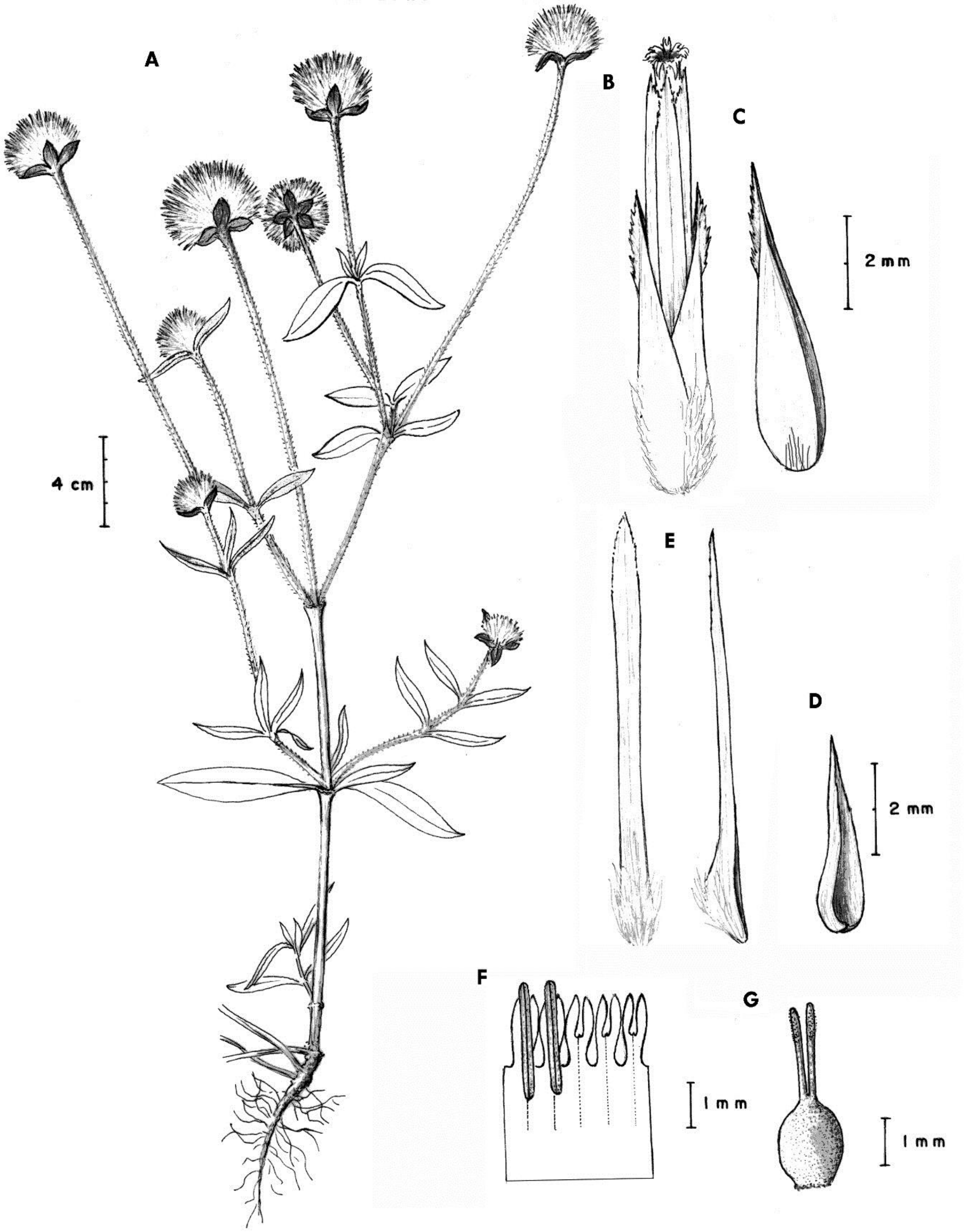


Fig. 4-13. *Gomphrena haenkeana* Mart. A) Habit. B) Flowers with lanate trichomes at the base. C) Bracteoles. D) Bract. E) Tepals. F) Detail of the androecium. G) Gynoecium. [voucher: Borsch & Ortuño 3585 (B, LPB)].

Micromorphology of trichomes. Multicellular uniseriate, on *stems and cauline leaves* with1-3 basal cells, thicker, the basal most subglobose, close to junctions with granulose and salicose ormanentarions. The 4-6 uppers cells with firm consistence, salicose, with spinous to granulose, ornamentation, with a strongly striated texture cuticule. Interlocking junctions, conspicuous linear, scars arranged in in parallel to trichome axis or in an angle of 45 degrees. A*pical leaves subtending paracladia trichomes,* with the lower part similar than the stems and cauline leaves, white, their upper surface glabrous. ***Trichomes on tepals*** only with long-elongate cylindrical cells, the upper collapsed, large, twisted and sinuous. ***Anatomy of tepals.*** Tissue is composed of elongate straight, cylindrical dermal cells, arranged in one row, the extremes fitting perfectly, the fibrous cells of tepals protrude in the margin as teeth. [voucher: Borsch, Ortuño & Fuentes, 3963].

Taxonomic remarks. The differences between *G. haenkeana* and the close species *G. trollii* are the texture and color of the tepals, and the annual condition of *G. haenkeana*, unlike a *G. trollii* that is perennial. The morphological patterns observed in the plants from Bolivia and Argentina examined in this work indicate that it is easy to distinguish the two species using the bracteole characters (presence or absence of crest/sizes and apex of bracteoles). Pedersen (1976) also thought that the annual life form distinguishes *G. haenkena* from *G. pulchella*.

The assumptions made by previous authors on the relationships of *G. haenkeana* and *G. pulchella* and the respective taxon concepts for these species are complex and many varieties for both species were described and then put into different synonymies by several authors. These taxon concepts were pre-phylogenetic and based on morphological characters (essentially following a morpho-species concept). Suessenguth (1934) considered *G. haenkeana* as a variety of *G. pulchella*, but Pedersen (1976) was not in accordance because he considered the two as different species. Here the treatment follows Pedersen. However, this study does not include *G. pulchella* because there are no samples or sequences of this species in Bolivia.

The type of *G. haenkeana* was collected by Tadeus Haenke, citing in the text only "Peruvia" as place of collection. This information was wrong because nobody else collected this species in Peru. For this reason and according to Pedersen this specimen came most likely from southern Bolivia; see also Bena (2017).

Habitat and ecology. The species grow in rocky slopes and in sandy soil, and it is common in the upper slopes of the river valleys of the "Rio Mizque", "Rio Parapeti", and "Rio Pilcomayo". It can form large populations with hundreds or even thousands of individuals in open places between trees

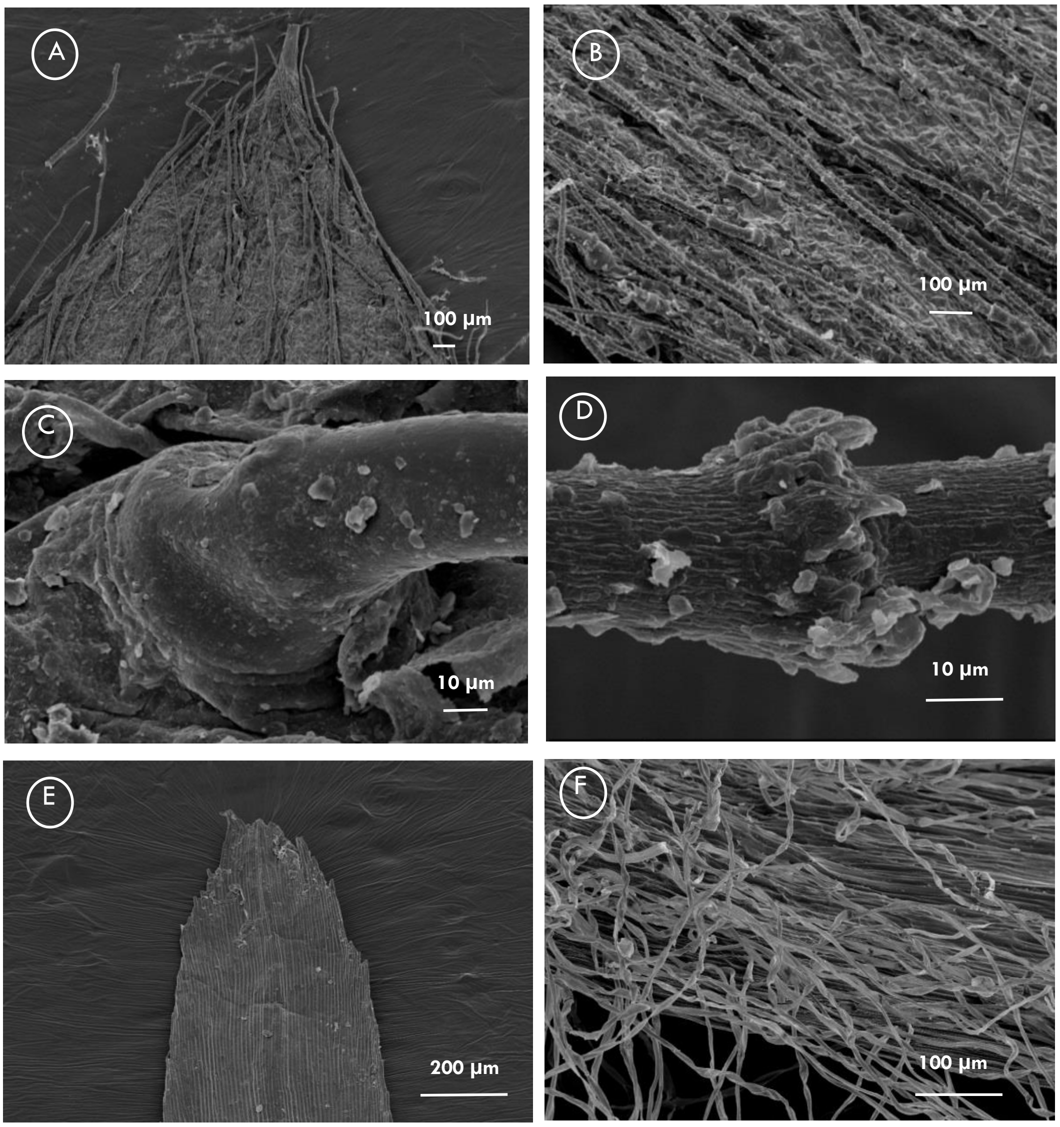


Fig. 4-14. *Gomphrena haenkeana* Mart. Cauline leaves: A) Upper leave surface with mucronulate apex, B) lower leaf surface with dense trichomes, C) detail of the basal cells of the trichomes, D) detail of the interlocking junction with the overlapping scar zero and forty-five angles degrees. Tepals: E) toothed apex, F) lanate trichomes on the dorsal part. [voucher: Borsch et al. 3963 (AC1051)].

and shrubs such as *Copernicia alba* Morong, *Schinopsis quebracho-colorado* (Schltdl.) F.A. Barkley & T. Mey.], *Senegalia emilioana* (Fortunato & Ciald.) Seigler & Ebinger, *Schinopsis cornuta* Loes. ex Herzog. Inter-Andean dry forest, Semi humid Puna, Dry Puna, Gran Chaco, Chiquitano dry forest, Tucuman- Bolivian forest, Chaco Serrano ecoregion. Altitudinal range of collections between (100) 320 – 3103 m.

Fig. 4-15. *Gomphrena trollii* Suess. A) Habit. B) Detail of the paracladia. C) Cordillera Colorada en Tupiza, photo Mario Giorgetta. *Gomphrena haenkeana* Pedersen. D & E) Habit. F) Detail of the paracladia.

Distribution. North East of Argentina, dptos. Jujuy, Salta, Tucuman. Southern Bolivia, province Luis calvo (Dept. Chuquisaca), province Cercado, Mizque, Narciso Campero, Aiquile, Punata (Dept. Cochabamba), provinces, Andres Ibañez (dept. Santa Cruz) provinces, Cercado, Gran Chaco. (Dept. Tarija) (see Fig. 16).

Specimens examined for distribution assessment. ***ARGENTINA, Jujuy***, Dr. Manuel Belgrano, Ruta Provincial 29 de Ruta Nacional 9 a Tiraxi, antes del Río Grande, [-65,425556, -24,04666699], 1635 m, 13, 2, 2010, *Zuloaga, F.O., 11604*, (SI). Ruta Provincial 1, de San Pedro a Santa

Clara, [-64,8400, -24,2972220], 566 m, 10, 2, 2010, *Zuloaga, F.O., 11482*, (SI). ***Salta***, La Capital, Ciudad de Salta. Playa de maniobras del FF.CC. frente a la estación, [-65,410556, -24,7883330], 1187 m, 3, 4, 1999, *Lázaro J. Novara, 11262*, (LPB). La Viña, Alrededores de La Viña, [-65,5747219, -25,4647219], 1230 m., 15, 2, 2010, *Zuloaga, F.O., 11829*, (SI). Orán, Ruta Prov. 5, 30 km de Pichinal camino a La Estrella, [-64,099, -23,5333299], 350 m, 2, 5, 2003, *Osvaldo Morrone, Maria E. Múlgura de Romero & Silvia S. Denham, 4567*, (LPB). ***Tucumán***, Trancas, Camino a Raco, [-65,3408330, -26,6111110], 850 m, 14, 11, 1920, *Venturi, S., 1056*, (LPB). ***BOLIVIA***, ***Chuquisaca***, ***Luis Calvo***, Centro El Salvador-CIMBOC., [-63,1666669, -20,616667], 783 m, 14, 4, 1993, *Saravia Toledo, C., 11811*, (LPB, CTES). ***Cochabamba***, ***Cercado*** camino Parotani-Capinota, Borde de camino terreno abandonado. [-66,302847, -17,5946810], 2447 m, 21, 1, 1991, *Antezana, C., 155*, (LPB). Camino La Paz a Cochabamba, a cerca a Cochabamba 6 km del puente Tapacari., [-66, 3568333333, -17, 6031666667], 2785 m, 1, 4, 2003, *Borsch, T.,* ***3572***, (LPB, B). Saliendo de Cochabamba hacia La Paz, en el Km. 46., [-67,33491667, -17,50916667], 2465 m, 12, 3, 2009, *Borsch, T.,* ***3963***, (LPB, B). Cerro San Pedro y Río Rocha, [-66,133888, -17,4005560], 2570 m, 14, 1, 1996, *De la Barra, N., 292*, (MO, LPB). ***Mizque***, Camino de Mizque a Aiquille, pasando el segundo puente antes de llegar a Mizque, [-65,354333, -17, 8956666667], 2196 m, 2, 4, 2003, *Borsch, T.,* ***3585***, (LPB, B). Rio Mizque, [-64,3333329, -18,6499], 1970 m, 28, 4, 1997, *Lara, D., 431*, (LPB). Rio Mizque, [-64,33333299, -18,6499], 1358 m, 28, 4, 1997, *Lara, D., 483*, (LPB). On N side of town, in weedy areas, [-65,333330, -17,9499], 2020 m, 4, 5, 2005, *Nee, M., 52941*, (LPB, NY). ***Narciso Campero***, Aiquile Villa Granado, Entre Aiquile y Villa Granado, [-65,18322499, -18,210839], 2270 m, 21, 3, 1999, *Antezana, C., 1138*, (LPB). Rumicancha (Aiquile), [-65,24305556, -18,12277778], 2360 m, 4, 1990, *Garcia, G.I.H., 40*, (LPB). Aiquile, [-65,1759109, -18,1995749], 2250 m, 16, 1, 1987, *Sigle, M., 305*, (LPB). En el camino de Aiquile a Totora, bajando al rio Mizque a 2 km de Chullkas, [-65,15201667, -17,9820667], 2076 m, 26, 3, 2003, *Wood, J.R.I., 19512*, (HSB,LPB). ***Punata***, 1 Km al N del puente sobre el Rio Pucara Mayu-Jatum Mayu 5 Km al NE de Punata por linea recta, [-65,8166669, -17,5], 3103 m, 5, 3, 1988, *Solomon, J.C., 17896*, (LPB, MO). ***Quillacollo***, Cerca de Parotani, [-66,333332, -17,4833329], 2655 m, 20, 3, 2002, *Ibañez, D., 80*, (LPB). On Cochabamba-Oruro highway between Parotani and Llavini, [-66,3616829, -17,6195780], 2900 m, 12, 2, 2003, *Wood, J.R.I., 19055*, (BOLV, LPB). ***Santa Cruz***, ***Andres Ibañez***, 3 km de Porongo hacia Santa Cruz, [-63,29277778, -17,82972222], 452 m, 10, 12, 2009, *Wood, J.R.I., 26660*, (LPB, USZ). ***Cordillera***, Misiones, Parque Nacional Kaa-Iya del Gran Chaco, 20 km al O del puesto Misiones, [-62,33250, -19,91250], 320 m, 19, 7, 1998, *Fuentes, A., 2634*, (LPB). Charagua, [-63,192768, -20,58333], 1300 m. 7, 4, 2011, *F. Estrada, 357*, (HSB). Camino a Boyuibe, entrando a mano derecha hacia plamarito, afloramiento de rocas, [-63,291029, -20,0081370], 759 m, 10, 6, 2006, *L. Arroyo, 3255*, (USZ, MO). Alto Parapetí, pequeña isla en el rio Paratetí, [-63, 6372222, -20.058333], 850 m, 28, 12, 1982, *Michel, R. de, 194*, (LPB). Alto Parapetí, [--63.636944, -18,00805556], 800 m, 28, 12, 1979, *Michel, R. de, 1*, (LPB, B, CTES, MO, NY, SI, USZ). Along highway from yacuiba to camiri, 2.2 Km. by road SE of Salinas and turnoff to Charagua, [-63,455278, -20,239722], 915 m, 13, 2, 2006, *Nee, M., 54147*, (LPB, NY). 10 km de Boyuibe a Camiri. Pasando el alambrado de una propiedad, orilla del camino, [-63,3361110, -20,3930560], 914 m, 26, 4, 2007, *Ortuño, T., 753*, (LPB). ***Florida***, Abra de San Juan, ca. 6 Km del pueblo de Samaipata, sobre el camino a Vallecito, ca 500 m, entrando por camino vecinal, lado derecho de la carretera, [-63,866667, -18,2166670], 1923 m, 25, 3, 2004, *Mendoza, M., 900*, (LPB, USZ). 3 Km. S of Mataral on road to Vallegrande, [-64,216667,-18,1333], 1425 m, 6, 2, 1988, *Nee, M., 36250*, (LPB, NY). ***Manuel María Caballero***, Camino de Aiquile a Santa Cruz carretera vieja. Cerca Saipina., [-64, 4688333333, -18, 1026666667], 1594 m, 6, 4, 2003, *Borsch, T., 3627*, (LPB, B). 2.5 km N of Tambo, rio San Isidro (Río Pulquina) Valley, [-64,43330,-18,1499], 1500 m, NW of bridge at San Isidro, [-64,451660, -18,023610], 1620 m, 17, 4, 2002, *Nee, M., 52178*, (NY). 5,7 Km al SE de San Isidro, [-64,40, -18,066], 1600 m, 9, 3, 1988, *Solomon, J.C., 17987*, (LPB, MO). San Isidro, ca. 4 km antes de San Isidro, sobre la carretera principal Santa Cruz-Cochabamba, [-64,3833329, -18,083333], 1636 m, 11, 4, 2003, *Wood, J.R.I., 19680*, (USZ, LPB). Saipina, A 4 Km al Este de la estancia El Canal, exposicion Oeste del cerro El Maguial, [-64,6083330, -18,0055559], 1567 m, 18, 3, 1995, *Balcazar, J, 243*, (LPB, USZ). ***Vallegrande***, SW del centro del poblado, [-64,1122220, -18,488610999], 2054 m, 11, 5, 2008, *Peñaranda postrasa, 824*, (HSB). Camino hacia el Rodeo, [-64,1469440, -18,4869440], 2365 m, 5, 3, 2011, *Luzmila Arroyo P., G.A. Parada, M. Betancur & M. Huanca, 5339*, (USZ). Potreros de los comunarios, [-64,411, -18,215], 1398 m, 10, 4, 2011, *M. Huanca, Miguelina Muñoz & F. Abasto, 12*, (LPB). Vallegrande [-64,1122220, -18,489], 2100 m, 4, 12, 2011, *Parada, G.A, 4013*, 23, 2, 1984, *Schmitt, G., 56*, (LPB). Along highway from Comarapa to San Isidro, 3 km (MO, USZ). 2 Km above Santa Rosa on road Pucara in Rio Grande valley, [-64,2911, -18,7088889], 1100 m, 12, 2, 1996, *Wood, J.R.I., 10654*, (LPB). ***Tarija***, ***Cercado***, Cerca Santa Ana, finca de Kohlberg, plano, [-64,616044, -21,592542], 1860 m, 11, 1, 1986, *Bastian, E., 397*, (LPB,B, CTES, NY). Yesera, [-64,551381, -21,416553], 2050 m, 12, 3, 1988, *Ehrich, R., 489*, (LPB). Along rio Guadalquivir w Tarija, [-64,75, -21,5333329], 1920 m, 19, 2, 2002, *Müller, J., 9092*, (LPB). ***Gran Chaco***, Carretera de Boyuibe a Villamontes, al borde de la via ferrea que va paralelo a la carretera, [-63,2805559, -20,500278], 822 m, 15, 3, 2007, *Atahuachi, M., 1121*, (BOLV, USZ, LPB). 0.5 Km E of Chuvere., [-63,802778, -21,5375], 870 m, 23, 3, 2007, *Nee, M., 54878*, (LPB, NY). Along highway from Yacuiba to Villa Montes, 1 km N of Palmar Grande town, [-63,46083, -21,538329], 480 m, 13, 5, 2005, *Nee, M., 53002*, (NY, LPB). ***José María Avilés***, Chocloca, 6 Km SW al camino, [-64,765172, -21,774830], 2000 m, 25, 3, 1979, *Beck, S.G., 743*, (LPB). Quebrada de Colón, [-64,599, -21,766], 1720 m, 25, 3, 1994, *Subieta, M., 213*, LPB.

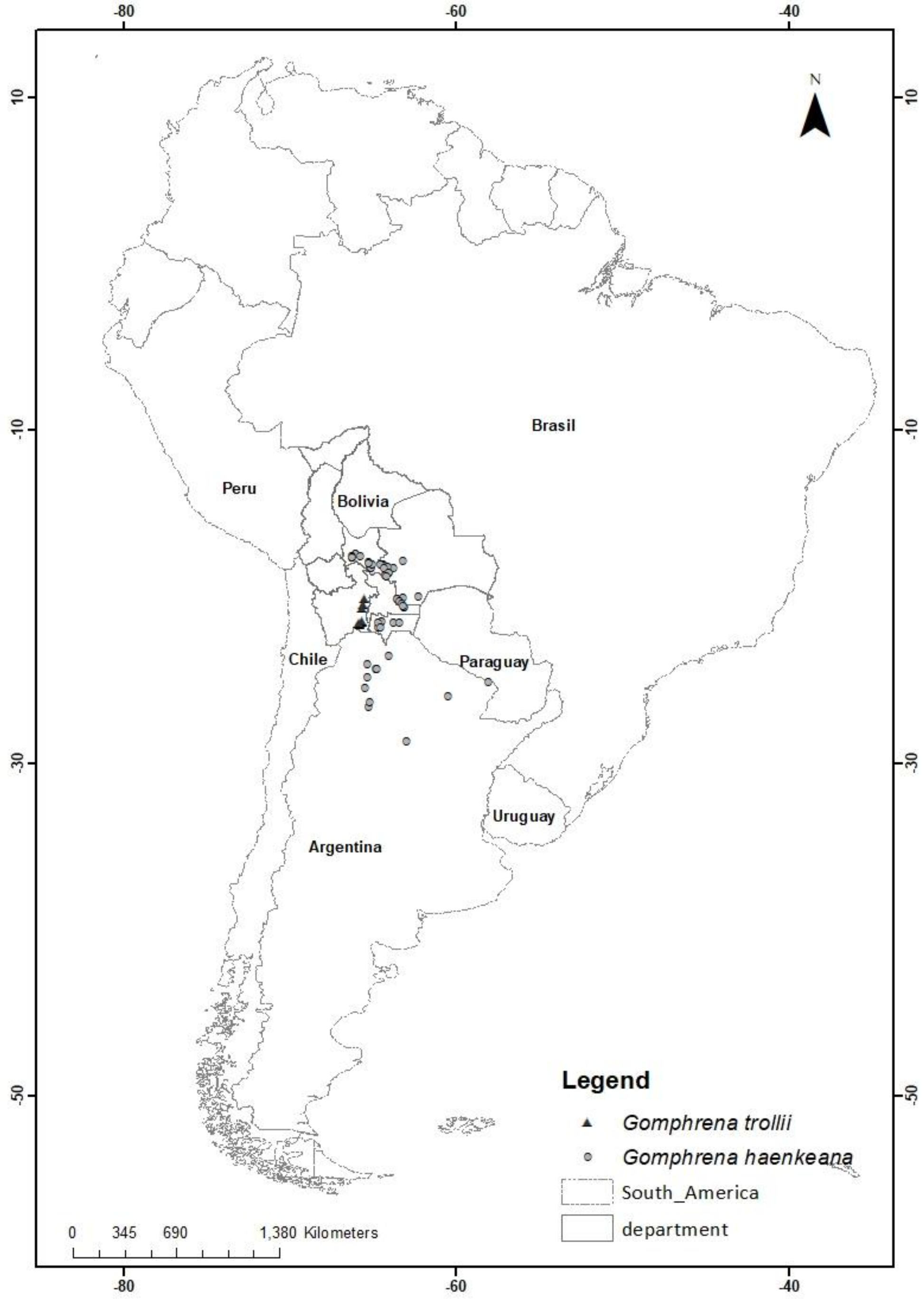


Fig. 4-16. Distribution of the species *Gomphrena trollii* and *G. haenkeana*.

4.3.3. Gomphrena phaeotricha CLADE

Gomphrena phaeotricha and allies form a subclade within the "Mostly Andean Clade A". The *matK-trnK* tree (Fig. 3-2, chapter 3) shows high support for the *G. phaeotricha* clade (1.00 PP, 92 BS, 61JK). Two further sublineages are found but there is no clear picture about relationships of all the samples in this clade (e.g. *G. pallida* subsp. *munda*, AC438 and AC439). One of these sublineages corresponds to the typical specimens of *G. phaeotricha* from Argentina described by Pedersen (1976), i.e. *G. phaeotricha* from Salta-Argentina, (Borsch & Ortuño 3738, AC441), close to Borsch & Ortuño 3647 (*G.* sp. nov. type b, AC489), and Borsch & Ortuño 3657 (*G. phaeotricha* (a), AC491). The second sublineage is composed by specimen Borsch & Ortuño 3648 (*G. sp. nov. type b*, AC168) and specimen Borsch & Ortuño 3753 (*G. sp. nov. (f. calva)*, AC447) supported by the Bayesian analysis (1.00 PP), but weakly by the parsimony and Likelihood inference (63BS, 74JK).

In the case of the ITS tree (Fig. 3-3, chapter 3) a *G. phaeotricha* clade appears monophyletic including two sublineages that can be distinguished. The first with samples *G. phaeoticha* Borsch & Ortuño 3648 (*G. sp. nov. type b*, AC168), Borsch & Ortuño 3657 (*G. phaeotricha* (a), AC491), and Borsch & Ortuño 3647 (*G. sp. nov. type b*, AC489). The second sublineage is composed by samples Borsch & Ortuño 3738 (*G. phaeotricha* AC441). and AC 438 (*G. pallida* subsp. *munda*). The third sublineage includes two samples, one is Borsch, Ortuño & López 3733 (AC439) and Ortuño 1677 (*sp. nov.* spec7, AC1007) that are well supported as sisters (1PP, 100 JK).

The principal difference between plastid and ITS trees is the sample Borsch & Ortuño 3753 (*G. sp.* nov. (f. calva), AC447), showing an incongruent isolated position. This incongruence can result from reticulate evolution or incomplete lineage sorting and in part explain the difficulty of achieving resolution within this clade. Further research including more genetic data and the sampling of populations as well as on ecology is required in this region, in order to get a better understanding about speciation in this clade. In this thesis the corresponding provisional taxon descriptions are made: *G. phaeotricha*, G. *sp. nov.* (type b) ined., G. *sp. nov.* (spec7) ined., *G. sp. nov.* (*flexuosa*), *G. sp. nov. (calva)*. The specimen Borsch & Ortuño 3753 (AC447) appears morphologically similar to the G. *phaeotricha* clade and is treated here according the position in the plastid tree.

The distribution maps of G. *phaeotricha* and allies (Fig. 4-28) show that all the species of this clade are occurring in a similar geographic area. The geomorphology of this region facilitates that populations are separated by the complex mountain topography, and as a result, there are isolated localities with probably specific microclimates, and different soil types. In this area other new endemic species were found (Ortuño & Borsch 2005, Beck St. 2008, Essi et al. 2010, Huaylla et al. 2010). The results of molecular clock dating for this clade indicate that the crown group has arisen about 1.5 Ma (Fig. 3-8, Chapter 3), indicating very recent speciation events.

The differences between the entities recognized here are mainly in the different degrees of fusion of the saminal tube and thus position of anthers, the shape of bracteoles, the position, morphology and colour of the trichomes, and main differences are in the indumentum on the apical leaves subtending the paracladia. See descriptions and taxonomic comments below.

Key to entities in the G. phaeotricha CLADE

1. All tepals completely glabrous. Bracteoles with wide, widely prominent crest extended on two thirds to three quarters along the dorsal part of the middle nerve. (2)

2. Filament tube completely united, anther appears sunken between two filament appendices. Inner tepals considerably shorter than the external ones, glabrous. …..…………………………………………………………………… *G. phaeotricha* (Fig. 4-17)

2'. Filament tube almost completely united……………………….. *G. sp. nov. (calva)* (Fig.4-26)

1' Inner tepalswith trichomes or trichomes on other tepals only in the dorsal part but never on the margin, filament tube completely united, anther sunken between two filament appendices (3)

3. All the tepals with trichomes in the dorsal part, bract dentate at apex (4)

4. Stems voluble and thin. Bracteoles ovate-lanceolate, crested for about a quarter, margin of actual bracteole entire. Trichomes in the adaxial part with two ovate to elliptic and broad interlocking junctions …………………………………………… *G. spec. nov. (flexuosa)* (Fig. 4-25)

4'. Stems firm. Bracteoles ovolanceolate to elliptical, the lateral blades of the bracteoles wide and deeply dentate at margin. Ovate to elliptic in shape, trichomes with narrow interlocking junctions ……………………………………………………………*G. sp. nov (spec7)* (Fig. 4-21)

3' Inner tepals with trichomes, apical leaves subtending the paracladia ovolanceolate to cordate, acute at apex, smaller than the inflorescence and glabrous. ….. *G. sp. nov. (type b)* (Fig. 4- 19)

4.3.3.1. ***Gomphrena phaeotricha*** **Pedersen**, Darwiniana 20 (1–2): 286, f. 3. 1976.

Type: Argentina, Tucumán Prov., Chicligasta Dept., Quebrada del Río las Pavas, between Puesto La Cascada and Cuevas Pajonales, 2800-3000 m, J.G. Hawkes, J.P. Hjerting & K. Rahn 3599. (HT: C C1005408, IT: CTES, CTES0000315, WAG WAG0000065).

Annual, herb, 2.5-19 (--30) cm. ***Root*** simple, fibrous. ***Stems*** decumbent to ascendent, with secondary and tertiary stems, striate, densely appressed indumentum, trichomes light to dark brown, darkest near the inflorescence, 0.4--2 mm long. ***Cauline leaves*** ovolanceolate, 1-3.2 (--4.2) x 0.5-1.2 (--1.6) cm, acute at apex, middle nerve prominent, the first pair of lateral veins conspicuous, indumentum appressed, denser at the margin and in the dorsal part. ***Apical leaves subtending paracladia*** *(inflorescences)*. 3-4 leaves located symmetrically, cordate to ovate, usually smaller than the paracladia, 0,4-0.8 (--1.0) x 0.4-0.8 (--1.1) cm, dense trichomes in the lower part and the margin, upper part glabrous, dark brown to black colour. ***Inflorescence*** globose, terminal on the vegetative axes, 0.5-1.7 (--2) cm, consisting of 1-5 partial florescences. ***Flowers*** 3-4.3 (--5.6) x1.5 -1.9 mm in size. ***Bracts*** ovate-lanceolate, cymbiform, 3- 3.5 (--3.7) x 1.2-1.4 mm, fine membranous in texture, white translucent, acute at apex, middle nerve excurrent for ca. 1 mm. ***Bracteoles*** ovolanceolate, 3-4.2 (--4.8) x 1.2-1.3(--1.5) mm, membranous, white, crest extending for three quarters in the dorsal part of the middle nerve, crest rounded, dentate at margin and apex, white. ***Tepals*** lanceolate narrowest at middle, fine membranous, white translucent, acute and dentate at apex, the size unequal, the external tepals 2.8-3 (--3.3) x 0.5 mm, intermediate tepals 2.5-2.8 (3.1) x 0.5 mm, inner tepals, 1.3-1.5 (--1.7) mm, more cymbiform, markedly smaller than the other (Fig, 17 E). ***Filaments*** 2-3.7 (--4.6), fused into a tube, 1.5-3.1 (--4.1) mm, free part 0.25-0.32 mm. ***Filament appendages*** conspicuous, 0.45-0.5 mm long, lanceolate, arising at the tip of filament tube. ***Anthers*** oblong, 0.8 mm long, inserted between the two filaments appendices (Fig. 4-17 G). ***Gynoecium*** with two filiform stigma branches of 1.2-1.4 mm length, style 0.4 mm, ovary subglobose, 0.6-0.5 mm. [voucher: Borsch & Ortuño, 3738 = AC441 (B, LPB)].

Micromorphology of trichomes: Multicellular uniseriate on stems and cauline leaves with 1-3 conspicuous and rounded basal cells (Fig.4-18B). The 3-6 upper cells with firm consistence, granulate ornamentation and cuticule with flat striae. ***Interlocking junctions*** conspicuous, linear scars arranged in an angle zero degrees overlapping, scars arranged in parallel to the axis of the trichomes (Fig. 18C). ***Trichomes on apical leaves subtending paracladia*** similar then on stems, but dark brown to black in the lower side of leaves and at margin. The upper side glabrous. ***Trichomes on tepals*** glabrous, the epidermic cells has strait form. Anatomy of ***tepals.*** Tissue are composed of elongate strait, cylindrical dermal cells, arranged in single rows, all fitting perfectly, in the margin protruding like fibers [voucher: Borsch. & Ortuño, 3657 (B, LPB)] (Fig. 4-18 F).

Taxonomic remarks. Pedersen (1976) described *G. phaeotricha* as a new species. This specimen (Hawkes, J. P, Hjerting & K. Rahn N° 3599) was identified before as *G. oligocephala*. However, it is clear that *G. oligocephala* is a different species because *G. phaeotricha* is annual and *G. oligocephala* is a perennial plant; furthermore *G. oligocephala* is endemic of Bolivia (Borsch, Ortuño & Nee 2014).

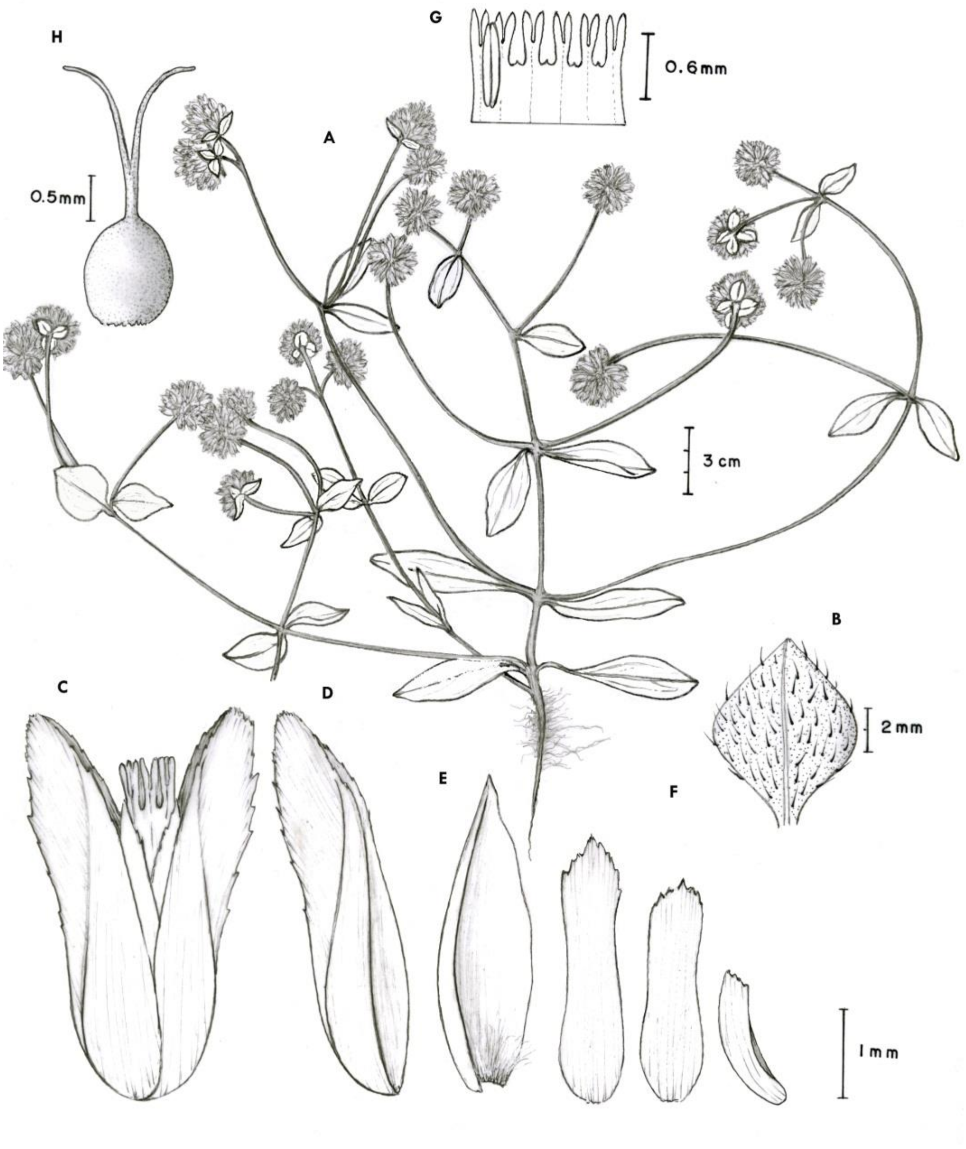


Fig. 4-17. *Gomphrena phaeotricha* Pedersen. A) Habit. B) Apical leaves subtending paracladia, detail of the lower part. C) Flower. D) Bracteoles. E) Bract. F) Tepals. G) Detail of the androecium. H) Gynoecium [voucher: Borsch & Ortuño 3738].

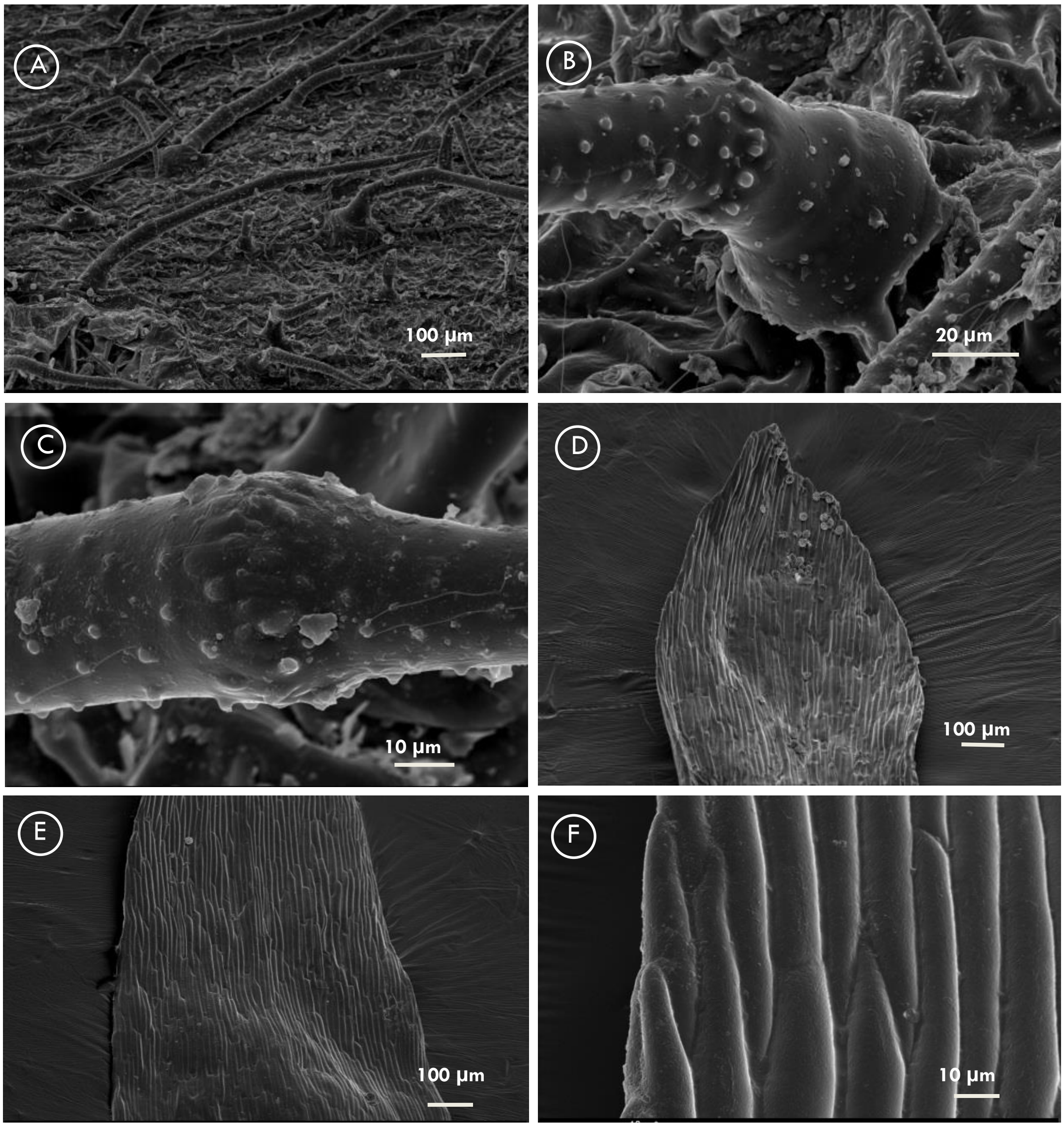


Fig. 4-18. *Gomphrena phaeotricha* Pedersen. Cauline leaves. A) Appressed trichomes. B) Rounded basal cells of a trichome with granulate ornamentation in the second cells. C) Thick interlocking junctions, conspicuous linear scars arranged in an angle of zero degrees overlapping. D) Apex of tepal. E) Dorsal part of the tepals without trichomes. F) Detail of the straight form of epidemics cells of tepals. [voucher Borsch & Ortuño 3657= *G. phaeotricha* a].

For Pedersen (1976) *G. phaeotricha* is distinguished by glabrous tepals, the size of the inner tepals is smaller with respect to the external. I found them usually half the length of the outer ones, but occasionally up to two-thirds of their length. The crest is widely winged and extending along the dorsal part, an important characteristic is the position of the anther in the completely fused filament tube, where the anther appears sunken between the laterally also partly fused filament appendages (of two adjacent filaments). Pedersen (1976) compared the insertion point of the filaments as similar to what can be found in *Pseudogomphrena*.

In this work, in addition to the characters proposed by Pedersen (1976), two additional characters are used to differentiate *G. phaeotricha* from the other annuals such as *G. pallida*. These characters are the form of the tepals, which are never narrow in the middle in *G. phaeotricha*, as well as the absence of trichomes in the margin of the tepals. To the contrast, trichomes are frequently found there in the clade of *G. pallida* and related species.

Although the molecular data do not fully resolve all samples or provide statistical support within the *G. phaeotricha* clade, it is possible to observe that the specimens included display morphological differences. The morphologically closest specimen to the type of *G. phaeotricha* is Borsch & Ortuño *3657 (*AC 491*)* and Borsch & Ortuño *3653,* both populations occur in Southern Bolivia (Cuesta de Sama).

The vouchers Borsch & Ortuño 3648 (*G. sp. nov. type b, AC168*), and Borsch & Ortuño 3647 (*G. sp. nov. type b, AC489*) are from Tarija, having trichomes in the dorsal part of inner tepals, but not at the margin, and the anther is on a completely fused staminal tube, thus between the filament appendices.

Habitat and ecology. In Argentina the sample Borsch & Ortuño 3738 (*G. phaeotricha*, AC441) was collected in the National Park of Cardones, in a place known as "Valle Encantado" (3100 m). There was one abundant population growing in humid and green grassland at the bottom of a valley with prominent rocks. In Bolivia the species is found in open scrub in rocky slopes in the Inter-Andean dry forest, Semi humid Puna, Prepuna, Tucuman-Bolivian forest ecoregions, where the plants were collected between 2100 – 3600(4000) m.

Distribution. The species is distributed in North-East Argentina and Southern Bolivia. Argentina Provinces of Jujuy, Quiaca. In Bolivia, Provinces of Chayanta and Charcas (Departament of Potosí), Provinces Oropeza, Tomina (Departament of Chuquisaca) and Provinces Mendez, O'connor, Aniceto Arce and José María Avilés (Departament of Tarija) (see Fig. 4-28).

Specimens examined for distribution assessment. ***ARGENTINA, Tucumán,*** Chicligasta, Quebrada del Río Las Pavas, between Puesto La Cascada and Las Cuevas Pajonales, [-65,9666670, -27,1833330], 2627 m, 24, 2, 1966, *Hawkes, J. G., 3599*, (MO). ***Salta***, Bajando de la entrada del Parque Nacional los Cardones en el lugar conocido como El valle Encantado, [-65,84038333, -25,19341667], 3100 m, 7, 4, 2004, *Borsch, Th., **3738***, (LPB, B). **BOLIVIA, Chuquisaca**, ***Tomina***, Saliendo de la comunidad El Villar camino a Alcalá, [-64,316666999, -19,21666700], 2100 m, 1, 7, 2004, *Carretero, A., 1135*, (BONN, HSB, MO). ***Potosí, Charcas,*** Parque Nacional Toro Toro. Ladera camino hacia escalon a 1km aprox., [-65,7671969, -18,132614], 2750 m, 12, 2, 1999, *Zamora, V., 6*, (LPB). ***Chayanta,*** Ravelo, -[65.611067, -18.865867], 3320 m, 9, 1996, *Sallés, C., 119*, (LPB). ***Tarija, José María Aviléz,*** Bajando del Abra de Turcamarca hacia Antigal, [-65, -21,80], 4000 m, 22, 4, 2000, *Beck, St.G., 27379*, (LPB). ***Mendez,*** Camino de Tarija a Potosí, subiendo la "Cuesta de Sama", [-64.866, -21.4499], 3151 m, 11, 4, 2003, *Borsch, Th., 3653,* (LPB, B). Camino de Tarija a Potosí subiendo la "Cuesta de Sama", [-64,5422899, -21,2987], 3834 m, 11, 4, 2003, *Borsch, Th.,* ***3657***, (LPB, B). 25 Km hacia Camargo, 2765 m, 26, 3, 1979, *Beck, St. G., 833,* (LPB). Sama, [-64,94498900, -21,483069], 3515 m, 15, 2, 1986, *Ehrich, R., 121*, (LPB). Sama, [-64,93794200, -21,48228299], 3556 m, 7, 2, 1987, *Ehrich, R., 319*, (LPB). Cantón Paycho, [-64,9266667, -21,295], 3600 m, 27, 2, 1991, *García, E., 2312*, (LPB). Cantón Paycho, subida a la cordillera, quebrada loma Kewiña, frente a la quebrada Pinta, [-64,93166667, -21,27972222], 3500 m, 28, 2, 1991, *García, E., 2457*, (LPB). Cantón Paycho. Subida a la cordillera, quebrada loma Kewiña, frente a la quebrada Pinta, [-64,93166667, -21,27972222], 3500 m, 28, 2, 1991, *García, E., 2484*, (LPB). **Aniceto Arce**, Cerro Pabellón, arriba de la población de Cañas, [-64,8666670, -21,866667], 2700 m, 15, 3, 1998, *Beck, St.G., 26129*, (LPB). ***José María Avilés***, Serranía Sama, bajando de la quebrada Corralitos hacia Antigal., [-64,95000, -21,800], 3200 m, 23, 4, 2000, *Beck, St.G., 27464*, (LPB).

4.3.3.2 ***Gomphrena*** *sp. nov. (type b)* T. Ortuño & Borsch, [ined.]

Type: Bolivia, Dept. Tarija, O'Connor, La cumbre del camino de Entre Ríos a Tarija, *Borsch, T. & Ortuño, T.,* 3648, 10 April 2003. 64°29'4.33 W 21°27'11421 S, 2329 m. (HT: LPB 0001621LPB,
IT: B).

Annual herb 9.2-9.4 (--12.5) cm. ***Root*** simple, fibrous. ***Stems*** decumbent, 6.3-9.5 (--12.5) cm long, with secondary stems, strigose, with dense villous indumentum, with white to light yellow colour trichomes. ***Cauline leaves*** sessile, lanceolate-oblong blades, 2.2 (--3.6) x 0.9 (--1.3) cm, acute, mucronate (0.2 mm), apex, decurrent, green olive, trichomes same as on stems, denser in the lower part. ***Apical leaves subtending paracladia*** *(inflorescences)* 3-6 leaves arranged symmetrically usually smaller than the paracladia, ovolanceolate-cordate, 0.4-1 (--1.2) x 0.3-0.6 (--0.8) cm, similar to cauline leaves in texture and indumentum, yellow to light brown, trichomes denser at the base of leaves and at the margin, the upper side of blade without trichomes. ***Inflorescences*** terminal on the vegetative axes, 1.1-1.6 (--1.8) cm in diameter, consisting of 2-6 paracladia. ***Flowers*** 4-4.2 (--4.4) mm long. ***Bracts*** ovate-lanceolate, cymbiform 2 (--2.2) x 0.8 mm, membranous texture, white colour, acute at apex, middle nerve prominent, cymbiform. ***Bracteoles*** ovate-lanceolate, 4-4.2 x 0.8-1 mm, membranous texture, white colour, acute at apex, a half of the dorsal part with moderately wide wing crest, toothed at apex crest. ***Tepals*** lanceolate and narrower at middle, membranous, white, acute and toothed at apex. The external and intermediate glabrous, the inner densely lanate in the dorsal part or glabrous, unequal size; external tepals 3.5-4 (--4.3) x 0.5 mm, intermediate tepal 3.5-3.9 (--4.2) x 0.4 mm, inner tepals 2.9-3.6 (--3.8) x 0.3 mm, (Fig. 4-15E). ***Filaments*** 4-4.8 (--5.9) mm long, fused into a tube, 2.8-3.6 (--4.7) mm. ***Filament appendages*** conspicuous, 0.8 mm long lanceolate shape, (base united 0.4) (Fig. 4-19 F). ***Anthers*** oblong, 1 mm, inserted between the two filament appendages. ***Gynoecium*** with two filiform branches of 1.2 mm length, style 0.4 mm, ovary subglobose, 0.6-0.5 mm. [voucher: Borsch & Ortuño 3648 = AC168 (LPB, B)].

Micromorphology of trichomes. Multicellular, uniseriate on stems and cauline leaves with 1-3 conspicuous basal cells, the first rounded, the others strait. The 4-7 upper cells with firm to flexible consistence, granulate, spinous and salicose ornamentation, cuticle with somewhat striated texture. Interlocking junctions simple conspicuous. ***Trichomes on apical leaves subtending the paracladia*** in the lower part of the leaves and the margin similar than on stems and cauline leaves, light brown, the upper side glabrous. *Anatomy of tepals*. Tissue composed of elongate strait, cylindrical dermal cells, arranged in one row, all fitting perfectly. [voucher: Borsch & Ortuño 3648].

Pollen. Diameter ~16 µm. Pore number 46-52. Pore ~2.8 µm in diameter, pore membrane with ektexinous bodies, widely arranged circularly in a mosaic-like pattern. Mesosporia hexagonal or pentagonal, rounded (sharp) angles, corners with spine-like protusions, tectum complete, columnellae visible. [voucher: Borsch & Ortuño 3648] (Fig. 20-A, B).

Taxonomic remarks. Molecular data do not resolve the position of this entity and there is inconsistence between ITS and *matK* trees. Morphologically an entity here called *Gomphrena sp. nov. (type b)* can be differentiated of the other species of the *G. phaeotricha* clade mainly through the anther placed at the tip of a completely fuesed filament tube between the filament appendices (Fig. 4-19). Some morphological difference was found among different specimens of *Gomphrena sp. nov. type b*, for example in the voucher Borsch & Ortuño 3648 (AC168) and Borsch & Ortuño 3647 (AC489), showing differences in the sizes of cauline leaves as well as the apical leaves subtending the paracladia

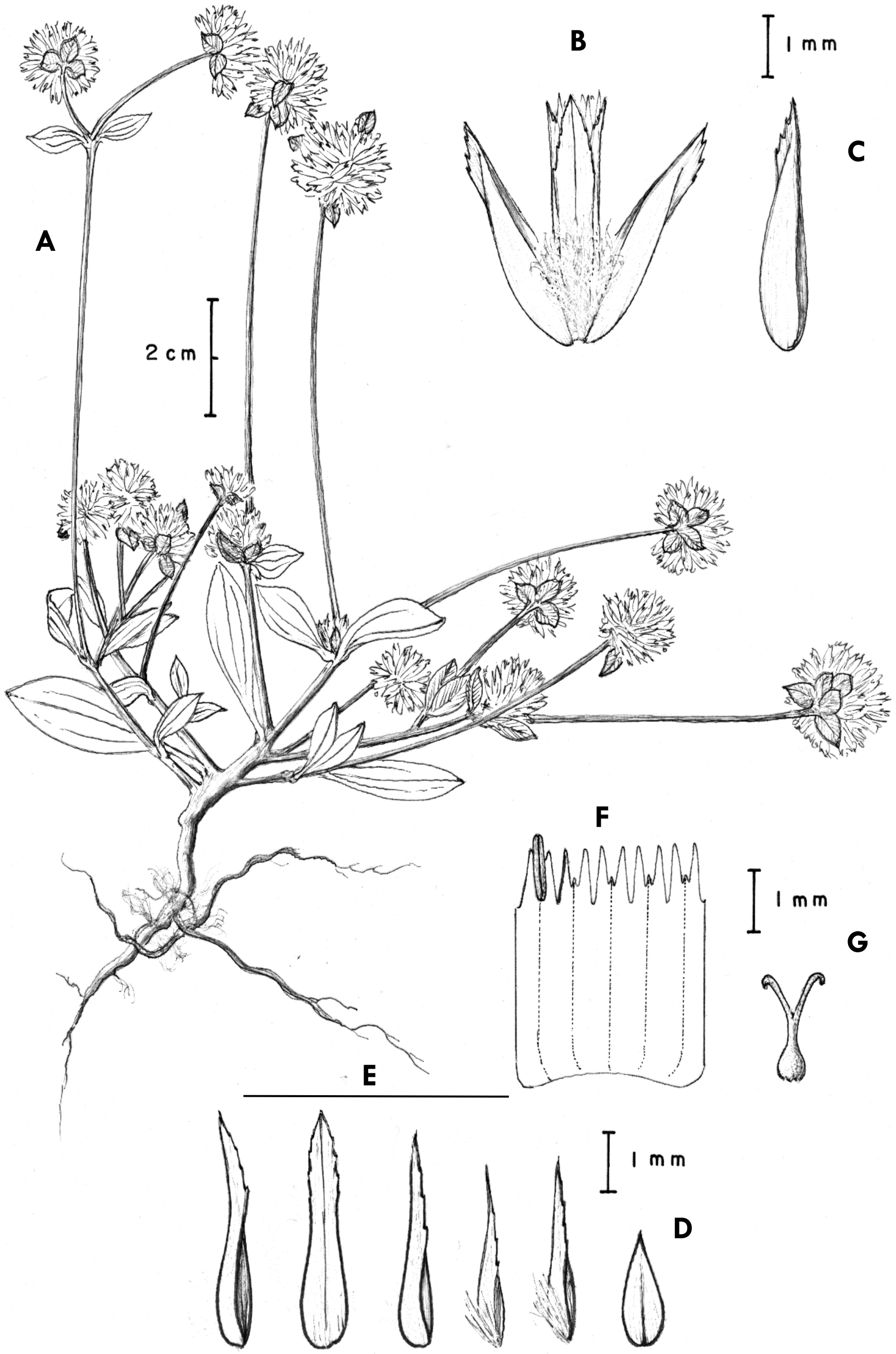


Fig. 4-19. *Gomphrena sp. nov. (type b)* Ortuño, T. & T. Borsch. A) Habit. B) Flower. C) Bracteoles. D) Bract. E) Tepals. F) Detail of the androecium. G) Gynoecium. [voucher: Borsch & Ortuño 3648].

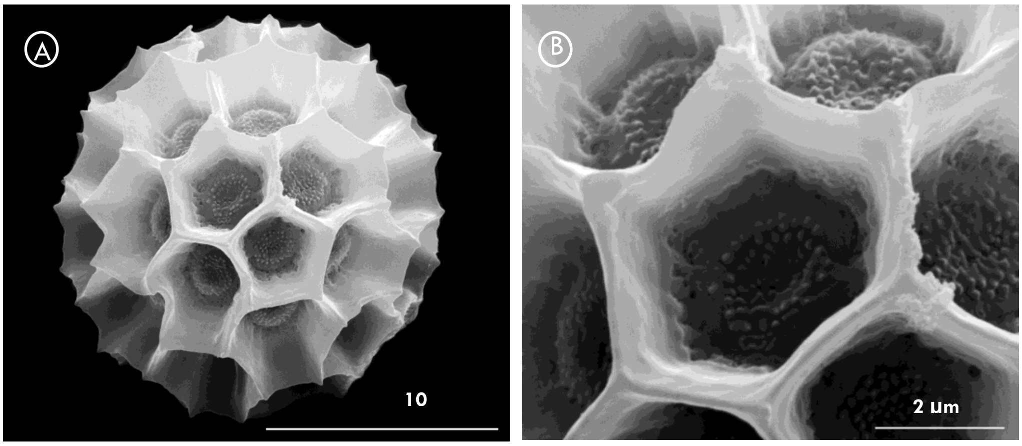


Fig. 4-20. *Gomphrena sp. nov. (type b)*. A) Pollen general overview. B) Detail of pore. Photo: Sara Kunz [voucher: Borsch & Ortuño 3648].

The difference among *Gomphrena sp. nov. type b* (Borsch & Ortuño 3648, AC 168) and Borsch & Ortuño 3657 (*Gomphrena phaeotricha* (a), Borsch & Ortuño *3657,* AC491) is that the second has all the tepals smaller than the bracteoles.

The entity provisionally called *G. sp. nov. (type b)* morphologically presents some similarities with *G. ferruginea* var. *rustica* Pedersen, for example by possessing inner tepals with trichomes and the anthers appearing attached between the filament appendices. However, the two mentioned species also have fundamental differences like the size and form the cauline leaves that are bigger in the *G. sp. nov. (type b)*. Moreover, in this last species the apical leaves subtending the paracladia are smaller than the inflorescence, the bracteoles are shorter than the tepals, the margin of the tepals is entire or only slightly dentate, and the plants in general are more erect and bigger.

The differences with the *G. sp. nov. (flexuosa)* and *G. sp. nov. (spec 7)* are discussed later (see below), and with respect to *G. pallida* this species (type b) has smaller inner tepals and the tepals never have trichomes at the margin of tepals. The apical leaves subtending the paracladia usually are glabrous, and the bracteoles have a large crest.

Habitat and ecology. This species is restricted to the ecoregion of the humid Puna of southern Bolivia, where it grows in open grasslands, in rocky places in areas of the humid Bosque Tucunamo boliviano with species of *Alnus*, and also in shrublands dominated by *Baccharis* sp., *Salvia sp.*, and Verbenaceae. Most the specimens were collected in habitats bordering mountains of South east Bolivia in the Tucuman-Bolivian forest. The distribution of collections range between 2094 to 3200 m of altitude.

Distribution. Province of Mendez, O'connor, Aniceto Arce and O'Connor (Dept. Tarija) (see Fig. 4-28).

Specimens examined for distribution assessment**:** **BOLIVIA**, ***Tarija***, ***Aniceto Arce***, [-64,6805, -21,9577780], 2130 m, 21, 2, 2006, *Beck, S.G., 31649*, (LPB). ***Aniceto Arce***, Cerro Pabellón, arriba de la población de Cañas [-64,8666, -21,866], 2700 m, 14, 3, 1998, *Beck, St.G., 26082*, (LPB). ***O'Connor***, Camino de Villamontes a Tarija. 45 km de Entre Ríos [-64,42546667, -21,4208833], 2669 m, 10, 4, 2003, *Borsch, Th., 3647* (LPB, B). 39,9 Km S of jct. Of road to Entre Rios on road to Padcaya, [-64,68, -21,89], 2100 m, 29, 4, 1983, *Solomon, J.C., 10267*, (LPB, MO). La cumbre del camino Entre Rios a Tarija., [-64,49055, -21,4519], 2329 m, 10, 4, 2003, *Borsch, Th.,* ***3648***, (LPB, B). [-64,4249, -21,421917], 2670 m, 22, 2, 2006, *Beck, S.G., 31692*, (LPB). ***Cercado***, Hacia la angostura entrando 11 Km hacia Papachacra, Serrania El cóndor, [-64,554, -21,6975], 2477 m, 24, 4, 2006, *Beck, S.G., 32049*, (LPB). ***Eustaquio Méndez***, Cuesta de Sama, 10 km de reten de Santa Barra Chica, cercanias del curce a Caña Cruz, [-*64,7999719, -21,446389], 2246 m, 13, 3, 2005, Mendoza, M., 1489, (USZ)*. Tomates grandes, campo experimental, [-64,81669, -21,2833], 2777 m, 12, 1, 1985, *Bastian, E., 351*, (LPB) **Chuquisaca**, ***Oropeza***, Side road from Punilla north along Rio Kollpa c. 4 km [-65,376322, -18,96220], 3200 m, 5, 4, 1997, *Wood, J.R.I., 12003*, (LPB).

4.3.3.3 *Gomphrena sp. nov.* *(spec7)* T. Ortuño & Borsch, [ined.]

Type: Bolivia, Dept. Potosí, Sud Chichas, Tupiza, camino al sillar, 65°27'52.92"W, 21°27'51.48"S, 3200 m. 26 February- 2012. *T. Ortuño, S. Beck, & A. Nuñez, D. Newman 1677*. (HT: LPB, IT: B).

Annual herb, up to 4.5 (--13) cm. ***Root*** simple, fibrous. ***Stems*** decumbent, unbranched or with secondary stems, slightly striated, indumentum appressed to villous, especially dense in the upper parts close to the inflorescence, the trichomes varying in colour from light to dark brown, 1-2 mm long. ***Cauline leaves*** sessile, lanceolate to oblong, 1.5-2 (--2.5) x 0.3-0.4 (--0.5) cm, mucronate at apex (midvein excurrent for 0.4 mm), with indumentum appressed denser in the lower part, white colour. ***Apical leaves subtending paracladia*** *(inflorescences)* 3-5, ovo-lanceolate, 0.5-0.8 (--1.4) x 0.4-0.7 (--1) cm, usually larger than the inflorescence, with acute to mucronate (0.4 mm) apex, in the lower part indument appressed, with trichomes light to dark brown; hirsute on upper side of leaf, intensely yellow in colour, trichomes short (Fig. 4-22G). ***Inflorescences*** terminal on the vegetative axes, 0.7-1.5 (--2.0) cm in diameter, consisting of 2-5 paracladia. ***Flowers*** 3.2-4 (--4.2) x 2.5 mm, grouped in 7-14 flowers forming one partial florescence. ***Bracts*** ovolanceolate, cymbiform, 3-3.2 (--3.5) x 2 mm, membranous in texture, white, acute at the apex, the margin dentate; with prominent middle nerve and with toothed crest. ***Bracteoles*** ovalanceolate to elliptical, 4-4.3 x 2 mm, membranous, white in colour, the lateral blades of the bracteoles wide and with toothed margin (see Fig. 4- 21E), at the apical lower part extended into a one third wide crest, toothed in the margin, bigger than tepals. ***Tepals*** lanceolate, narrowest in the middle, fine membranous, white, obtuse at apex, deeply dentate at apex and margin, with lanate indumentum in the dorsal part of all tepals, without trichomes at the margin, middle part scarious and green at anthesis. Sizes unequal, external tepals 2.4-3.8 x 0.6-0.8 mm, intermediate tepal 2.2-3.7 x 0.6-0.7 mm, inner tepals 2-3.6 x 0.3-0,4 mm. ***Filaments*** 2.1-3,2 (--3.5) mm long, fused into a tube, 1,1- 2.2 (--2.5) mm, free part 1mm long. ***Filament appendages*** conspicuous, 0.6 mm long, lanceolate in shape, (united basally for 0.4 mm; Fig. 4-21G). ***Anthers*** oblong, 1 mm long, attached between the filament appendages. ***Gynoecium*** with two filiform stigma branches of 0.8-1.1 mm length, style 0.2 mm, ovary subglobose 0.5-0.6 mm. [voucher: Ortuño et al. 1677 = AC1007 (B, LPB)].

Micromorphology of trichomes. Multicellular, uniseriate; on stems and cauline leaves, the 1-3 basal cells differning, first basals cell rounded and the others straight, all with firm consistence, surface of cuticle smooth. The upper cells 3-6, firm in consistence, with salicose and granulate ornamentation and prominently striated sculpture of the cuticule walls cells. ***Interlocking junctions*** **simple**, inconspicuous. The trichomes of the ***cauline leaves*** often collapsed and flattened, this most conspicuously on the upper leaf surface (Fig. 22C, F). ***On apical leaves subtending paracladia*** the trichomes of the lower surface with basal cells similar to the stems and cauline leaves; the upper cells with firm consistence, granulose ornamentation and incospicuos interlocking junctions. On the upper surface of leaf trichomes with one rounded firm basal cell, and two upper cells with ovate to elliptic shape, narrow interlocking junctions; cuticule smooth in sculpture (Fig. 22G). ***Anatomy of tepals.*** Composed by elongate straight, cylindrical cells, arranged in one row, the extremes fitting perfectly, the fibrous cells of tepals protruding at the margin as teeth.

Taxonomic remarks. The nuclear (ITS) and plastid (*matK-trnK*) molecular data show that *Gomphrena sp. nov.* spec7 belongs to the *G phaeotricha* clade, with low support (PP 0.76, 54 JK) in ITS, and with high support (1PP, 61JK, 92BS) in the plastid tree. In both trees the species level is not well resolved. However, in the nuclear ITS tree the *Gomphrena sp. nov. (spec7)* and *G. nov. comb. (flexuosa)* appear as sisters in the same subclade with high support (1PP, 100 JK).

The morphological characters that distinguish the G. *sp. nov.* (spec 7) are the size of the apical leaves subtending the paracladia, which are bigger than the inflorescence. The differences of the indumentum between the lower and the upper surface of the leaves, and the distinct hirsute indumentum on the upper surface composed of small intensely yellow trichomes formed by peculiar elliptic to ovate cells, with narrow interlocking junctions. The latter characteristic is the main difference between *G. sp. nov. (flexuosa)*.

The principal difference between G. sp. nov. (spec7) and *G. phaeotricha* is the insertion point of the anther, where in *G. sp. nov. (spec7)* they are attached between filament appendices and in *G. phaeotricha* are in middle part of two filament appendices (see Fig. 4-21 in description of *G. phaeotricha*).

Habitat and ecology. *G. sp. nov. (spec7)* grows in open rocky sites, between spinous shrubs e.g. *Prosopis ferox* Griseb., *Cercidium andicola* Griseb., columnar cacti such as *Trichocereus* ssp., globose cacti such as *Oreocereus celsianus* (Lem. ex Salm-Dyck) Riccob. and *Opuntia ssp.* In the Prepuna, the species is abundant in the localities around Tupiza (Department Potosí). Some specimens grow in Inter Andean Dry forest and in the Semi humid ecoregions, where the plants are collected between 2400-3700 m.

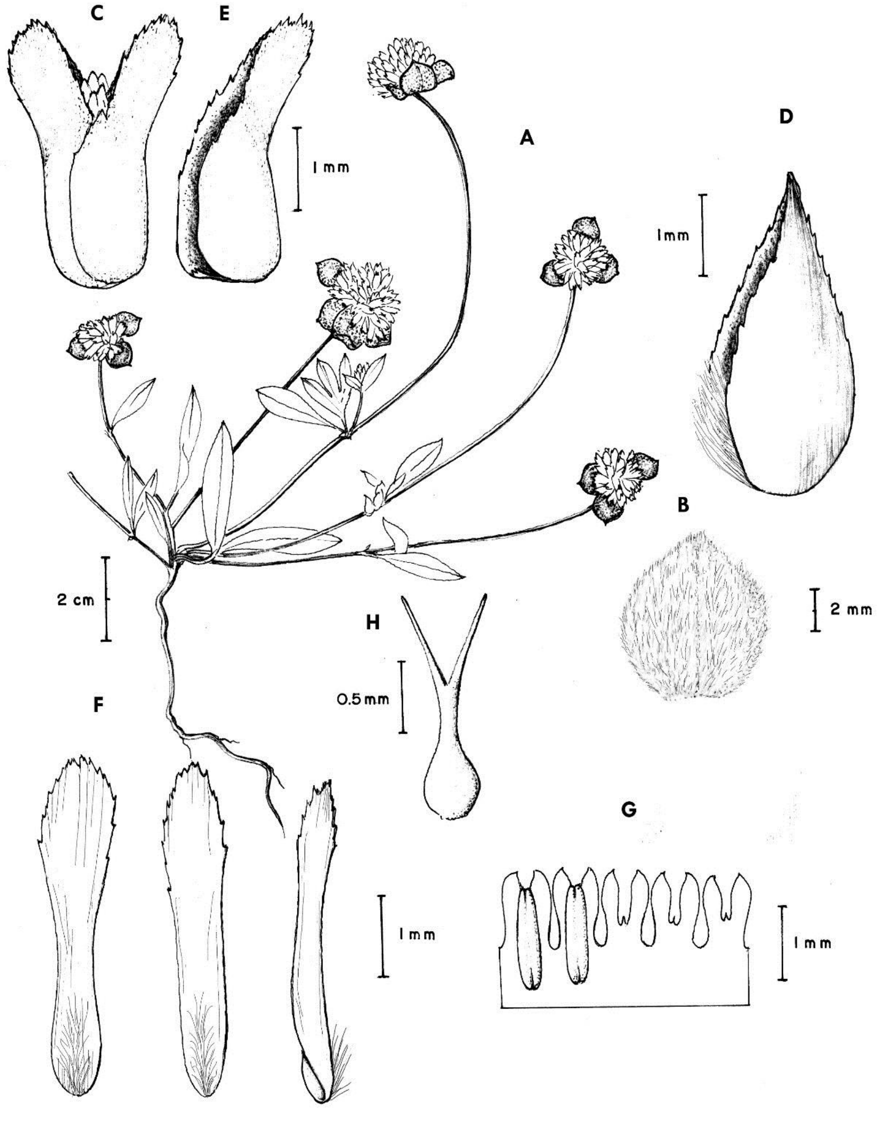


Fig. 4-21. *Gomphrena sp. nov. (spec7)*. A) Habit. B) Detail of the upper leaves, apical leaves subtending paracladia. C) Flower. D) Bract. E) Bracteoles. F) Tepals. G) Detail of the androecium. H) Gynoecium [voucher: Ortuño et al. 1677].

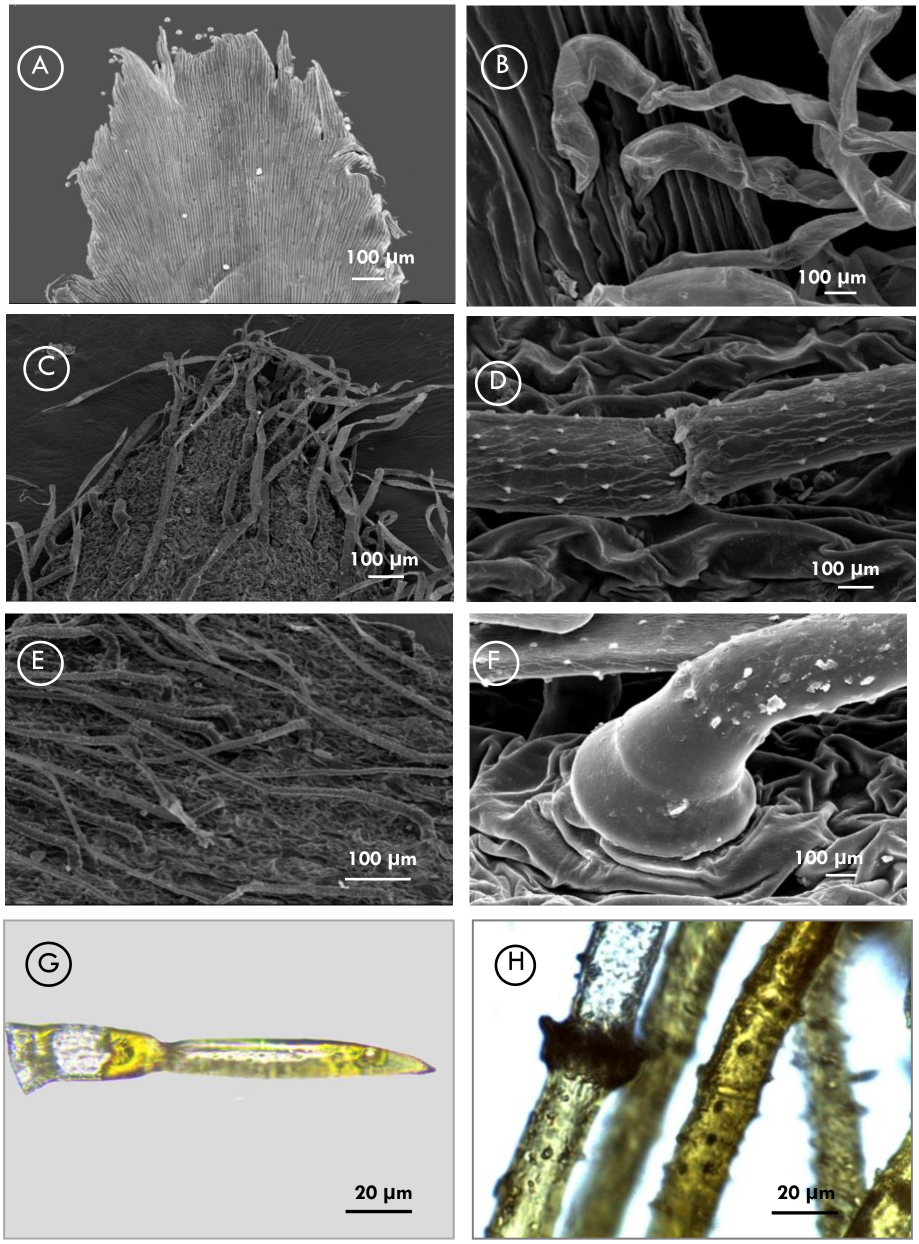


Fig. 4-22. *Gomphrena sp. nov. (spec7)*. A) Tepals with toothed apex. B) Trichomes with collapsed cells, arose of the fibrous cells of the dorsal part of the tepals. Cauline leaves. C) Apex of the upper part of the cauline leaves, trichomes with collapsed cells. D) Inconspicuous interlocking junctions between two collapsed cells. E) Trichomes the lower part of the cauline leaves. F) Detail of the rounded broad basal cells of the trichomes. Apical leaves subtending the paracladia. G) Trichomes of the upper part of leaf with ovate to elliptic cells and narrow interlocking junctions. H) Trichomes of the lower part of the subtending leaves, with firm and conspicuous interlocking junctions and spine ornamentation of cuticule wall cells [voucher: Ortuño et al. 1677 (B, LPB)] strong yellow colour trichomes plus forming with elliptic to ovate peculiar cells, with narrow interlocking junction.

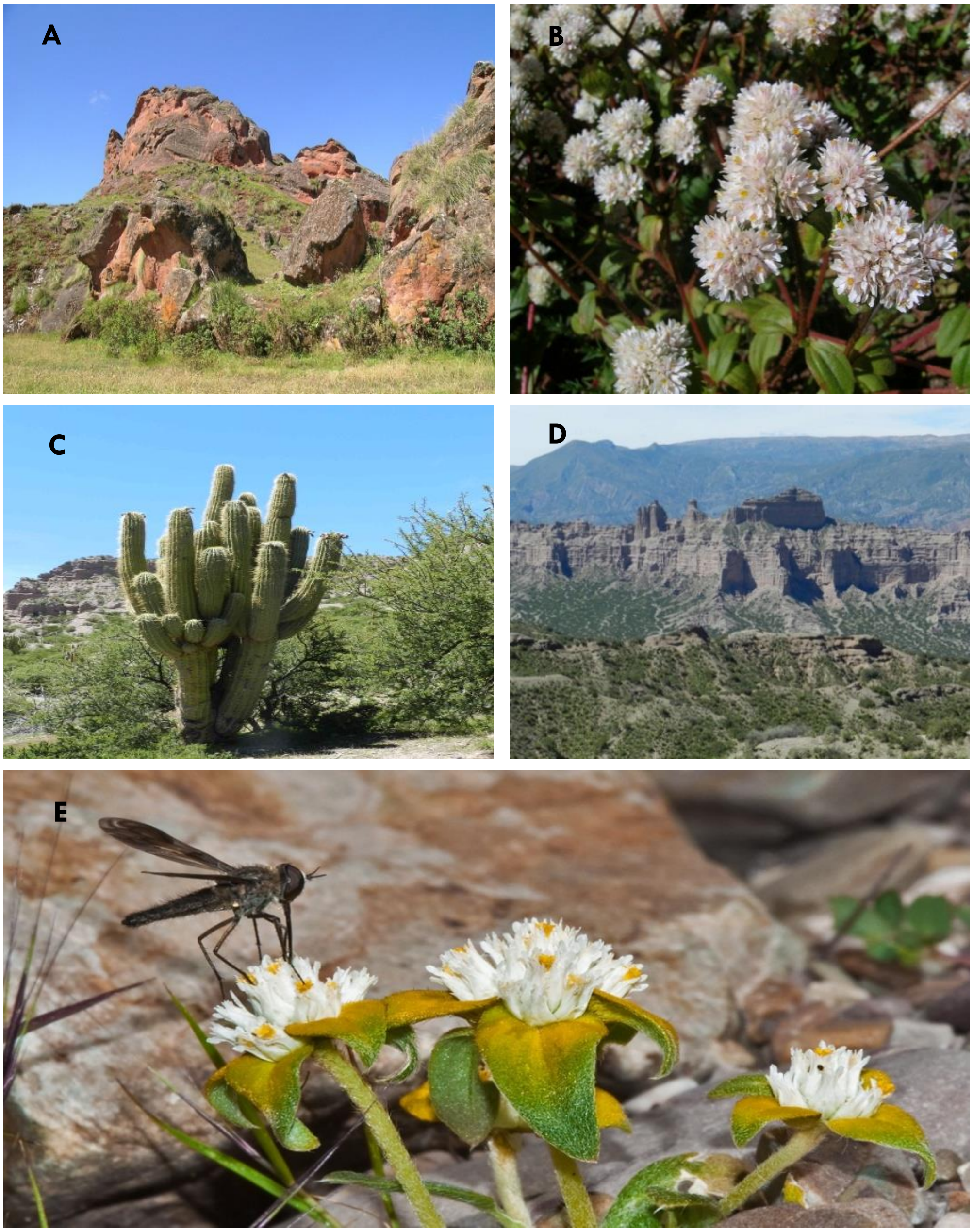


Fig. 4-23. Habitats. A) Valle Encantado, Salta, Argentina. B) *Gomphrena phaeotricha* Pedersen. C) *Trichocereus pasacana*. D) Sud Chichas, Tupiza, Quebradas del Palala. E) *Gomphrena* sp. nov. (spec7).

Distribution. Southern part of Bolivia: Province Sud Chichas and Nor Chichas (Dept. Potosí), Province. Yamparáez (Dept. Chuquisaca), Province Narciso Campero (Dept. Cochabamba) (see Fig. 4-28).

Specimens examined for distribution assessment. ***BOLIVIA, Potosí, Sud Chichas***, en línea recta de la comunidad de Espicaya aprox. 7.92 km, [-65,868217, -21,588067], 3820 m, 29, 2, 2012, *Beck, St.G., 33822*, (LPB). Subiendo la quebrada Palala y entrando hacia el Sillar, al Oeste en línea recta de la ciudad de Tupiza, aprox. 6,89 Km, [-65,783333, -21,4333], 3450 m, 26, 2, 2012, *Beck, St.G., 33725*, (LPB). Tupiza, camino al sillar, [-65,77988889, -21,44536111], 3200 m, 26, 2, 2012, *Ortuño, T.,* ***1677***, (LPB). Parinolqui, [-65.4888, 20.69638889], 2486 m, 17, 4, 2010, *Ortuño, T., 1246*, (LPB). Tupiza, camino al sillar, [-65.4647, 21.2644], 3200 m, 26, 2, 2012, *Ortuño, T., 1679, (*LPB). Tupiza, camino al sillar, [-65,77416667, -21,43363889], 3609 m, 26, 2, 2012, *Ortuño, T., 1674*, (LPB). Tupiza, camino al sillar, [-65,78155556, -21,44577778], 3200 m, 26, 2, 2012, *Ortuño, T., 1676*, (LPB). Al Sud-oeste en línea recta de la comunidad de Espicaya, [-65,846824, -21,596923], 3409 m, 29, 2, 2012, *Zenteno, R.F., 11607*, (LPB). Tupiza, camino al sillar, [-65,77138889, -21,43080556], 3571m, 26, 2, 2012, *Ortuño, T., 1673*, (LPB). Churquipampa, al Sud Este en línea recta de la ciudad de Tupiza. Aprox 5.11 km, Santa Rosa y Churquipampa, [-[65,691775, -21,478092], 3300, 2, 3, 2012, *Zenteno, R.F., 11709*, (LPB). Road from Tupiza vía Quebrada de Palala to El Sillar (& Uyuni). [-65,7625, -21,41861111], 3100 m, 29, 3, 1997, *Wood, J.R.I, 11946*, (HSB). Al Oeste-Nor-Oeste en línea recta de la comunidad de Oploca, aprox. 1.04 km., [-65,814481, -21,336365], 3205 m, 26, 2, 2012, *Zenteno, R.F., 11470a*, (LPB). Tupiza, camino al sillar, [-65,76347222, -21,42347222], 3700 m, 26, 2, 2012, *Ortuño, T., 1672*, (LPB). ***Nor Chichas***, Colina con laderas, 3300, 15, 4, 1993, Torrico, G., 389, (LPB). Parinolqui, [-65,76880556, -21,44705556], 3119 m, 18, 4, 2010, *Ortuño, T., 1252*, (LPB). ***Chuquisaca*****, Oropeza** Ca. 1/2 Km del cruce camino al señor de Maica Palamana, [-65.1715, -19.3178333], 21, 2, 2004, *Wood, J.R.I., 20212*, (LPB). ***Yamparáez***, 15 km hacia Tarabuco, [-65,1958333, -19,145555], 3000 m, 7, 3, 1981, *Beck, St.G., 6215*, (LPB).

4.3.3.4. ***Gomphrena*** *spec. nov. 8b (flexuosa)*. T. Ortuño & Borsch [ined.]

Type: Argentina, Jujuy, 15 km al W de la Quiaca, 13 km entrando por el camino que va al cerro Toroque, 65°25'17.58"W, 22°4'30", 3600 m, 4 April 2004, Borsch, T., Ortuño, T. & R. López 3733 (HT:LPB, IT: B).
= *Gomphrena pallida* ssp. *munda*, Darwiniana 20 (1-2): 285.1976.
Type: Argentinae prov. Jujuy in loco Abra de Yavi dicto die 20. Novembris anno 1963 legit A.L. Cabrera sub: n° 15328. (HT: LP LP010409, IT: CTES CTES0000313, Herbario auctoris PT: LP LP010410).

Annual herb, 3.5-7.5 (--8.5) cm long. ***Root*** simple, fibrous. ***Stems*** decumbent, with secondary stems, slightly striated, with undulate (Fig.4-24), appressed to villous indument, denser especially along the upper parts (close to the inflorescences), with trichomes variable in colour from white to light or dark brown. ***Cauline leaves*** sessile, ovolanceolate to linear, 0.9-1.3 (--2) x

0.2 (--0.4) cm, acute mucronate (0.2 mm) at apex, midvein prominent, with dense trichomes in the lower part, appressed, white. ***Apical leaves subtending paracladia*** 4-5, ovolanceolate, 0.8-1 (--1.5) x 0.4 (--0.7) cm, acute to mucronate (0.4mm) at apex, dense trichomes appressed in the lower part, dark brown colour, hirsute indumentum on the upper leaf blade, white-light yellow. ***Inflorescence*** globose, terminal, 0.7 (--2.0) x 0.7 (--1.5) cm diameter, consisting 2-5 partial florescences. ***Flowers*** 4.4 x 4.2 mm, consisting in 7-14 flowers forming a partial florescence. ***Bracts*** ovate-lanceolate, cymbiform, 3(--4) x 1.5 mm, membranous texture, white, acute apex, the margin dentate, a little crest in the apex scarcely toothed. ***Bracteoles*** ovate-lanceolate, cymbiform, 4.5 x 1.5 mm, membranous texture, white, crest ¼ portions in the apex of the dorsal part, biggest than tepals. ***Tepals*** lanceolate, narrowest at middle, the inner tepals cymbiform, texture finely membranous, around mid-vein scarious and green after anthesis commonly white, acutely dentate at apex, indumentum denser and lanate in the dorsal part. Size of tepals unequal, external and intermediate tepals 4.2 x 0.5 mm, inner tepals 3.9 x 0.3 mm. ***Filaments*** 4.5-5.9 mm long, fused into a tube for 3.5-4.9 mm, free part c. 1 mm long. ***Filament appendages*** conspicuous, 0.7 mm long, lanceolate in shape. ***Anthers*** oblong, 1.5 mm. ***Gynoecium*** with two filiform stigma branches of 1 mm, the style 0.5 mm, and ovary is subglobose 0.5-0.6 mm long. [voucher: Borsch, Ortuño & López 3733 = AC 439 (LPB, B)].

Micromorphology of trichomes. Multicellular uniseriate on stems and cauline leaves with 1-3 basal, rounded cells. The 4-6 upper cells of trichomes with salicose and granulate ornamentation, sculpture of cuticule striate; **interlocking junctions** simple, not conspicuous. The first cells of the trichomes firm consistence and the last cells flexible (Fig. 4- 25 A, B). ***Apical leaves subtending paracladia*** with lower part and margin similar than on the stems, but with light to dark brown colour, the upper cells of trichomes with firm consistence (Fig. 4-25D). The upper surface of leaf, with short trichomes, one rounded broad firm basal cells, the upper cells ovate to elliptic in shape, ***interlocking junctions*** broad and simple, dark yellow (Fig. 4-25E, F). ***Trichomes of tepals*** with firm basal cells, the upper cells numerous often with walls collapsed. ***Anatomy of tepals.*** Tissue composed by elongate strait, cylindrical dermal cells, arranged in one row, all fitting perfectly, the fiber cells constitute a coarsely dentate margin especially at the apex.

Taxonomic remarks. The entity of *Gomphrena nov. (spec 8b)* was first recognized by Pedersen (1976) as *Gomphrena pallida* ssp. *munda* who thought that it belongs to the infraspecic variation of *G. pallida*. The main difference to describe the subspecies (Pedersen 1976) were the ovolanceolate to linear or narrowly lanceolate leaves, and the bracteoles with almost the same size as the tepals. Here more morphological characters are added, to better clarify the differences to the close species using the voucher Borsch, Ortuño & López 3733 (*G. nov. spec. 8b)*, AC439).

The molecular data of the specimens clearly show the distant relations of this plant with the *G. pallida* clade, but point to the relationship within the *G. phaeotricha* clade. This is a sufficient reason to recognize these specimens as new species. The molecular results, with the ITS marker show voucher Borsch, Ortuño & López 3733, (G. *sp. nov.* spec.8b as a sister to specimen Ortuño et al. 1677 (G. *sp. nov. spec7*) in the same subclade within the *G. phaeotricha* clade with high support (1PP, 100 JK). The *matK-trnK* tree confirms that this species nested in the *G. phaeotricha* clade (PP 1, BS 61, JK 92).

Morphologically, the specimen Borsch, Ortuño & López 3733 (*sp. nov. spec8b*) differs of *G. pallida* because it has a glabrous margin of the tepals, while *G. pallida* has margins of the tepals with trichomes. On the other hand, it differs from *G. phaeotricha* by the presence of a dense indumentum in the dorsal part of the tepals, considering that *G. phaeotricha* has completely glabrous tepals.

An obvious characteristic of *G. spec. nov. (spec 8b)* are the thin, flexible and undulate stems. This character is not observed in other species of *Gomphrena*. The probably most closely related species to *G. spec. nov. (spec 8b)* is *G. sp. nov (spec 7)*, but both are different in the type, consistence and ornamentations of the trichomes on the cauline leaves. Moreover, in *G. spec. nov. (spec 8b)* the trichome cells have a firm consistence and salicose ornamentation, while the trichomes in *G. sp. nov. (spec 7)* shows collapsed cells and a spinous ornamentation. Also the trichomes the apical leaves subtending the inflorescence are different.

Habitat and ecology. On open places in rocky slopes of mountains of the Argentinian Puna; a specific place with collections is the “Cerro toroque”. The steep hillsides on the Northern Puna are surrounded by striking mountain chains, with reddish mineral colors. In the region dominant scrubs are *Baccharis boliviensis* (Wedd.), *Adesmia spinosissima* Meyen ex Vogel, as well as grassland with *Jarava ichu* Ruiz & Pav., *Bouteloua simplex* Lag., *Puna subterranea* (R.E. Fr.) R. Kiesling. As indicated correctly by Pedersen (1976), these species grow in high mountains of Jujuy, Argentina, representing a species group that reaches considerably high altitudes, considering that the altitudinal range of collections is between 3450-3900 m.

Distribution. Northern Argentina, province Jujuy, locality Yavi, La Quiaca (see Fig. 4-28).

Specimens examined for distribution assessment. ***Argentina, Jujuy***, 15 km al W de la Quiaca. 13 km entrando por el camino que va al Cerro Toroque, [-65,70258333, -22,12531667], 3600 m, 4, 4, 2004, *Borsch, T, Ortuño, T. & López, R,* ***3733***, (LPB, B). 15 Km de la Quiaca, Cerro Toroque, [-65,43648, -22,1304], 3628 m, 4, 4, 2004, *Borsch, T. & Ortuño, T., 3731*, (LPB, B). Yavi, [-65,461879, -22,13043], 3459 m, 20,11, 1963, *Cabrera, A.L., 15328*, (LPB). Localidad Cajas, [-65,2865199, -22,2182169], 3920 m, 18, 3, 1982, *Vignale, N.D., 151*, (SI).

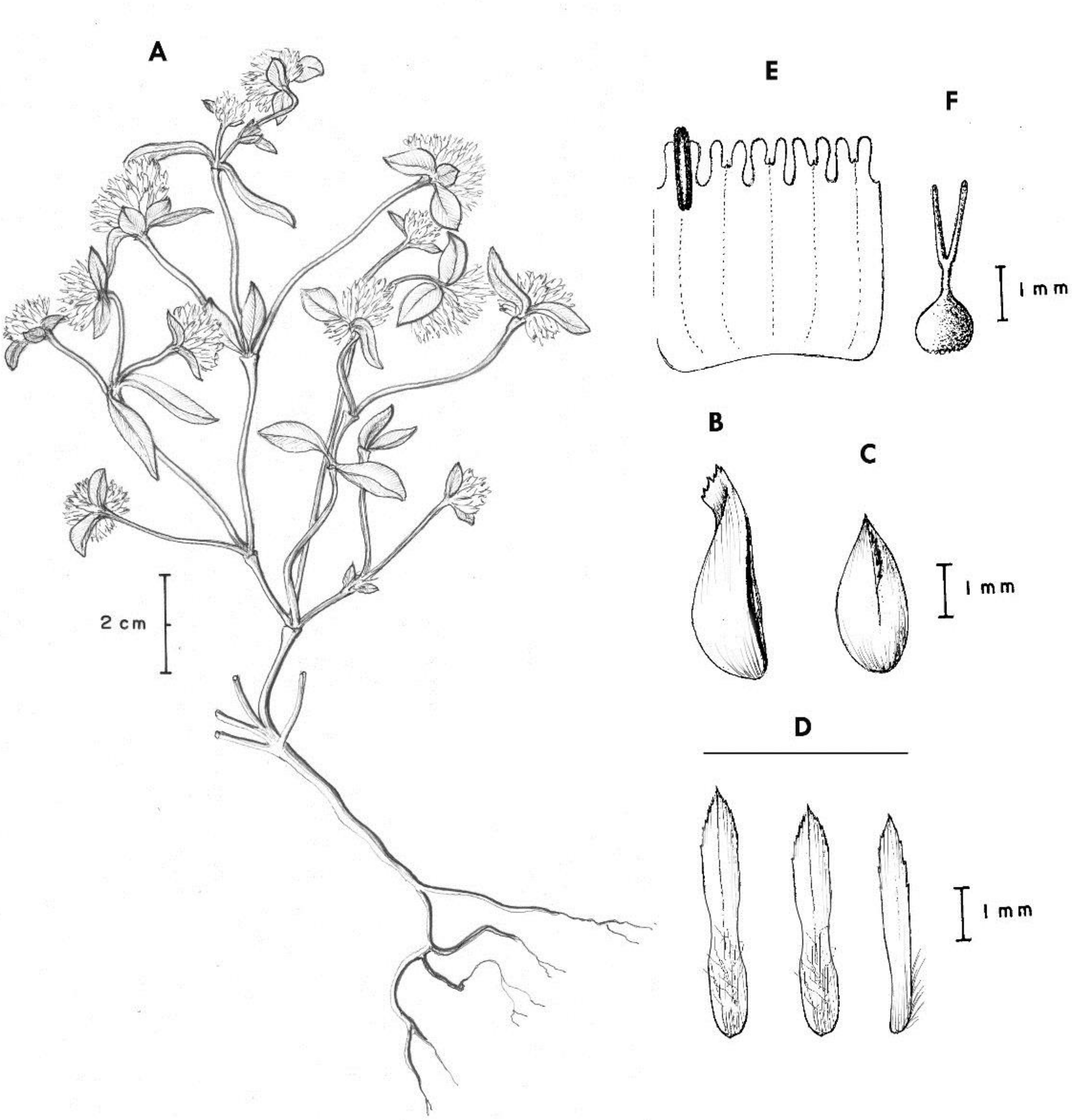


Fig. 4-24. *Gomphrena sp. nov. 8b (flexuosa)*. A) Habit. B) Bracteoles. C) Bract. D) Tepals. E) Detail of the androecium. F) Gynoecium [voucher: Borsch, Ortuño & López 3733 (LPB, B)].

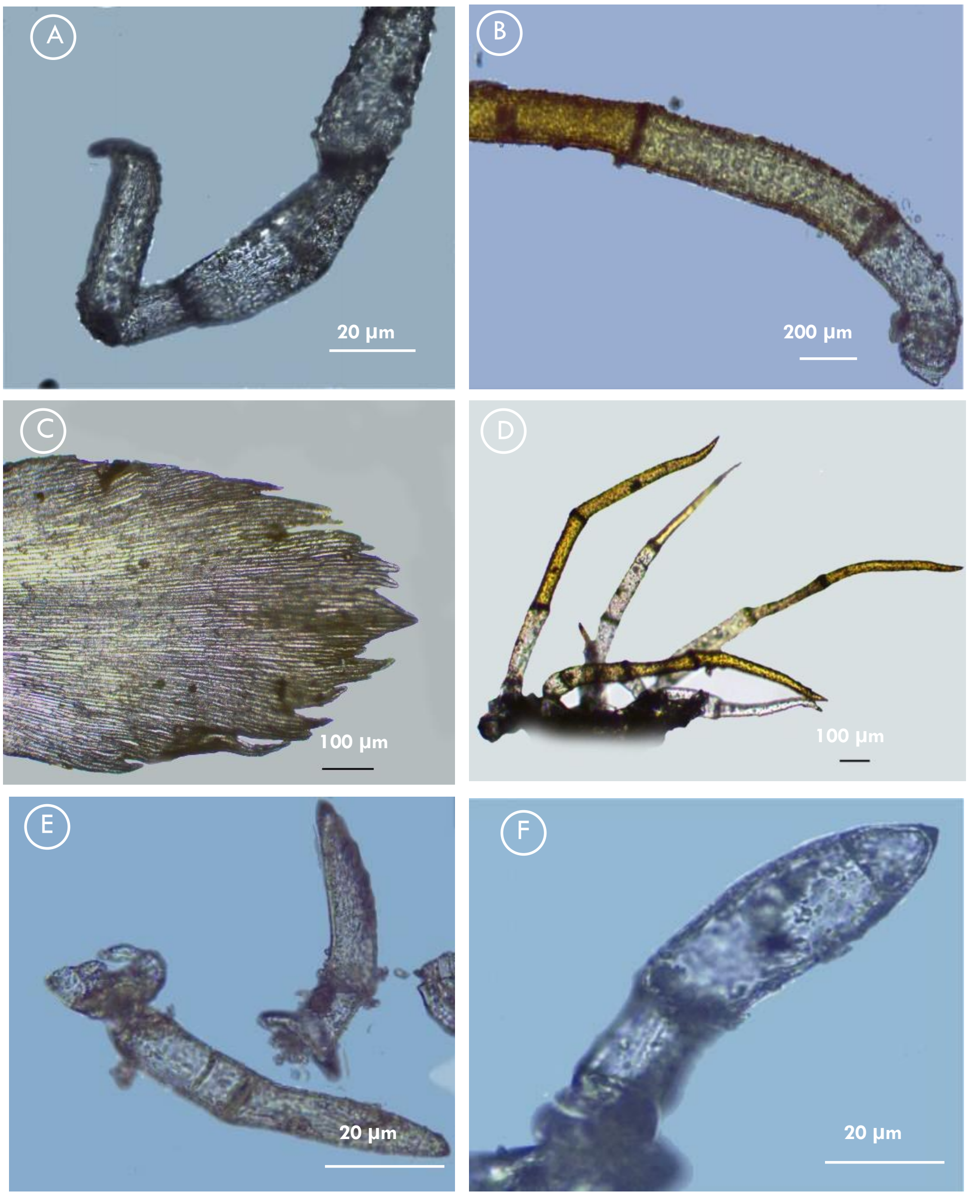


Fig. 4-25. *Gomphrena. spec. nov. 8b (flexuosa)*. A) Trichomes of the cauline leaves and stems, detail of the upper cells of trichomes with salicose ornamentation and striate texture. B) Detail of the basal leaves. C) Tepal tissue with elongate, fiber cells and dentate apex. Apical leaves subtending the paracladia. y D) Trichomes of the margin and from the abaxial surface. E and F) trichomes of the adaxial side of the leaf, with ovate to elliptic cells and broad interlocking junctions. [voucher: Borsch, Ortuño & López 3733].

4.3.3.5. ***Gomphrena* spec. nov. *(spec 9 f. calva)*** Ortuño, T. & Borsch, T. [inded.]

Type: Argentina, Salta, San Isidro, 7 km de Iruya por camino a herradura. 3 km de San Isidro hacia el SE sobre el río. *Borsch &Ortuño, 3753* (HT: LPB, IS: B).
= *Gomphrena pallida* subsp. *pallida* forma *calva* Pedersen, Darwiniana 20: 285. 1976. Type: Argentina, El Alisal at 2800 m, Mar. 1914, *Rodríquez* 1420 (M-0241766. Here is proposed the Lectotype in next publication).

Annual herb, 13-16 (--22) cm long. ***Root*** simple, fibrous. ***Stems*** decumbent, with secondary stems, villous indumentum, denser especially in the upper parts (close to the inflorescence), the trichomes 0.5-0.8 ((--1) mm of long, colour varying from white to brown, and dark near the inflorescence. ***Cauline leaves*** lanceolate to oblong, 2-3.5 (--5) x 0.7-1 (--1.5) cm, acute apex, prominent midvein, appressed indumentum, denser in the abaxial part, hirsute in the margin and villous in the adaxial side. ***Apical leaves subtending paracladia*** 4-5, ovolanceolate, 0.8-1 (--1.5) x 0.5 (--0.7) cm, apiculate apex, mucronate (1mm), dense appressed in the abaxial surface, hirsute indumentum in the margin, dark brown colour, glabrous in the adaxial side of leaf. ***Inflorescence*** terminal, 1.5 (--1.8) cm in diameter, consisting 3-4 partial florescences. ***Flowers*** 4.4 x 4.2 mm, consisting in 7-14 flowers forming a partial florescence. ***Bracts*** ovolanceolate, 1.4 (--3) x 1.5 mm, membranous texture, white, acute apex, the margin dentate, a little crest in the apex without toothed. ***Bracteoles*** ovolanceolate, cymbiform, 3.6-3.8 (4) x 1.5 mm, membranous texture, white, crest 1:2 portions in the apex of the dorsal part, smaller than tepals. ***Tepals*** lanceolate narrowly at middle, finely membranous texture, around mid-vein scarious and green after anthesis commonly white, the acute dentate apex, glabrous. Size unequal, external 4.4 x 0.5 mm, intermediate tepals 4 x 0.5 inner tepals 3.6 x 0.3 mm. ***Filaments*** 4.2-.4.4 mm of long fused into a tube 3-3.2 mm long, free part 1.2 mm long. ***Filament appendages*** conspicuous, 0.8 mm long, lanceolate shape (unit base 0.4 mm) (Fig. 4-26E). ***Anthers*** oblong, 1.5 mm, inserting between two filament appendages. ***Gynoecium*** with two filiform stigma branches of 1 mm long, the style 0.5 mm, and ovary is subglobose 0.5-0.6 mm long. [voucher: Borsch & Ortuño 3753 = AC447 (B, LPB)].

Micromorphology of trichomes. Multicellular uniseriate on stems and cauline leaves with 1-3 rounded basals cells. The 4-6 upper cells of trichomes with salicose ornamentation, cuticule striated; ***interlocking junctions*** conspicuous, linear scars or projections of the extreme border cells in angle of zero degrees (Fig. 4-27 C). ***Apical leaves subtending paracladia*** with trichomes on the lower part and margin similar than on the cauline leaves. ***Trichomes on tepals*** have the firm basal cells, the upper cells numerous with collapsed cell walls. ***Anatomy of tepals***. Tissue composed by elongate strait, cylindrical dermal cells, arranged in one row, the extremes fitting perfectly, the fibrous dermal cells of tepals protrude in the margin as teeth.

Taxonomic remark. Pedersen recognized *Gomphrena pallida* subsp. *pallida* forma *calva* Pedersen, Darwiniana (20: 285, 1976) as one of three intraspecific taxa of *G. pallida*. He described the form with the type specimen from Argentina, El Alisal at 2600 m, April. 1914, *Rodríquez* 1420 (HT: M-0241766). The molecular data from plastid *matK-trnK* show *G. sp. nov.* (type b) in the same sublineage close to G. spec. nov. spec9 (= f. calva, AC447) with quite some support (0.98 PP, 62 JK, 81 BS). However, the ITS tree shows an incongruence with respect to the *matK-trnK* tree. In ITS the specimen AC447 is isolated in the Andean clade A, and not inside the *G. phaeotricha* clade. Perhaps this can be explained by reticulate evolution (hybrid speciation), with the maternal ancestor having been a plant close to *G. phaeotricha* and the paternal probably close to *G. ferruginea*. However, it is necessary to carriy our more studies for clarifying this complex, including further sequenes, population level sampling and best cytological data. In this work, this plant is treated as a new entity at species level. In contrast, the treatment of Pedersen (1976) is just based on an alpha-taxonomic comparison of individual characters whithout considering and evolutionary patterns. Also the recognition of forms as taxa is not adequate for plants that substantially deviate. For this reason here it is proposed to accept *Gomphrena spec. nov. 9* (f. *calva*) and *G. spec. nov.* (spec 8b = *flexuosa*) at the level of species based on phylogenetic evidence and morphological data. *Gomphrena spec. nov. 9 (f. calva)* have tepals without trichomes; inner tepals are shorter than the outer and bracteoles have a conspicuous crest prolonged narrowly until their base. Considering the Code of Botanical Nomenclature the rule of priority only applies within ranks at the level of genera and below. Since the historic type of the fa. *calva* cannot be investigated easily with phylogenetic methods, and therefore the possibilities to place the regarding specimen will be limited, it is preferred in these cases to describe such entities at a species with a new type.

When comparing this species morphologically to *G. ferruginea,* the differences are that *G. ferruginea* has bigger cauline leaves, tepals navicular in shape, bracteoles more hooded at the apex, light brown to yellow trichomes with a denser spinous to granulate ornamentation. With respect to the habitat, *G. ferruginea* is collected more frequently in the Tucumano forest at a lower altitudinal range (1600-2800) whereas *G. spec. nov. 9 (f. calva)* occurs at 2770-3200 m.

Habitat and ecology. It grows preferably on rocky, open, slopes, semi humid, among scattered trees of *Alnus* sp., close to low herb and grasses as *Plantago* sp., *Trifolium* sp., *Senecio* sp. *Begonia* sp. The plant has been collected between 2770-3200 m.

Distribution. Argentina, Province Salta 7 km de Iruya, Cachi, las Pailas. Bolivia, Province Méndez (Dept. Tarija) (see Fig. 4-28).

Specimens examined for distribution assessment. ***Argentina*, *Salta***, San Isidro, Iruya San Isidro (7 Km de Iruya por camino de herradura). 3 km de San Isidro hacia el SE sobre el río, [-65.25298333, -22.72776667], 3215 m, 10, 4, 2004, *Borsch & Ortuño, 3753* (B, LPB). Cachi, las Pailas 3000 m, *E. Nicora, E. Gomez-Sosa & J. Pensiero,* 9130 (SI). ***Bolivia, Tarija, Eustaquio Méndez***, Camino de Tarija a Potosí empezando de la "Cuesta de Sama", [-64,84608333, -21,46823333], 2774 m, 11, 4, 2003, *Borsch, T., 3652*, (LPB, B).

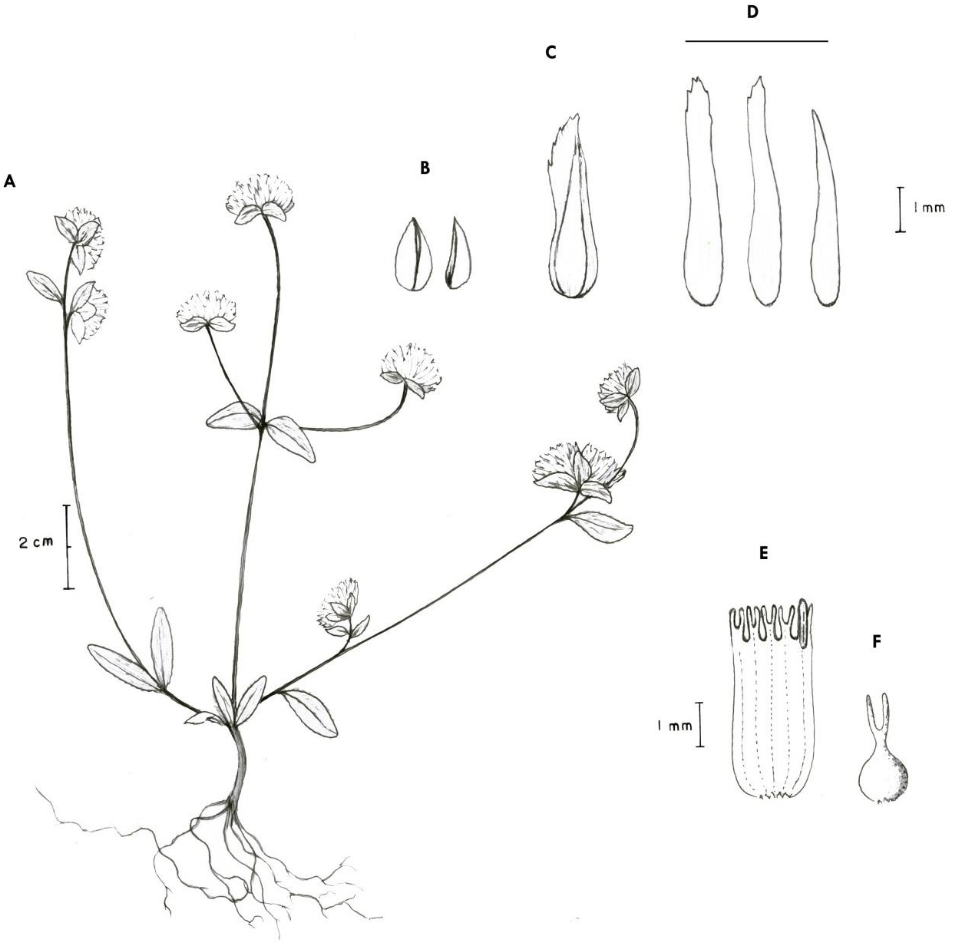


Fig. 4-26. *Gomphrena spec. nov. 9 (f. calva)*. A) Habit. B) Bracteoles. C) Tepals. D) Bract. E) Detail of the androecium. F) Gynoecium. [voucher: Borsch & Ortuño 3753 (B, LPB)]

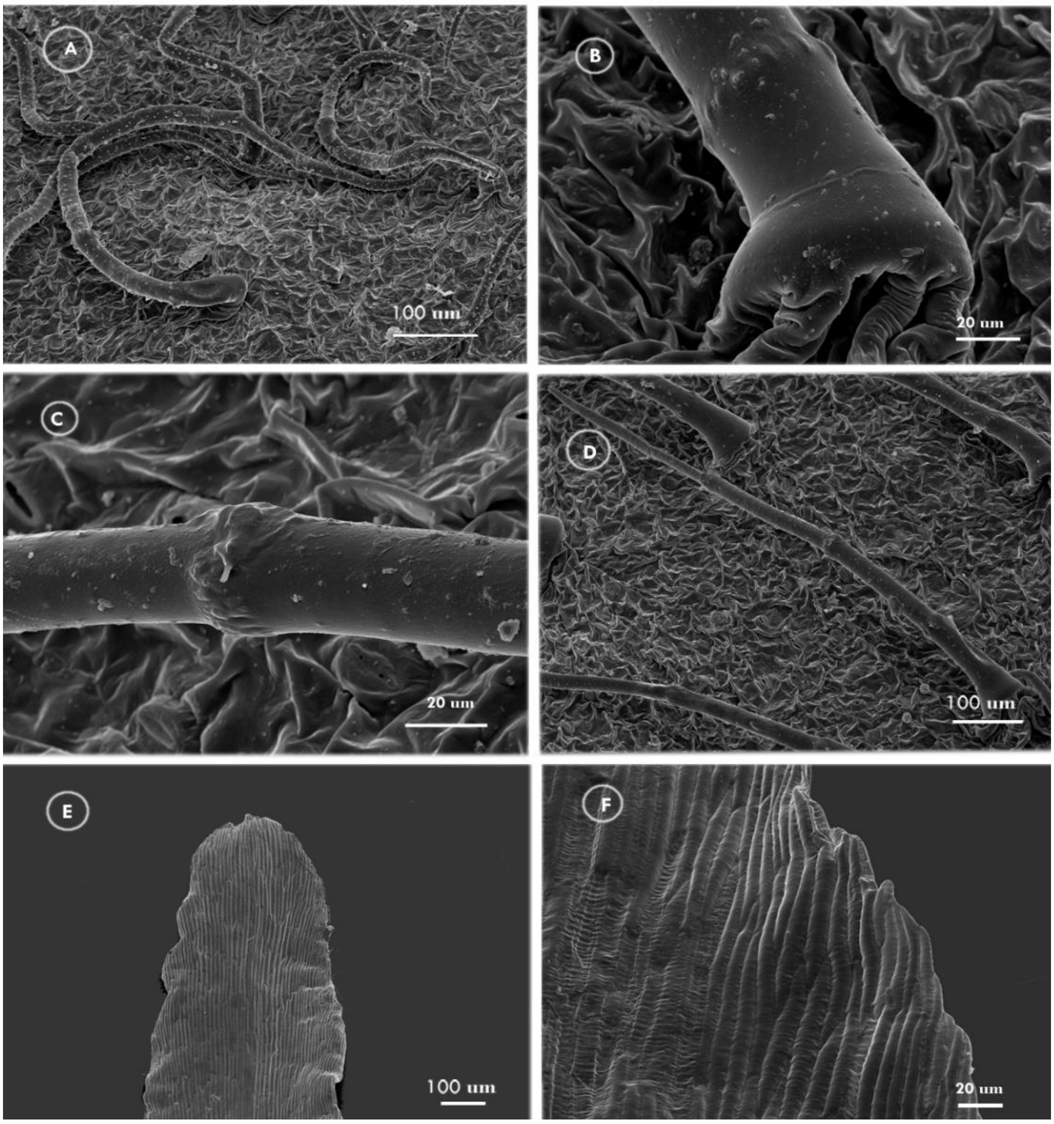


Fig. 4-27. *Gomphrena sp. nov. 9 (calva)*. Trichomes in the cauline leaves. A) Villous indumentum in the adaxial size leave, and salicose ornamentation. B) Detail of the rounded, flat basal cells of the trichomes. C) Interlocking junction, conspicuous linear scars and projection of the extreme border cells positioned at angle of zero degrees. D) Abaxial part of the leaves with appressed indumentum and salicose ornamentation. Tepals E) and F). Glabrous surface with slightly dentate margin, tissue composed by elongate straight, fibrous cells.

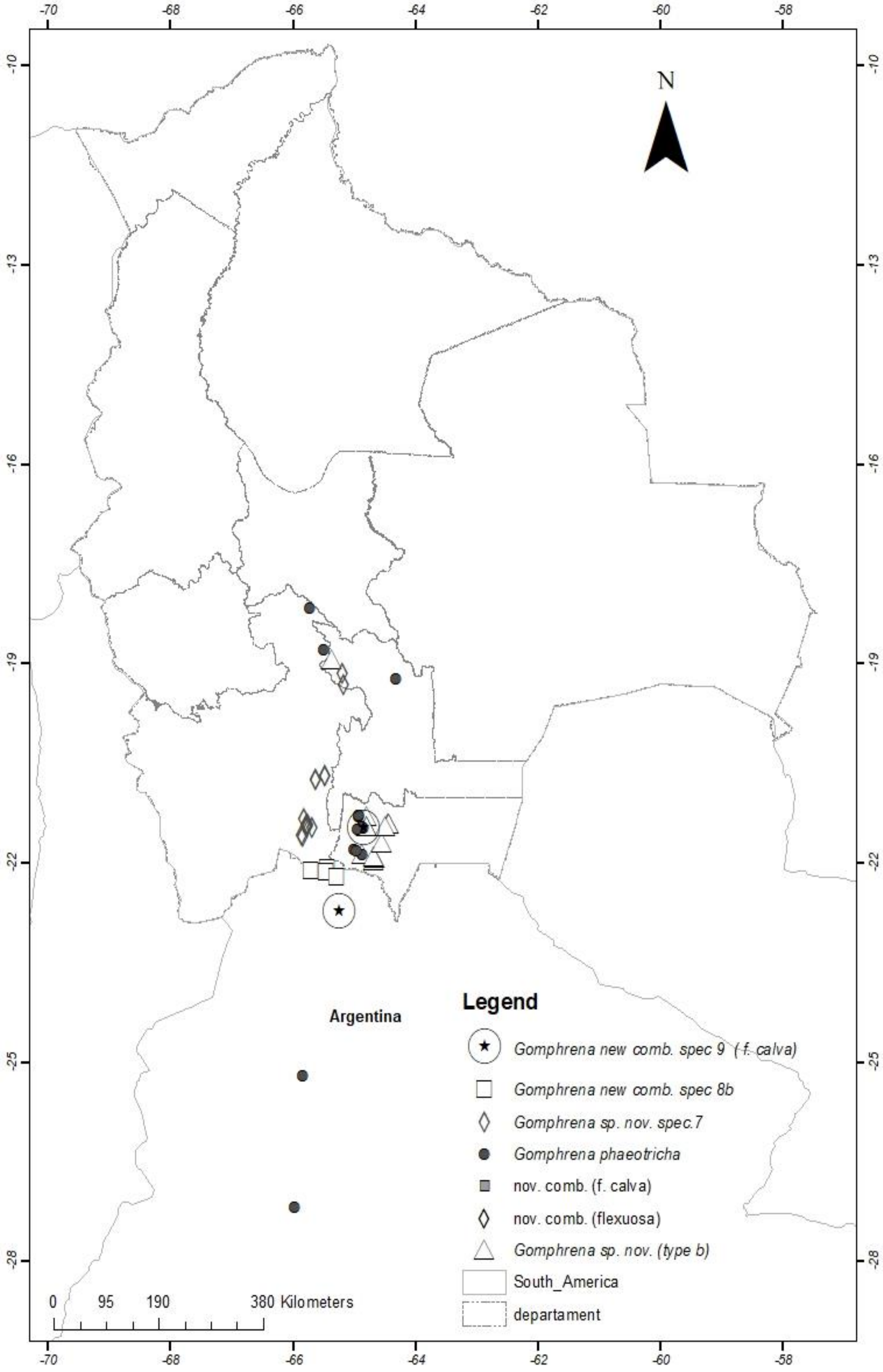


Fig. 4-28. Distribution of species the *Gomphrena phaeotricha* clade.

4.3.4. *Gomphrena lanigera* –G. cardenasii CLADE

The plastid *matK-trnK* tree shows a monophyletic *Gomphrena lanigera* clade, with high support (1.00 PP, 97BS, 92JK). This clade includes the species *G. lanigera*, *G. agrestis*, and *G. macrocephala*. Similarly, the nuclear tree shows that *G. cardenasii*, *G. agrestis*, *G. demissa*. (0.96 PP, 91 JK) belong to this clade. The most notorious difference among both trees is that the nuclear tree exhibits a *G. lanigera* sister to *G. celosioides* (see *G. celosioides* clade) but this is statistically unsupported and therefore rather inconsistent.

The morphological data show similarities in this group. For example, all the species of the clade have a perennial life form, erect habit and are woody in the basal part of the stems. They possess large paracladia, trichomes dorsally at the lower part and margin on the tepals, which are large in size, with firm to collapsed cells, and erect, appearing like a brush (in particular *G. macrocephala*). The trichomes of the apical leaves subtending the paracladia in general not different among the lower and upper side, as in the *G. pallida* clade. *Gomphrena agrestis* and *G. cardenasii* have bracteoles distinctly shorter than the tepals, and *G. macrocephala* and *G. lanigera* have bracteoles nearly equal in size of the tepals. These two species have a deepely dentate crest as characteristic feature, contrary to *G. agrestis* and *G. cardenasii* that have a small crest in the upper dorsal part of the bracteoles.

Another interesting point to remark in this group is the distribution. All species are distributed the in the Cerrado region. The biogeographic province of the Cerrado is one of the largest in South America, extending generally throughout the center of Brazil to the east of Bolivia and northeast of Paraguay. The species grown in places with a current presence of several vegetation elements of the Cerrado flora, in predominantly closed and/or isolated areas, which mostly are disconnected or semi-connected in the present area of the Cerrado Province. This could indicate a greater paleo-historical extension of this province, possibly in the course of fluctuations during the Quaternary (Pleistocene) in the lowland of South- America (Navarro 2002). Apart from *G. cardenasii*, which is an endemic of Bolivia, the other species are more widespread and just reach Bolivia as part of their range.

Key to the species of *G. lanigera* CLADE

1. Plants erect, up to < 15 cm, covered with hirsute indumentum of long trichomes, inflorescence 3.2-3.3 (--4) cm in diameter, apical leaves subtending the paracladia lanceolate to linear ….. *G. lanigera* (Fig. 4-29)

1' Plants erect to decumbent > 30 cm (up to 100 cm), with appressed to villous indumentum, inflorescence 1-1.3 cm in diameter (2).

2. Plants with only basal leaves, ovate lanceolate in shape, 2.5-4 (--12) x 0.6- 2 (--3) cm, apical leaves subtending paracladia 2-5, arranged symmetrically, cordate to ovate, 0.5-0.8 (--1) x 0.4 (--0.8) cm, acute at apex.. *G. agrestis* (Fig. 4-33)

2'. Plants with cauline leaves, oblong lanceolate in shape, 1.5 (--1.7) x 0.5 (--0.7) cm, acute mucronate, inflorescence subglobose, apical leaves subtending paracladia 2-5, arranged symmetrically, cordate to-ovate, 0.5-0.6 (--1) x 0.3 (--0.5) cm, acuminate at apex.. *G. cardenasii* (Fig. 4-31)

4.3.4.1. ***Gomphrena lanigera*** Seubert, Prodr. ser. 13, (2): 406. 1849.

Type: Brazil Northeast, Brasilia, in serra de S.-Felix prope Rio Trahira cap. Goyaz., Pohl. 2234 (HT: P P00622694).

≡ *Xeraea lanigera* Kuntze, Revis. Gen. Pl. 2: 543 1891.

= *Gomphrena aurea* Lopr. ex Urb., Bot. Jahrb. Syst. 30(67): 31. 1902. Bot. Jahrb. Syst. 30(1, Beibl. 67): 37. 1901.

Type: in civil Goyaz inter As Antas et pedro Sardinha in campo, Glazio n. 21966, m. Aug. fl. (HT: S S07-12664, IT F F0BN003241).

= *Gomphrena scapigera* var. *lanigera* Stuchlík, Beih. Bot. Centralbl. 30(2): 403. 1913.

Type: Brasilia, Mina Geraes!, Gardner!, Goyaz, Glaziou s/n (HT: K).

Perenial herb, 9-11.5 (--13) cm. ***Root*** a woody taproot. ***Stems*** erect, only with unbranched principal, yellow/green stems; with dense hirsute trichomes of 2 to 4 mm length, yellow to light brown in colour. ***Basal leaves*** ovolanceolate, 2.0-3.5 (--4) x 0.7-0.8 (--1.3) cm, acute at apex, midvein prominent, decurrent at base, dark green, trichomes hirsute, sparse in all the leaves and at the margin, light to dark brown in color. ***Cauline leaves*** lanceolate to linear, 0.8 (--1.5) x 0.2 (--0.4) cm, acuminate apex and midrib excurrent as a short spine, trichomes similar to those on the stems, yellow and light brown. ***Apical leaves subtending paracladia*** *(inflorescences)* 4-5, arranged symmetrically, lanceolate-linear 7 (--9) x 1.2 (1.3) cm, acute at apex, dark green, on both surfaces with dense hirsute trichomes. ***Inflorescences*** globose to subglobose, terminal, 3.2-3.3 (--4) cm in diameter, consisting 3-5 partial florescences, yellow to light brown. ***Flowers*** 3.2-3.8 (--4) mm of long. ***Bracts*** ovate to lanceolate, 9.0 (--10) x 1.5 mm, coriaceous in texture, light brown, glabrous, entire at margin. ***Bracteoles*** ovate-lanceolate to linear (Fig. 4-29 D), 10-11 (--12) x 1.5 mm, membranous to coriaceous in texture, light brown, conspicuous with a dentate crest that extends on three quarters in the upper part in the dorsal side, tepals bigger than bracteoles. ***Tepals*** linear to lanceolate, membranous but hard coriaceous in the middle, yellow to light brown colored, acuminate at apex, connate in the base, margin deeply dentate, with 5 mm long trichomes (Fig. 4-29 E) in the abaxial part and the margin. Size of tepals unequal. External tepals 10.4 x 1.2 mm, intermedian tepal 10.3 x 1 mm, and inner tepals 10 x 0.7 mm. ***Filaments*** 8.1-10.2 (11) mm long, fused into a tube, 7.9-10.2 (--11) mm long, free parts 0,4 mm long, ***Filament appendages*** 0.2-0.3 mm long, the free part has two shortly acute conspicuous lobes (Fig. 4-29F). ***Anthers*** oblong, 2.8 mm long, inserted between the lobes at the tip of the filament tube. ***Gynoecium*** with two filiform branched stigma branches, of 1.8 mm length; style 0.2 0.3 mm, ovary subglobose, 0.8 mm [vaucher: J. Wood et al. 19964].

Micromorphology of trichomes. Multicellular, uniseriate. On ***stems and caulinar leaves*** with 1-3 basal cells, the basal one rounded, the upper cells 4-8, straight with granulose to spiny ornamentation, firm consistence, and striate sculpture of the cuticle walls (Fig. 4-30A). ***Interlocking junctions*** conspicuous linear, scars arranged in zero angle angle or up to forty-five degrees. ***Trichomes on apical leaves subtending paracladia*** on the abaxial part similar than on the stems, on the adaxial surface without ornamentation, and smooth texture. ***Interlocking junctions*** light yellow. ***Trichomes on tepals*** in dorsal and marginal position, 2-4 (--5) mm long, hirsute-erect, with 1-2 firm rounded basal cells, and smooth surface. ***Interlocking junctions*** conspicuous with scars and linear overlapping ornamentation, with firm consistence at the base but collapsed upper cells. [Voucher: Wood, Goyder, Bigg & Mercado 19964]. ***Anatomy of tepals.*** Tissue is composed of elongate straight, cylindrical dermal cells, arranged in one row, the extremes fitting perfectly.

Pollen. Size c. 23.1 µm. Pore number 18-20. Pore 6.3-5.3 µm in diameter, pore membrane with ektexinous bodies arranged circularly in a mosaic-like a pattern. Mesosporium consisting of hexagons and pentagons, acute (sharp) angles in the connection points. Tectum with columellae visible in the lower near middle of the vertical part, arranged around the pore (Fig. 4-30F).

Taxonomic remark. *G. lanigera* is easily distinguished by the morphological characters from the other species of the genus: the erect habit, small size of plants that are covered by a peculiar hirsute indumentum of brown to yellow firm cells, and the inflorescence that is much bigger than in the other species, the androecium with short filament appendages, and the deeply dentate bracteoles.

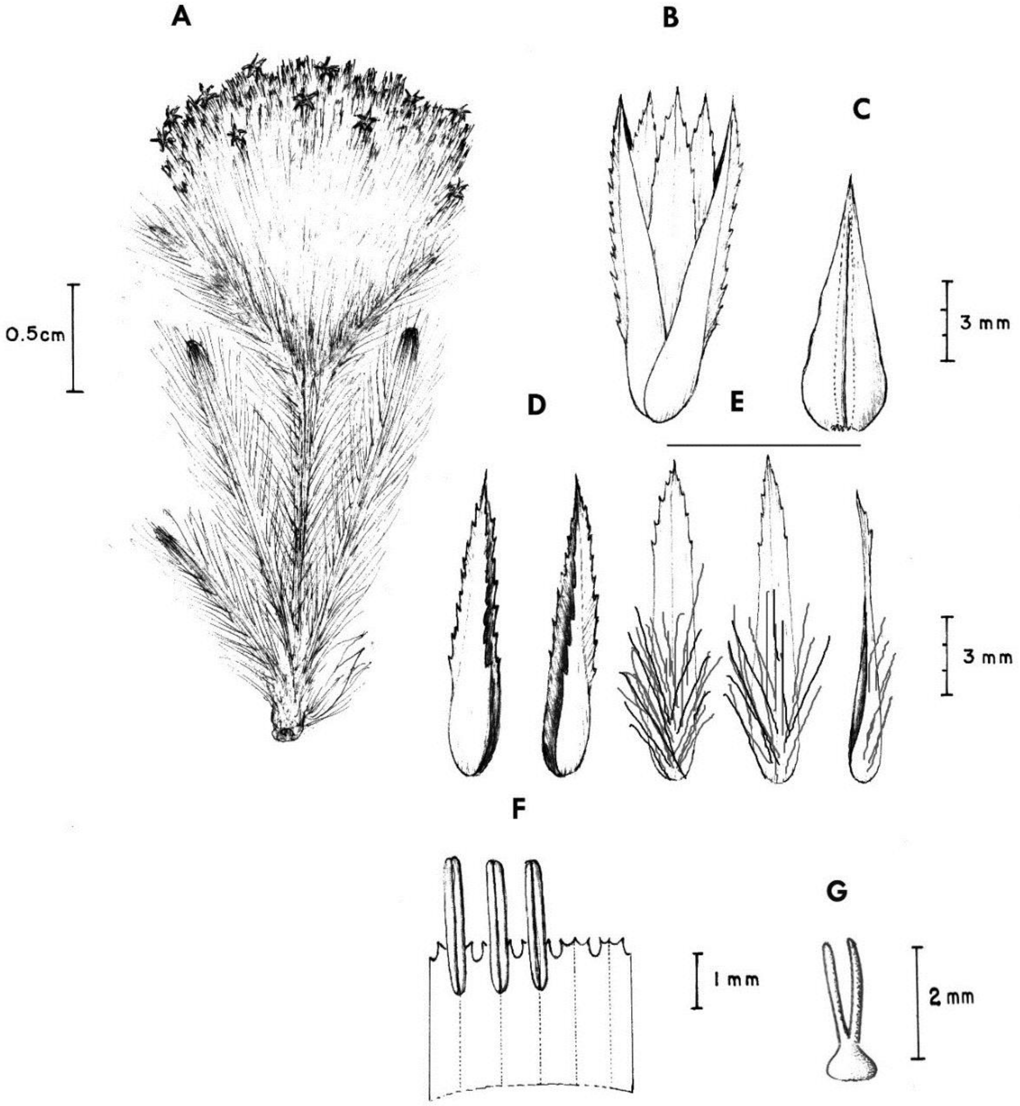


Fig. 4-29. *Gomphena lanigera* Seubert. A) Habit. B) Flowers. C) Bract. D) Bracteoles. E) Tepals. F & G) Detail of the androecium with anthers inserting at the tip of very shortly free filaments [voucher: Wood, Goyder, Bigg & Mercado 19964].

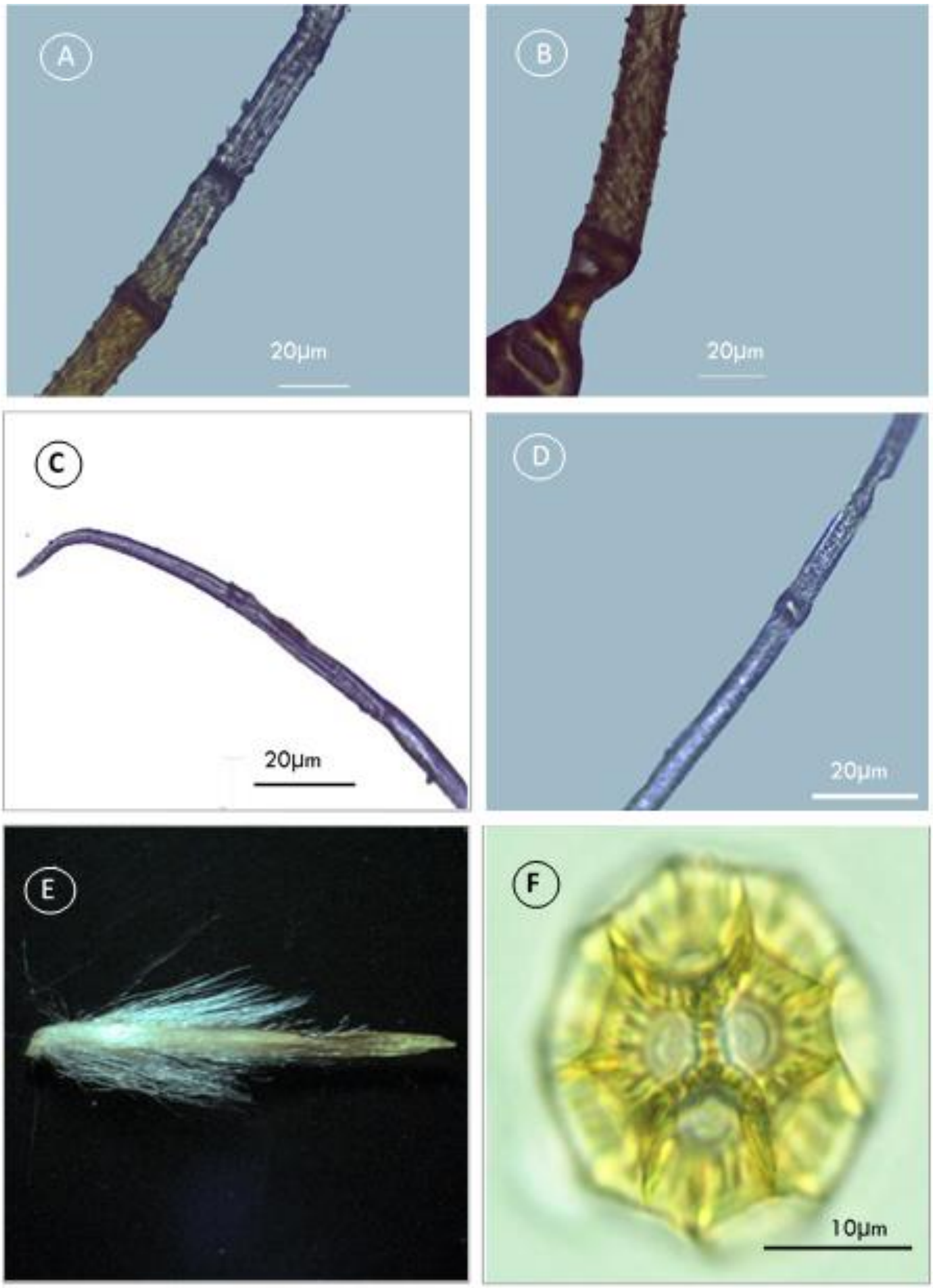


Fig. 4-30. *Gomphrena lanigera* Seubert. Firm trichomes of cauline leaves. A) Detail of the upper cells. B) Detail of the basal cells. Trichomes on tepals. C) Detail of the upper cells. D) Detail of the intermedite cells. E) External tepal with dorsal and marginal trichomes. Pollen. F) Overview with penta and hexagonal pores [voucher: Wood, Goyder, Bigg & Mercado 19964].

Habitat and ecology. In Bolivia this species is restricted to the "Serrania de Huanchaca", which belongs to the “Chiquitano Precambrian shield”. This ecoregion belongs to the “Cerrado boliviano”, which has some typical species of the chiquitano forest such as *Acosmium cardenasii*

H.S. Irwin & Arroyo. And there grow species such as *Ateleia guaraya* Herzog, *Buchenavia grandis* Duncke, common in humid places, possible better described as transitional zone, and a remarkably high diversity and dominance of lianas and bejucos. *Gomphrena lanigera* was collected on flat open places "Pampas" in undulating, stony areas, frequently between disperse scrub, growing widely dispersed after burning. In more general terms the species belongs to the Cerrado Chiquitano ecoregion, where the plants are collected in a range between 300-955 m.

Distribution. Brazil, Brasilia, Serra de las Vertentes. Distrito Federal: Brasilia, Goias "Serra dos Pireneus", Mina Gerais, Belo Horizonte. Bolivia, department Santa Cruz, province José Miguel de Velasco F., Parque Nacional de Noel Mercado. Campo rupestre. Bosque húmedo con influencia amazonica. (see Fig. 4-35).

Specimens examined for distribution assessment. ***Bolivia, Santa Cruz, José Miguel de Velasco F.***, [-60,36, -14,75], 738 m, 9, 11, 1951, *Schmidt, E., 35*, (M). Parque Nacional Noel Mercado. Serrania de Caparuch, senda hacia los farellones, a los 20 km al SE del campamento los Fierros, [-60,769167, -14,561389], 500 m, 1, 11, 1994, *Killen, T.J., 7077*, (USZ). Velasco, Catarata Encanto, [-60,716667, -14,6333], 300 m, 31, 10, 1994, *Guillen, V., 2512*, (USZ). Meseta de Caparuch, [-60,749972, -14,549972], 771 m, 15, 11, 2003, *Wood, J.R.I., 19964*, (B, K, LPB, USZ). ***Brasil, Brasilia***, Serra das Vertentes, [-49,5, -26,55], 955 m, 8, 4, 1894, *Glaziou, A., 25435*, (Herbarium IGN.Urban).

4.3.4.2 *Gomphrena cardenasii* Standl. Ex E. Holzh., Mitt. Bot. Staatssamml. München 2: 187. 1955.

Type: Bolivien, Santa Cruz, Robore of Chiquitos, 10/1934, M. *Cárdenas 2953* (HT: M M0241702; IT: F F0093016F, LIL LIL001833).

Perennial plant, 30-35 (--40) cm. ***Root*** a woody taproot, fleshy. ***Stems*** erect, unbranched or with secondary branches, racemose, the main stems woody in the lower part; above green, with dense, 1-2.5 mm long, white trichomes. ***Cauline leaves*** sessile, oblong to lanceolate, 1.5 (--1.7) x 0.5 (--0.7) cm, acute mucronate at apex (Fig.4-32A), decurrent at base, middle nerve prominent, margin entire, densely covered with appresed trichomes both on the blade and the margin, on adaxial side of leaf bright white, on abaxial side of leaf more light yellow; trichomes multicellular 1.6 (--2.5) mm long. ***Apical leaves subtending paracladia*** (inflorescences) 2-5, leaves arranged symmetrically, cordate to-ovate, 0.5-0.6 (--1) x 0.3 (--0.5) cm, acuminate at apex, green to olive colour, densely covered with white to light yellow trichomes. ***Inflorescences*** globose to subglobose, terminal, 0.5-0.8 (--1.2) cm in diameter, white. ***Flowers*** 5-(--6) mm long, sessile. ***Bracts*** ovolanceolate, cimbiform 2-(--2.4) x 1.5 mm, membranous in texture, white opaque colour, acute at apex, margin entire. ***Bracteoles*** ovate-lanceolate, 3.4 x 1.5 mm, membranous charinate in texture, white-translucent, acuminate at apex, with a crest in the third of the upper dorsal part, which is wide and toothed at the margin, tepals bigger than bracteoles. ***Tepals*** oblong-lanceolate, chartaceous in texture, acute at apex, connate in the base, navicular, white, the middle part coriaceous and yellow; with straight, erect trichomes in the basal dorsal part. Size of tepals unequal, external tepals 4-4.4 (--5) x 0.7 mm. Intermediate tepal 3.9-4.3 (--4.9) x 0.7 mm, inner tepal 3.6 (--4.2) x 0.4 mm. ***Filament*** 5.4 (--5.6) mm long, fused into a tube for 5.0 mm long, free part 0.8 mm long. ***Filament appendages*** 0.2-0.3 mm long, acute at apex (Fig. 4-31). ***Anthers*** oblong, 1.6 (--2) mm long, attached between the parts of the filament appendages free (two lobes). ***Gynoecium*** with two filiform stigma branches, 0.6 mm long, style 0.4 mm long, ovary ovate 0.6 mm long [voucher: Wood 18813 = AC 460, LPB, B)].

Micromorphology of trichomes. Multicellular, uniseriate. On ***stems and cauline leaves*** with 3 basal cells, these rounded and with a granulate ornamentation, or spiny with apex divided in two as "T"(Fig. 4-32G), the 4-8 upper cells with firm to flexible consistence, granulate to spiny ornamentation, striated sculpture of cuticule walls. Interlocking junctions conspicuous, scars arranged in > forty-five (as spines) degree, overlapping. ***Trichomes on the apical leaves subtending paracladia*** similar than on stems, only finer in the upper part. ***Trichomes on tepals*** in dorsal and marginal position, 2-4 (--5) mm, hirsute to hispid-erect (Fig. 4-32G), firm to collapsed but always rigid, the 1-2 basal cells rounded, with firm walls, and smooth surface; ***interlocking junctions*** simple, conspicuous, without ornamentation. ***Anatomy of tepals.*** Tissue is composed of elongate straight, cylindrical dermal cells, arranged in one row, the extremes fitting perfectly.

Habitat and ecology. This species is endemic to Bolivia, so far collected only in the Chiquitano dry forest and Cerrado Chaqueño ecoregion. The characteristic habitat are forests with trees 20 to 25 m tall. Typical tree species are *Centrolobium microchaete* (Mart.ex Benth.) H.C. Lima, *Peltogyne heterophylla* M.F. Silva, in steep slopes *Anadenanthera colubrina* (Vell.)Brenan. *Gomphrena cardenasii* grows specifically on black (Laja) and granitical rock, and in sparse vegetation over shelving rocks passing to dry forests on deeper soil. Scattered plants were also found on bare rock in open “Campo rupestre” type vegetation with much open vegetation and some dry forest and moist areas. Altitudes range between 268-660 m. This is the only species of *Gomphrena* in Bolivia that has flowers all the year.

Distribution. Bolivia, province Chiquitos (Dept. Santa Cruz) (see Fig. 4-35).

Specimens examined for distribution assessment. ***Bolivia, Santa Cruz, Chiquitos***, Roboré, [-59,733, -18,33], 416 m, 10, 1934, *Cárdenas, M., 2953*, (F, LIL, M). Camino a Roboré, 5 km NW de Robore, [-59,65527, -18,3955], 268 m, 25, 4, 2012, *Mostacedo, B., 2839*, (USZ). c. 4 a 5 km de la rodovia Roboré-Santa Cruz, al frente de la Comunidad San Pedro, hacia la serranía Santa Bárbara, [-59,49110, -18,16209], 344 m, 11, 6, 2009, *Soto, D., 1171*, (USZ, LPB). Roboré c. 2 block north of the main square and beyond railway in Roboré town, [-59,749234, -18,3094369], 300 m, 13, 3, 2004, *Wood, J.R.I., 20678*, (LPB, B, K). Chiquitos, By path from airstrip south towards el Pozo de Ingeniero, [-59,625, -18,344166], 660 m, 29, 12, 2002, *Wood, J.R.I., 18813*, (USZ). 9 a 10 km de Santiago de Chiquitos sobre el camino a Roboré, [-59,6583329, -18,3366], 597 m, 30, 4, 2008, *Wood, J.R.I., 24604*, (USZ, LPB). Chiquitos, By path from airstrip south towards el Pozo de Ingeniero, [-59,625, -18,344166], 660 m, 29, 12, 2002, *Wood, J.R.I., 18813*, (LPB, K). Zona de paurito y el pozo del ingeniero, south of Santiago de Chiquitos, [-59,549, -18,35], 400 m, 14, 4, 2004, *Wood, J.R.I., 20685*, (BOLV, LPB).

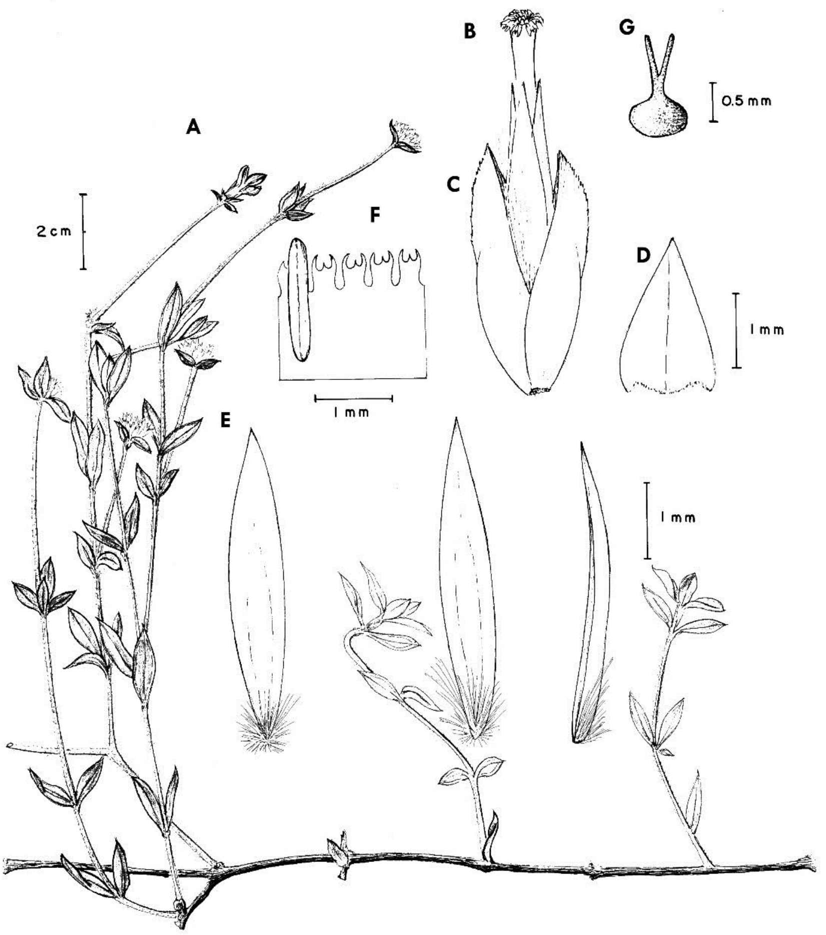


Fig. 4-31. *Gomphena cardenasii* Standl. ex Holzh. A) Habit. B) Flowers. C) Bracteoles. D) Bract. E) Tepals. F) Detail of the androecium. G) Gynoecium [voucher: Wood 18813 (LPB, B)].

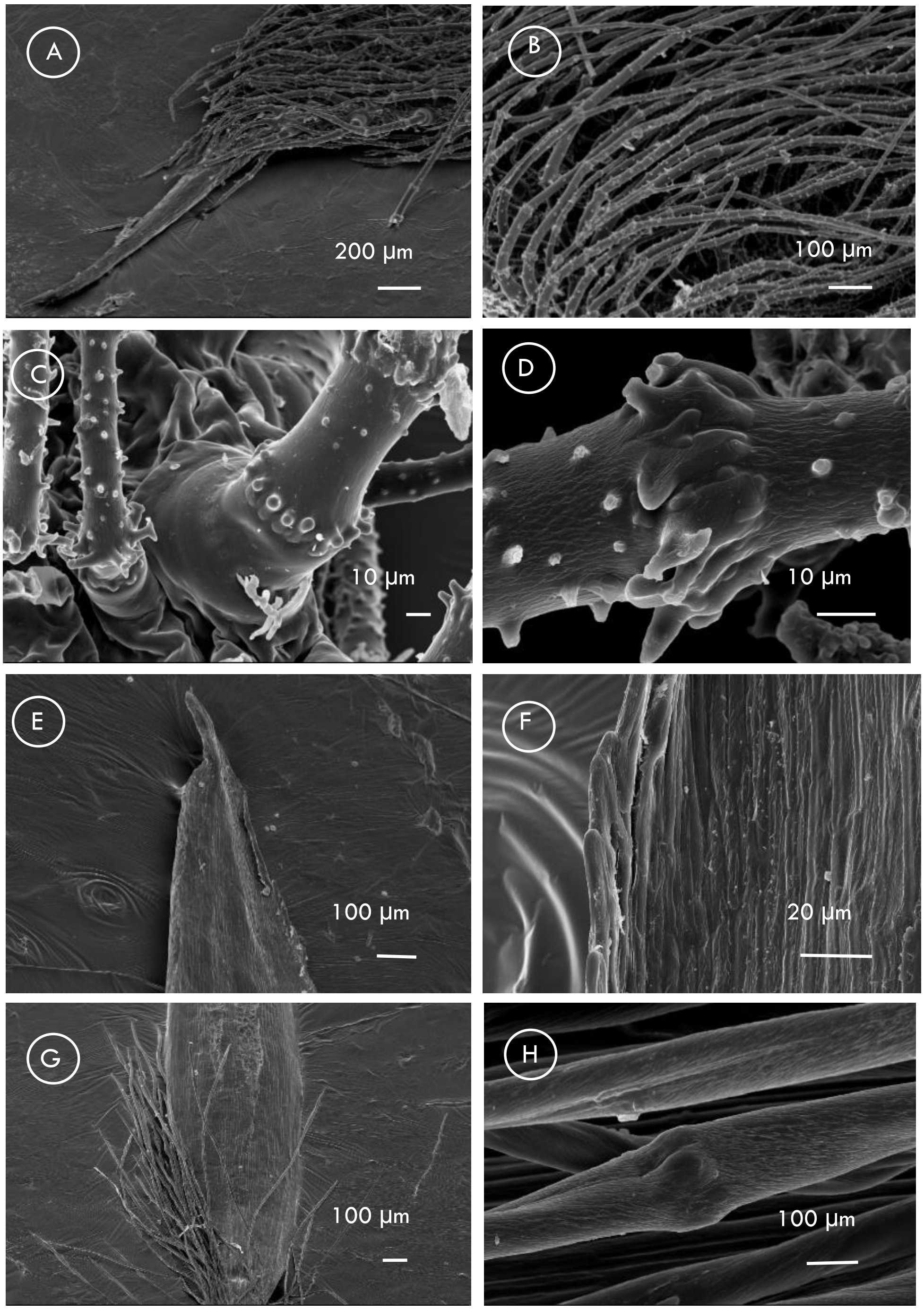


Fig. 4-32. *Gomphrena cardenasii* Standl. ex Holzh. Cauline leaves with trichomes. A) Detail of the mucronate leaf apex. B) Densely appressed trichomes on the lower leaf surface. C) Detail of the basal cells. D) Detail of the interlocking junctions. Tepals. E) Detail of the acute apex. F) Straight and fibrous tissue cells. G) Detail of the basal dorsal part of a tepal. H) Detail of the trichomes [voucher: Wood, 18813].

4.3.4.3. *Gomphrena agrestis* Mart., Nov. Gen. sp. pl. 2: 13, t.

Type: Crecit in campis montanis, in deserto Procinciae Minas Geraes, prope Serra de S. Antonio, inque mediterraneis Provinciae Bahiensis as Caeteté Villam. In provincia Cisplatin legit clar. Sellow. Pe Serra de Gram Mogol et prope Villam do Rio da Contas. Provinciae Minas Geraës et Bahiensis, Florebat Julio et Octobri, altitude 1600 pedum supra Oceanum. *Martius, C.F.P. von s/n* (HT: M, M0241688).

≡ *Xeraea agrestis* (Mart.) Kuntze., Rev. Gen. Pl.2: 545. 1891. 1891.

= *Gomphrena riedelii* Seub, Mart. Fl. Bras. 5:212.1875. Type: In campis ad Chapada d'Uberorana prov. Minarum: Riedel n. 2424 (HT: S S-R-2453 IT: BR BR 00000006950552, LE LE00001708, P P00622641, P00622641, C C10005416, K K000583085, M M0241796, GH, GH00037087.

= *Gomphrena rigidula* Glaz, Bull. Soc. Bot. France 58(3): 567. 1911.

Type: Entre Barbacena et Resaera, dans le campo, Minas, *Glaziou n°10016* (P).

≡ *Gomphrena agrestis* var. *genuina* (Mart.) Stuchlík., Beih. Bot. Centralbl. 30(2): 401. 1913.

Perennial subshrub, 28-50 (--100) cm tall. ***Root*** a woody taproot. ***Stems*** erect, only with unbranched principal stems, brown to light brown, with appressed to villous indumentum, trichomes brown to ligth brown. ***Basal leaves*** ovate lanceolate, blades 2.5-4 (--12) x 0.6- 2 (--3) cm, acute at apex, decurrent at base, trichomes hirsute to villous, white in the abaxial part, and light brown in the adaxial part. ***Cauline leaves*** ovate to elliptical, 1-4 (--4.5) x 0.3-0.6-(--2) cm, acute apex, midvein prominent, dark green, margin entire. ***Apical leaves subtending paracladia*** *(inflorescences)* 2-5, leaves arranged symmetrically, cordate to ovate, 0.5-0,8 (--1) x 0.4 (--0.8) cm, acute at apex, green to light brown, similar in texture to trichomes of caulinar leaves, trichomes are light brown to dark brown. ***Inflorescences*** globose to subglobose, terminal, 1-1.2 (--1.35) cm in diameter, solitary, white to light yellow. ***Flowers*** 5-6 (-- 7.5) mm long. ***Bract*** ovate to lanceolate, cimbiform, 2.5-3.5(--4.5) x 1.5 mm, membranous in texture, light brown, acute at apex, margin entire. ***Bracteoles*** ovolanceolate, 5-6 x 1.3 mm, membranous in texture, ligth brown, midvein prominent, the bracteole owns a crest extending widely for a fifth of the upper dorsal midvein, and narrowly extending to the base of the bracteole. ***Tepals*** lanceolate, membranous to coriaceaus at maturity, yellow-light brown, acuminate at apex, margin entire, trichomes dense at the base and abaxially. Sizes unequal. External tepals 7 x 1 mm, intermediate 6.8 x 0.7mm, inner tepals 6.4 x 0.3 mm. ***Filaments*** 8.5 mm long, fused into a tube for 7.2 mm long, free part 1.3 mm long. ***Filament appendages*** conspicuous, 0.5 linear shaped, united part 0.8 mm long (Fig. 4-33G). ***Anthers*** thin, oblong, 2 mm long. ***Gynoecium*** with two filiform rbranches, 1.5-1.8 mm in length, style 1.3 (--1.5) mm, ovary 0.5 mm [voucher: Stannard 6552].

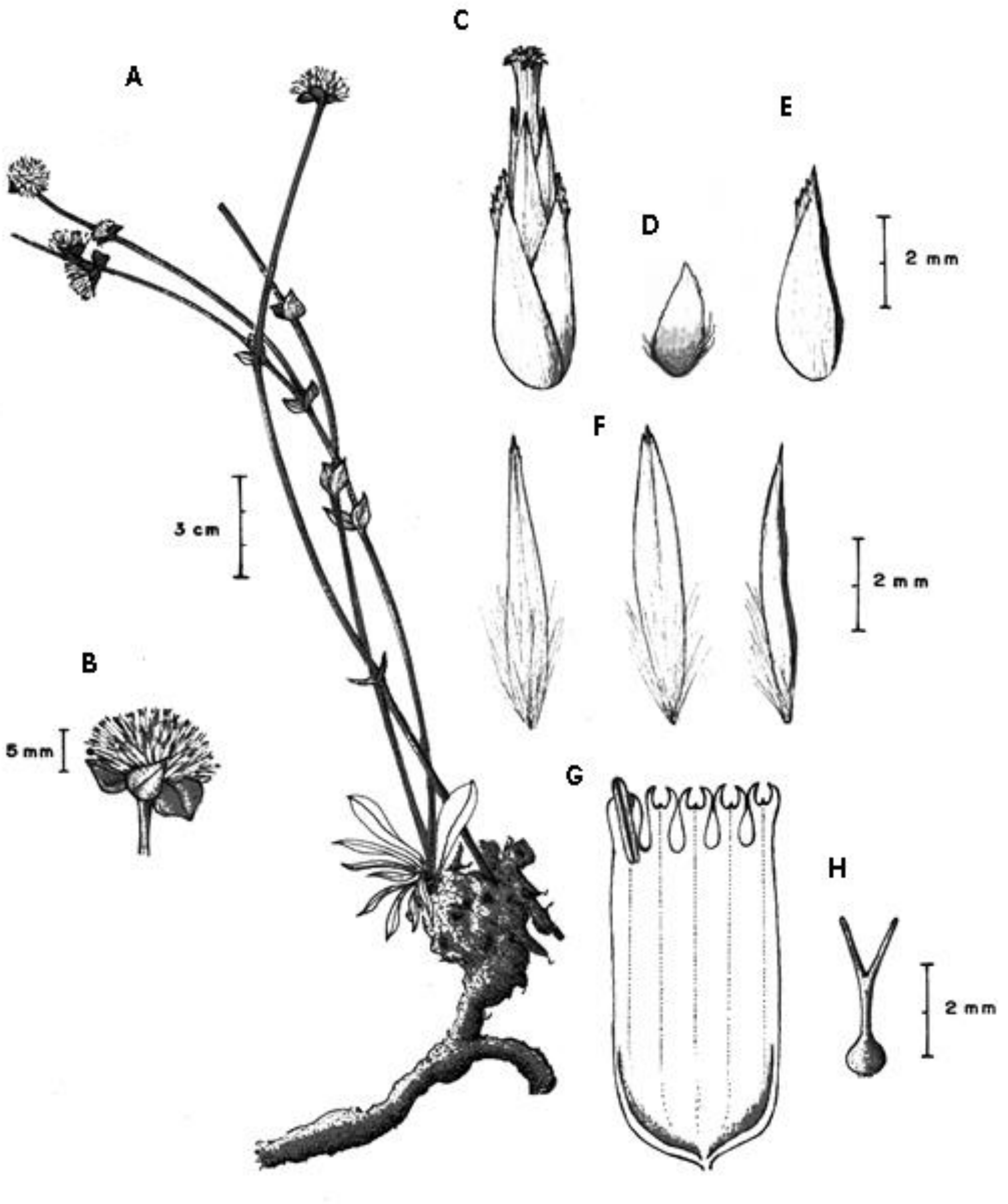


Fig. 4-33. *Gomphrena agrestis* Mart. A) Habit. B) Inflorescence head. C) Flowers. D) Bract. E) Bracteoles. F) Tepals. G) Detail of the androecium. H) Gynoecium [voucher: Stannard 6552].

Micromorphology of trichomes. Multicellular, uniseriate: 3-5 cells, 0.4 (--2) mm in length. On ***stems and cauline leaves*** with 1-2 rounded and broadly shaped basal cells, the upper 4-8 cells straight, salicose, with sparse granulose or palilose ornamentation, firm to flexible in consistence, conspicuously striated sculpture of the cuticule walls. ***Interlocking junctions*** conspicuous, broad, scars in zero angle degrees, overlapping. ***Trichomes on apical leaves subtending paracladia*** similar than on stems and cauline leaves, but cells larger and more flexible in the lower part. ***Trichomes on tepals*** *in* dorsal and marginal position, 2-4 (--5) mm, hirsute to hispid-erect, the 1-2 basal cells firm rounded, cell walls smooth, ***interloking junctions*** conspicuous, with firm consistence in the base, and collapsed cells in the upper cells [voucher: Stannard 6552]. ***Anatomy of tepals.*** Tissue is composed of elongate straight, cylindrical dermal cells, arranged in one row, the extremes fitting perfectly.

Taxonomic remark. The species has a characteristical basal leave rosette and erect umbranched stems. However, a detailed comparison of specimens from Bolivia and Brazil and Paraguay still needs to be made. It is necessary to make more collections of the genus in the East of Bolivia.

Habitat and ecology. Growing on quartzite rock outcrops, black stone "laja" or in sandy soils. The species is widely distributed in Brazil, in the region Paranence of the "Cerrado", "Campo rupestre" and "campos limpos", seldom on humid places on the West of Bahia (Senna et al. 2010). In Bolivia it was collected in Otuquis National Park, Santiago lookout in the chiquitana marginal high land, belonging to regions with savannahs (grassland), transitional forests mostly influenced by cerrado elements, Chiquitano semideciduous forest and Chaco deciduous forest, in semi-humid climate. Predominant tree species of the chiquitano forest ar *Schinopsis brasiliensis* Engl., *Aspidosperma pallidiflorum* Müll. Arg., *Astronium urundeuva* (Allemão) Engl. and it includes elements of the cerrado and Chaco such as *Anadenanthera macrocarpa* (Benth.) Brenan, *Calycophyllum multiflorum* Griseb. In Bolivia in the Chiquitano dry forest and the Cerrado Chaqueño ecoregion the plants of G. agrestis were collected between 140-1600 m.

Distribution: Brasil, Bahia, Maranhão, Minas Gerais, Paraná. Bolivia province of Chiquitos and Germán Busch Becerra, (Dept. Santa Cruz) (see Fig. 4-35).

Specimens examined for distribution assessment. ***Brasil, Bahia***, Trilha na beira da estrada de chão que liga Cocos a Minas Gerais (estrada paralela ao caminho para Tamanduá), [-44,732, -14,25], 595 m, *Conceição, S.F., 171*, (HUEFS). Catolés, Lagoinhas, [-41,854166, -13,3161109], 1380 m, 22, 7, 2003, *Conceição, A.S., 650*, (HUEFS). Abaira, [-41,549, -13,1], 1120 m, *Ganev, W., 129*, (HUEFS). Abaira, Serra do Atalho, complexo serra da tromba. Campo entre serra do atalho e a serra da tromba, [-41,830727, -13,2140210], 1400 m, 18, 4, 1994, *Melo, E., 1014*, (HUEFS). Abaira, [-41,916, -13,316667], 1250 m Ganev, W., 252, (HUEFS). Serra da Serrinha, caminho Capao-Serrinha-Bicota, [-41,85, -13,33], 1645 m, 26, 4, 1994, Ganev, W., 3126, (HUEFS). Alcobaca, West side of BA 001, 1.6 km south of junction with road from Teixeira de Freitas to Alcobaca, [-39,25, -17,533], 21, 10, 1993, Thomas, W.W., 10048, (HUEFS). [-45,8269439, -11,8788], 760 m, Cotrim, A., 1634, (HUEFS). Cocos, ca. 35-37km W de Cocos. Proximidades de Jacaré, [-44,7586110, -14,2458329], 580 m, 17, 5, 2001, França, F., 3641, (HUEFS). Correntina, Estrada para Mucambo, [-44,63388, -13,31472], 671 m, 16, 7, 2003, Oliveira, A.A., 229, (HUEFS). Estrada para Mucambo, [-44,62749, -13,293], 668 m, 16, 7, 2003, Oliveira, A.A. de, 232, (HUEFS). Jaborandi, ca. 58km L de Posse (Goiás), [-45,8352780, -14,1472219], 870 m, França, F., 3713, (HUEFS). Jacobina, Serra da Jacobina. Morro do Cruzeiro, [-40,5183, -11,1806], 478 m, Furlan, A., 7528, (HUEFS). Lencois, Mucugezinho, subida em direcao a Serra da Chapadinha, [-41,41694439, -12,4572], 792 m, 23, 10, 2000, Nunes, T.S., 177, (HUEFS). Mucugê, Entrada da Fazenda Florestal, [-41,4838, -13,0969440], 1150 m, 0, 0, 0, Giulietti, A. M., 2317, (HUEFS). Rio de Contas, Kaiambola. Serra da Mesa, [-41,861944, -13,39527], 1568 m, Giulietti, A. M., 2269, (HUEFS). Campo alto da Cruz. Próximo alto da Cruz a populacao de Melocactus do Projeto FNMA, [-41,8333, -13,5166], 20, 4, 2003, Santos, A.K.A., 102, (HUEFS). Serra Geral de Caitité. 9.5 km S of Caitité on road to Brejinhos das Ametistas. By small reservoir and stream. Scrub among rocks by stream, & with nearby woodland. This plant growing in cerrado, Serra Geral de Caitité. 9.5 km S of Caitité on road to Brejinhos das Ametistas. By small reservoir and stream. Scrub among rocks by stream, & with nearby woodland. This plant growing in cerrado, [-42,5, -14,11666], 1000 m, 13, 4, 1980, Harley, R.M., 21332, (MO). Umburanas, Delfino, estrada para Campo Formoso, após 1km dobrar à esquerda na estrada para Lages dos Negros, depois de 4,6km chega-se no povoado de Lagoa da Barra, dobrar à esquerda antes do campo de futebol, pegando a estrada para Boa Vista, depois de 8,7km chega, [-41,195556, -10,363611], 925 m, Machado, M., 266, (HUEFS). Maranhão, Mirador, Parque Estadual do Mirador, Aldeia, [-44,3631, -6,370829], 175 m. Félix, L.P., 8106, (HUEFS). Minas Gerais, Buritizeiro, Ligazao da Rod BR-365 a Sao Romao, Galhao, [-45,150188, -17,302012], 750 m, 12, 5, 2001, Hatschbach, G., 71962, (Museu botánico Municipal), Mato Verde, Estrada Rio Pardo de Minas sentido Mato Verde, [-42,636944, -15,476], 914 m, 21, 4, 2006, Carneiro-Torres, D.S., 700, (HUEFS). Paraná, Curitiba. Joaquim Felício, Serra do Cabral, [-44,17219, -17,7575], 676 m, Hatschbach, G., 72019, (HUEFS). Bolivia, Santa Cruz, Chiquitos, Mirador de Santiago de Chiquitos, [-59,57, -18,32472], 868 m, 7, 3, 2011, Wood, J.R.I., 27193, (LPB). Germán Busch Becerra, "Área natural de manejo integrado y Parque Nacional Otuquis", Estancia Quebracho, [-58,0983299, -19,358329], 140 m, 5, 11, 1998, Carrión, A.M., 683, (MO, USZ).

Fig. 4-34. Habitats of *Gomprena lanigera* Seubert. A) Serrania de Huanchaca, (photo Museo Noel Kempff Mercado). Area where *G. agrestis* Mart. Was collected B) Santiago de Chiquitos, photo J.R.I. Wood.

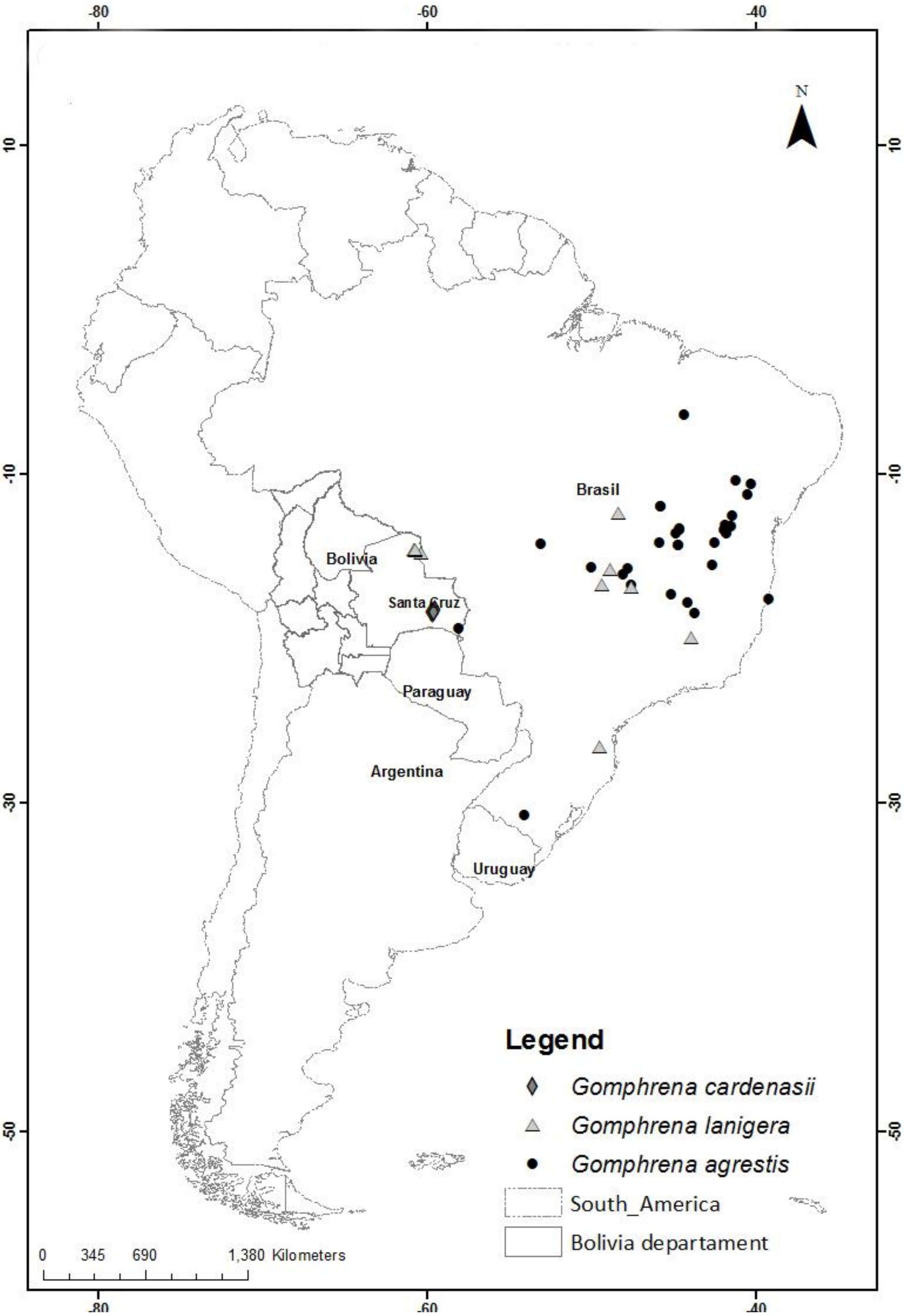


Fig. 4-35. Distributions of *Gomphrena agrestis, G. cardenasii* and *G. lanigera.*

4.3.5. *Gomphrena celosioides* CLADE

The nuclear marker (ITS) shows that the two specimens of *G. celosioides* appear in an isolated position in a polytomy with a clade of the species of the mostly Andean subclade (has high support values 1 PP, 100JK; see Chapter 3), and the clade that includes *G. agrestis*, *G. cardenasii, G. lanigera* and *G. macrocephala* (1PP, 100BS, 100JK). The latter species has not been found in Bolivia and only occurs in the Chaco of Argentina, Brazil and Paraguay.

But the sampling of this clade is a bit sparse, still. There are several morphologically similar taxa described from South America that need to be sampled with sequences. Some of them were introduced to the Old World Tropics where the two samples included here come from.

4.3.5.1. *Gomphrena celosioides* Mart., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 13: 301. 1826

Type: Crescit in Brasiliae, province Cisplantina, Brazil, Sellow s/n (HT: F F0047617F, IT: K 000195047, 000195048, 000195049, P 00622662, 00622663, 00622664).

≡ *Xeraea celosioides* (Mart.) Kuntze, Rev.Gen. Pl. 2: 545 (1891) nom. illeg.

= *Gomphrena decumbens* Jacq. Plantarum Rariorum Horti Caesarei Schoenbrunnensis 4: 41–42, pl. 482. 1804.

Type: Spain, M. H. R. Matritensis. Not on sheet, #s.n., (HT: SEV SEV-H4054).

= *Gomphrena decumbens* var. *albiflora* Stuchlík in Repert. Spec. Nov. Regni Veg. 11: 158. 1912.

Lectotype "in hoc loco designatus": Paraguay. Paraguarí: "In campo pr. Paraguari", IX.1885-1895, *Hassler, E. 945* (LT: G, G00103387, Barbey-Boissier!, ITLT: G, G00103426! K).

= *Gomphrena decumbens* fo. *albiflora*. Chodat. Bulletin de l'Herbier Boissier, sér. 2 3: 389. 1903. (nom. nud.)

= *Gomphrena decumbens* subf. *villosa* Chodat in Bull. Herb. Boissier ser. 2.3: 389. 1903 (nom. nud.)

Type: Nanbia, Bastardland, Aefners Farm. South West Africa, 19/11/.1934, *Dinter, K. 8002* (HT: S S0712687).

= *Gomphrena celosioides* f. *grandifolia* Stuchlík in Repert. Spec. Nov. Regni Veg. 11: 158. 1912.

Type: Paraguay. Canindeyú, regione vicine Igatimí, XI.1898-1899, *Hassler, E. 5474* (HT: G G00103446, IT: G G00103447, G, G00103448, G, G00103449, G, G00103450, K, P, P04960015, P P04960025!).

Annual or perennial herb, 26.5(--30.5) cm. ***Root*** a woody taproot and fibrous. ***Stems*** erect, with secondary and terciary stem, striated, with appesend to villous trichomes sparsely or densely hairy. ***Basal leaves*** absent. ***Cauline leaves*** subsessile, lanceolate to oblong, 1.7-2.7(--3.7) x 0.5-1(--1.2) cm, cuspitate-mucronate at apex, glabrous or sparse, appressed trichomes, on adaxial surface densely appressed. ***Apical leaves subtending paracladia*** *(inflorescence)* 3-5, leaves arranged symmetrically, ovolanceolate 0.9-1.5 (--1.8) x 0.9-1.5 (--1.8) cm, cuspitate to rounded at apex, green olive, with villous indumentum, trichomes white. ***Inflorescences*** globose to subglobose, terminal, 1.2-1.8 (--2.5) cm, spikes solitary and terminal on the main vegetative axes. ***Flowers*** 4.9-5 mm long. ***Bracts*** ovolanceolate, cymbiform 3 (--3.5) x 1.5 mm, membranous in texture, white color, acuminate at apex and with prominent midveine, margin entire, glabrous, translucent throughout or opaque and white at apex only. ***Bracteoles*** ovolanceolate, 3.4 x 1.5 mm, membranous in texture, white, acute to aristate at apex, midveine prominent, entire margin, straight, equal to or slightly longer than tepals. The bracteole owns a crest located in a third of the upper dorsal part; crest is thin and toothed in the margin. ***Tepals*** ovolanceolate, membranous more or less thick in texture, white, yellow or pink, acuminate at apex, entire at margin, with lanate trichomes on the dorsal part. Sizes unequal. External tepals 4.8 x 0.7 mm, intermediate 4.8 x 07 mm, and inner 4.6 x 0.4 mm. ***Filaments*** conspicuous 4.2 mm long, fused into a tube for 3.8 mm, free part 0.6 mm long. ***Filament appendages*** conspicuous 0.4 mm (united on the basal part 0.2 mm) (Fig. 4-36E). ***Anthers*** oblong, 0.8-1 mm long. ***Gynoecium*** with two filiform stigma branches, of 0.5 mm length, style 0.2–0.3 mm long, ovary 1 mm. [voucher: Medd 160837].

Micromorphology of trichomes. Multicellular, uniseriate. On ***stems and cauline leaves*** the 1-2 basal cells straight, at the border with large spinous and salicose ornamentation. The 4-6 upper cells with firm to flexible consistence, spinous ornamentation, and sculpture of cuticle walls smooth. ***Interlocking junctions*** conspicuous, linear prolonged in the border cells, overlaping scars arranged in zero degree (Fig. 4-37C). ***Trichomes on apical leaves subtending paracladia*** in the abaxial surface, with 1-2 rounded basal cells. The 4 to 6 upper cells with firm to flexible consistence, salicose and spinous ornamentations, striated sculpture, the ***interlocking junctions*** conspicuous, linear scar arranged in zero degrees. ***Trichomes on tepals*** with 1, 2 basal cells of firm consistence, the upper with collapsed, sinuous, twisted cells. ***Anatomy of tepals.*** Tissues are composed by elongate straight, cylindrical dermal cells, arranged in one row, all fitting perfectly, the fiber cells form a tooted irregular margin [voucher: Medd, R. 160837 (NSW)] (see Fig. 4-37).

Fig. 4-36. *Gomphrena celosioides* Mart. A) Habit. B) Bracteoles. C) Bract. D) Tepals. E) Detail of the androecium, F) Gynoecium. [voucher: Medd R. 160837 (NSW)].

Taxonomic remark. *Gomphrena celosioides* has a peculiar wide distribution: it is common in more humid places than the other species of *Gomphrena* s.str., and also it is frecuently present in Africa and Asia where is naturalized and common in the ruderal vegetation. This wide distribution created a complex and confusing nomenclature history. Still, the mayor problem is that the molecular analyses in this study do not yet include all the different varieties accepted by Pedersen (2016) and Ramella (2016). This is the reason why the present study describes just the species *G. celosioides* without discussing or recognozing varieties.

Habitat and ecology. The species occurs in open areas with sandy soil, ruderal vegetation, in scrub of *Dodonaea viscosa* Jacq. and *Acanthostyles buniifolius* (Hook. ex Arn.) R.M. King & H. Rob.. Also in Humid Savanna, semi-heigh humid grassland, and wet meadow with fan palms. Also at margins of forest of Anacardiaceae, *Cecropia* and Cactaceae, and *Jatropha*, and in secondary forest of the pre-Andean amazon; the ecoregions are inter-Andean dry forest, North Puna, Yungas, Gran Chaco, Chiquitano dry forest, Southwest Amazonia, flooded savannas, Cerrado Chaqueño, where the plants have been collected between 144- 4286 m.

Distribution. The species is native in South America, in Brazil, Paraguay, Humid Chaco, Argentina, and Uruguay, adventitious in Africa, Asia, Australia and Oceania. In the latter areas it as a markedly invasive tendency. In Bolivia it occurs in Provinces of Cercado, José Ballivián, Yacuma, Moxos, Vaca Diez (Dept. of Beni), Campero (Dept. Cochabamba), Abel Iturralde, J. Bautista Saavedra (Dept. La Paz), Andrés Ibáñez, Sara, Chiquitos, Cordillera, Germán Busch Becerra, José Miguel de Velasco F., Ñuflo de Chávez (Dept. Santa Cruz).

Specimens examined for distribution assessment. ***Bolivia, Beni*, *Cercado***, Trinidad "nordlich der Stadt, Wegrand ruderal", [-64,903,-14,803], 157 m, *Rilke, S., 576*, (LPB). Trinidad, Centro Nacional de Mejoramiento de Ganado Bovino del Beni (CNMGB-BENI), en potreros de investigacion (8-12), ubicado a 2.5 km, lado Noreste de la ciudad de Trinidad, [-64,895, -14,8113], 155 m, 7, 11, 2006, *Hayashi, H., 942*, (LPB). Vicinity of campus of the Universidad Tecnica del Beni, 2,5 Km N of center Trinidad, [-64,883, -14,8], 150 m, 26, 2, 1987, *Nee, M., 34274*, (LPB, NY). Vicinity of campus of the Universidad Tecnica del Beni, 2,5 Km N of center Trinidad, [-64,883, -14,8], 157 m, 26, 2, 1982, *Nee, M., 34275*, (LPB, NY). A 3 km de San Javier hacia la laguna de Coitarama, [-64,866, -14,566], 200m, 12, 3, 1999, *Orellana, M.R., 127*, (LPB). Trinidad. Nördlich der Stadt, Wegrand ruderal, [-64,9, -14,833], 159 m, 9, 11, 1986, *Rilke, S., 572*, (LPB). 34 Km de Trinidad - San Joaquin, [-64,833, -14,166], 144 m, 2, 11, 1993, *Moraes, M., 1479*, (LPB, RM). ***José Ballivián***, Rurrenabaque, Borde del camino al aereopuerto, [-67,504, -14,431], 217 m, 11, 3, 1982, *Beck, S.G., 8289*, (LPB). ***Yacuma***, Espiritu, en la zona de influencia del río Yacuma, [-66,375277778, -14,12861111], 200 m, 8,4, 1980, *Beck, S.G., 3215*, (LPB). Espiritu, en la zona de influencia del río Yacuma, [-66,38416667, -14,15777778], 200 m, 28, 4, 1980, *Beck, S.G., 3396*, (LPB). Espiritu, en la zona de influencia del Río Yacuma, [-66,616, -14,192], 200 m, 6, 2, 1987, *Gunnemann, H., 1*, (LPB). Estación Biológica del Beni, [-66,616, -14,5], 200 m, 14, 12, 1994, *Balderrama, J., s/n.*, (LPB). Estacion Biologica del Beni. Comunidad Villa Dorita, [-6,616, -14,5], 200 m, 22, 1, 1995, *Balderrama, J., 340*, (LPB, NY, CTES). Estacion Biologica del Beni, 60 Km de San Borja, hacia San Ignacio de Moxos, [-66,366, -14,816], 300 m, 21, 9, 1998, *Beck, S.G., 24569*, (LPB). Estacion Biologica del Beni, borde de la Laguna Normandia, [-66,354,-14,869], 178 m, 29, 9, 2000, *Beck, S.G., 27623*, (LPB). Espiritu, en la zona de influencia del río Yacuma, [-66,37527778, -14,12861111], 165 m, 1, 10, 1979, *Beck, S.G., 2618*, (LPB). Espiritu, en la zona de influencia del río Yacuma, [-66,37527778, -14,12861111], 164 m, 8, 4, 1980, *Beck, S.G., 3214*, (LPB). Estación Biológica del Beni, Tierra Santa. Lado canchón de la escuela, [-66,616, -14,55], 200 m, 4, 19, 1995, *Rivero, E., 330*, (LPB, B, CTES, NY, USZ). Espiritu, semialtura, zona 2, [-66,4, -14,133], 189 m, 22, 2, 1990, *Moraes, M., 1228*, (LPB). ***Moxos***, territorio Indigena, Parque Nacional Isiboro Sécure (TIPNIS), sector Tres pistolas. Modulo ganadero, semialtura, alternada con bajíos, [-65,266, -15,816], 150 m, 3, 6, 1996, *Gutiérrez, E., 2035*, (LPB). Territorio Indigena. Parque Nacional Isiboro Sécure; localidad: Tres pistolas. Bosque abierto, [-65,233, -15,516], 150 m, 6, 6, 1996, *Gutiérrez, E., 2130*, (LPB). ***Vaca Diez***, Riberalta, vereda de la plaza principal, [-66,074, -10,998], 138 m, 13, 8, 1985, *Moraes, M., 167*, (LPB). Riberalta, [-66,066, -11], 170 m, 23, 5, 1987, *Solomon, J.C., 16760*, (LPB, MO). ***Cochabamba***, ***Campero***, A 34 km de Lagarpampa hacia Aiquile, cerca a Panama, [-65,178, -18,212], 2820 m, 25, 3, 1993, *Atahuachi, M., 260*, (BOLV). ***La Paz***, ***Abel Iturralde***, Madidi, alrededores de San Buenaventura, [-67,536, -14,438], 200 m, 2, 12, 2004, *Araujo-M, A., 1265*, (BONN, LPB, MO). ***J. Bautista Saavedra***, Charazani; en Carijana, [-68,74138889, -15,22333], 4286 m, 20, 3, 1992, *Gutte, P., 171*, (LPB). A 30 Km de Charazani en el camino a Apolo, [-68,75, -15,216], 1543 m, 11, 2, 2003, *Wood, J.R.I., 18991*, (LPB). ***Santa Cruz***, ***Andrés Ibáñez***, City of Santa Cruz, [-63,2, -17,766], 400 m, 28, 11, 1984, *Nee, M., 30491*, (NY). Vicinity of abandoned old Jardín Botánico along Rio Piraí and roadsides on W side of Santa Cruz, [-63,216, -17,783], 420 m, 28, 11, 1984, *Nee, M., 30485*, (NY, LPB). Andres Ibañez, Abundant prostrate herb in moist sandy grassy mowed lawn next to Estacion de Servicio Guayacon on main road between Santa Cruz de la Sierra and Cotoca, [-63,093, -17,767], 528 m, 13, 12, 1999, *McCauley, R.A., 9925*, (LPB). 12 km E of center of Santa Cruz on road to Cotoca, [-63,066, -17,766], 375 m, 12, 8, 1987, *Nee, M., 35641*, (NY, LPB). Municipio de Porongo, localidad del Monumento Natural Espejillos. A 1.5 Km en direccion sureste de la casa de Dn Jose Osinaga, [-63,438, -17,901], 500 m, 3, 6, 2007, *Linneo, I., 1081*, B, (LPB, USZ, MO). ***Sara***, 5.8 Km al este de La Bélgica (surtidor de gasolina) por el camino entre La Bélgica y Buena Vista (cerca Estancia Salsipuedes), [-63,25, -17,566], 400 m, 2, 7, 1988, *Solomon, J.C., 18589*, (LPB, MO). Municipio de Santa Rosa, localidad Laguna Juan Chulo, bordes de la laguna y camino de ingreso, [-63,746, -16,987], 240 m, 10, 11, 2006, *Linneo, I., 888*, (LPB, USZ, MO). ***Chiquitos***, Roboré, c 2 blocks north of the main square and beyond railway in Roboré town, [-59,733, -18,333], 300 m, 13, 4, 2004, *Wood, J.R.I., 20674*, (LPB, BOLV). ***Cordillera***, Alto Parapetí "Hacienda Yapuimbia". Potrero abandonado,[-63,6369444, -20,0638], 800 m, 5, 1, 1984, *Michel, R. de, 269*, (LPB, MO). Camino a Totai. Saliendo de Santa Cruz hacia Camiri, desvío a Totai, [-63,387, -18,944], 28, 4, 2007, *Ortuño, T., 801*, (LPB). ***Germán Busch Becerra***, Puerto Quijarro, 6 Km hacia Puerto Suárez (de arroyo Concepción), [-57,716, -19], 145 m, 9, 9, 2000, *Beck, S.G., 27545*, (LPB). ***José Miguel de Velasco F.***, Finca Bonanza. Ca. 105 Km north of San Ignacio, and ca 22 Km S of San Simon, [-60,95, -15,63], 320 m, 26, 7, 1983, *Hopkins, M.J., 111*, (NY, LPB, B, CTES, MO). 1 Km debajo de la presa Guapomó, [-60,944, -16,38], 400 m, 29, 12, 1985, *Seidel, R., 21*, (LPB, NY). San Ignacio, [-60,983, -16,337], 400 m, 7, 5, 1986, *Seidel, R., 471*, (LPB). ***Ñuflo de Chávez***, [-62,5, -16,63], 241 m, 0, 0, 0, *McCauley, R.A., 126*, (LPB). Common prostrate to ascending (to 15 cm) herb in sandy soil along roadsides at edge of Chiquitanos, [-62,511, -16,633], 246 m, 14, 12, 1999, *McCauley, R.A., 9928*, (LPB). Near San Julian (S), [-62,595, -16,951], 274 m, 27, 2, 2003, *Rico, L., 1409*, (LPB).

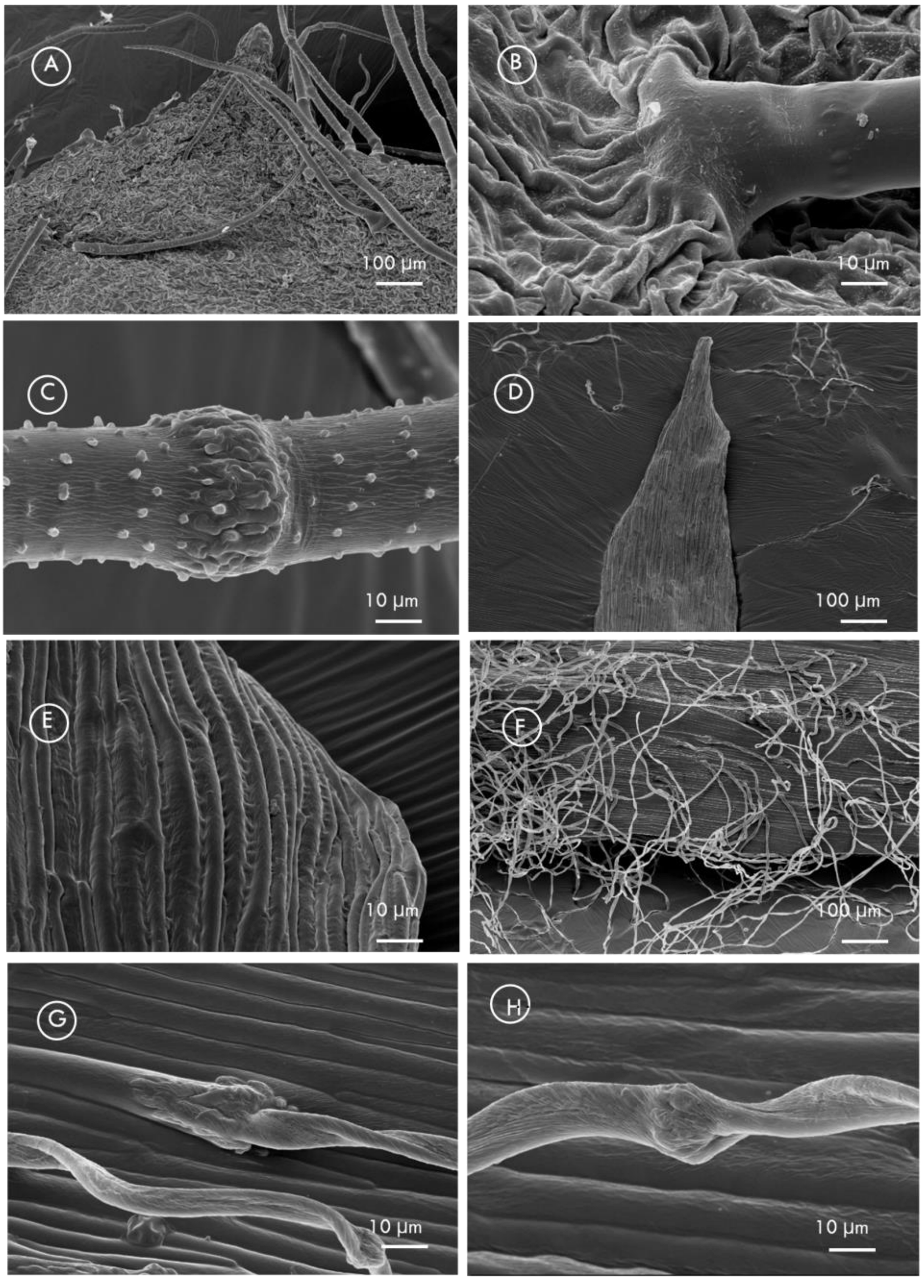


Fig. 4-37. *Gomphena celosioides* Mart. A) Trichomes on the cauline leaves and stems, trichomes appressed to villous. B) Detail of the basal cells. C) Detail of the interlocking junctions. Tepals. D) Apex of the tepals. E) Straight and fibrous tissue cells. F) Detail of the trichomes in general view. G) Detail of the collapsed cells. H) Detail of interlocking junctions [voucher: Medd, R. 160837 (NSW)].

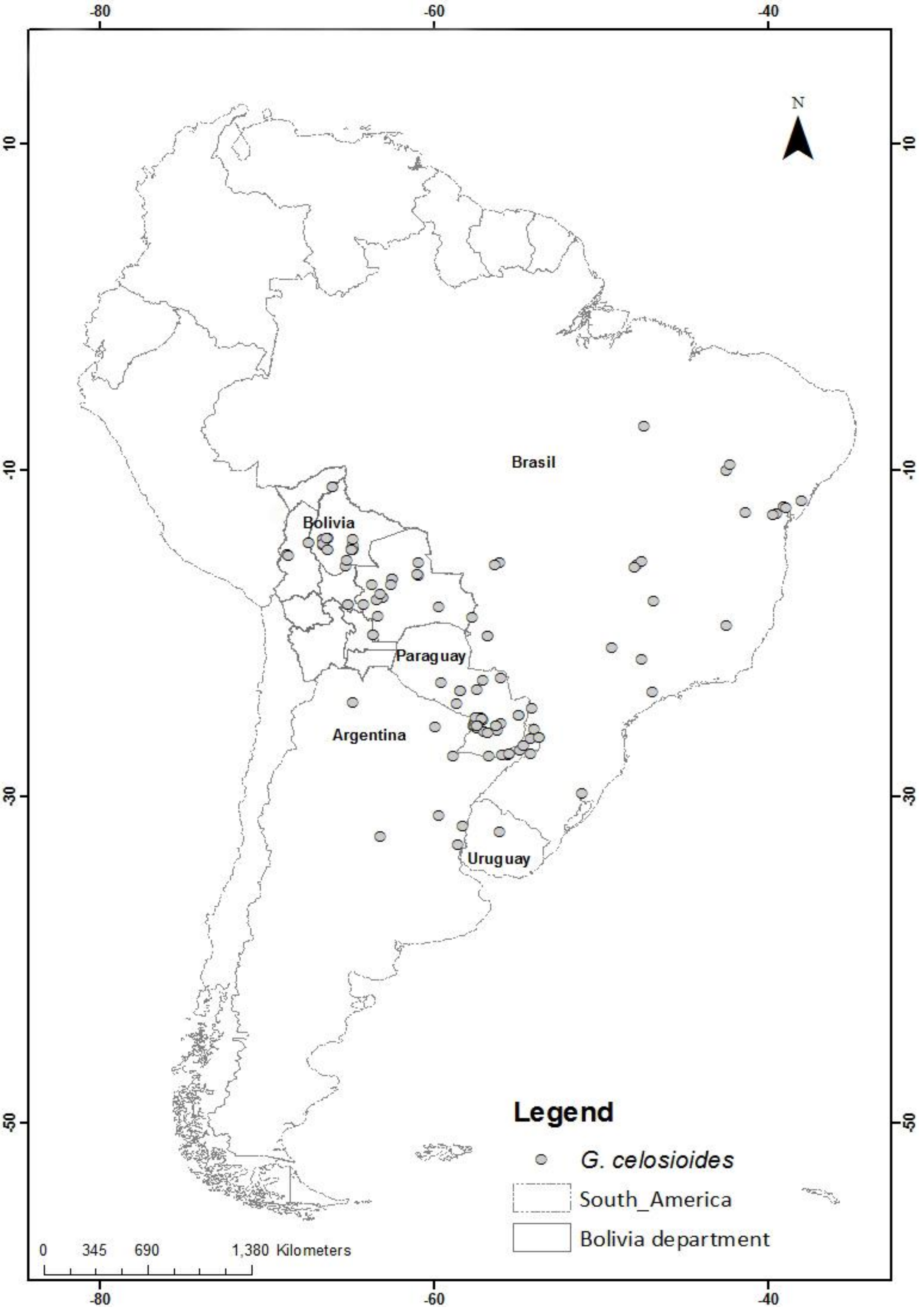


Fig. 4-38. Distribution of *Gomphrena celosioides*.

4.3.6. Annuals allied to *Gomphrena pallida* in the "Mostly Andean CLADE B"

This part includes a sublineage of the "Mostly Andean Clade B" (see Chapter 3). Nuclear ITS data separated specimens of *Gomphrena pallida* in two subclades. The latter one is with *G. pallida* s.str. and includes annual plants (1 PP, 100JK) together with the perennials (0.995 PP, 99JK). Othe samples formerly identified as *G. pallida* were treated above (in the *G. phaeotricha* clade). In this context the specimens of the true *G. pallida* subclade follow the concept of the species by Pedersen (1976). They are characterized by their subequal, basally united ungiculate sepals (narrowest in the center), which have trichomes on the dorsal surface and are "laciniate" or dentate or with trichomes on the margins. The main differences with respect to *G. phaeotricha* relate to the size of tepals, where *G. phaeotricha* much shorter inner tepals, and a glabrous margin of the tepals. There are also differences in the leaves whose abaxial surface is covered with long trichomes whereas the adaxial surface has shorter, very straight trichomes (see taxonomic remark in description species).

In general terms the species concept of *G. pallida* by Pedersen (1976), seems to be largely consistent with one of the clades in the ITS dataset. However, it may be necessary to designate a lectoptype, which could be the specimens Bang 933 (K), and as the istolectotype (E: 00394848) in a subsequent publication.

For the case of the description of *Gomphrena oligocephala* var. *pallida* Suess., this taxon was based on Rodríguez 1420, collected in the Sierra del Cajón, Salta Province, Argentina and distributed under this number to various herbaria (M, LIL, CTE, SI, LP), even though it represents several collections made from different localities and on different dates. Pedersen examined all of them in detail, finding all of them are similar with exception one which he described as *f. calva,* corresponding to the specimen Rodriguez 1420 in M (0241766). However, this specimen differs from the protologue in having been collected in April (not March) 1914 and at the height of 2600 m. As this appears to be unique, it should be selected as the lectotype of this form.

Suessenguth cited Rodriquez 1420, Venturi 3571 (LP 006807), Schreiter 5490 (M 021765) and Troll 1143 as syntypes of *Gomphrena oligocephala* var. *pallida,* but did not specify in which herbarium he saw these specimens. It must be supposed that the protologue was based on specimens seen at Munich (M), so Holzhammer annotated Rodriguez 1420 (M-0241762) as the type of this variety but did not nominate any one of the four, (M 0241762, 0241763, 0241767) sheets of this number at M as the type in Mitteil. Bot. Staats. München 14-15: 195. 1956. As Bena (2017: 139) simply interpreted this as lectotypification, without using the terms "designated here" or the equivalent, as demanded by the code, it is doubtful whether effective lectotypification has ever been made. Accordingly, Rodriguez 1420 (M-0241762) is here is proposed to be selected as lectotype of *Gomphrena oligocephala* var. *pallida* Suess. with isolectotypes: M-0241763!, M-0241764!, CORD-00002560!, CTES-0000310!, SI000719!. As this specimen originates from LP, it is likely that there is an isolectotype there although this cannot be confirmed.

In summary, Pedersen (1976, 1990) recognized four specific intraspecific taxa, three of which are analysed here: *Gomphrena pallida* ssp. *pallida* as the type of the species, (variety and forma), *G. pallida* subsp. *munda*, Darwiniana 20: 285. 1976. Type: Argentina, Jujuy, Abra de Yaví, 26 Nov. 1963, A.L Cabrera 15328 (HT: LP010409), *Gomphrena pallida* f. *calva*, Darwiniana 20: 285. 1976. Type: Argentina, El Alisal at 2600 m, April. 1914, Rodríquez 1420 (HT: M-0241766), and as the fourth *G. pallida* var. *diffusa* Pedersen, Bull. Mus. Natl. Hist. Nat., B, Adansonia ser. 4, 12(1): 86. 1990. Type: Argentina, Jujuy, 2 Nov. 1974, A. Schinini, C. Quarín, M.M. Arbo, S.M. Pire 10114 (HT: CTES0000312). The last is not including here, because no recent material was found in any herbarium or collected in the field.

Key to the annual species in the "Mostly Andean CLADE B" *(G. pallida* and allies)

1. Plants 5 - 20 (--40) cm tall, stems decumbent to ascendant or to erect, with firm consistence, and branched into secondary or tertiary stems. Inflorescence terminal, usually more than >1.5 cm (in the range of 0.7-2.5 cm in diameter (2)

2. Tepals lanceolate, narrowest at middle part (unguiculate), dentate in the margin, trichomes of the stems and cauline leaves white or light yellow. Upper part of filament free with clearly raised appendages……………………………………………………*G. pallida* (Fig. 4-39, 4-40)

2' Tepals lanceolate to spatulate, deeply dentate especially at the apex, trichomes of the stems and cauline leaves light to dark brown, darker especially near the inflorescence. Anther appears sunken between laterally fused filament appendages ……………….. *G. mizqueensis* (Fig. 4-42)

1'. Plants usually not more than 15 cm tall, usually <10 cm, decumbent to erect, with secondary or tertiary stems. Inflorescence terminal, usually not more than <1.1 cm (in the range of 0.7-1.1 cm) in diameter (3)

3. Cauline leaves lanceolate to cordate , light to dark green marmolate colour, acute at apex, scarcely villous indumentum (only in the middle part), bract semiforcate (broadest in the apex). Anther appears sunken between laterally fused filament appendages. (4)

4. Stems decumbent to erect, trichomes dark brown to black (Toro Toro).
…………………………………………………………………………… *G. sp. nov. (spec2 a)* (Fig. 4- 44)

4.' Stems decumbent to ascendent, trichomes white (Chataquila)...*G. sp. nov. (spec2 b)* (Fig. 4- 46)

3.' Cauline leaves ovolanceolate, light green in colour, apiculate to mucronate at apex, covered with homogeneous indumentum, the apical leaves hirsute, with short trichomes (2-3 cells). Upper part of filament free with clearly raised appendages ………… *G. sp. nov. (sarijchi)* (Fig. 4-. 48)

4.3.6.1. *Gomphrena pallida* (Suess.) Pedersen, Darwiniana 20(1–2): 282, f. 2. 1976

≡ *Gomphrena oligocephala* var. *pallida* Suess., Repert. Spec. Nov. Regni Veg. 49: 9. 1940 Type: Argentina, Salta, Sierra de Cajón. Rodriguez, 1420.
(to be proposed the LT: M-0241762. ISLT: CORD 00002560: M 0241762, M 0241763, M 0241764, SI 000719, LP 006807)
= *Gomphrena decumbens* var. *boliviana* Stuchlík, Repert. Spec. Nov. Regni Veg. 12: 519. 1913; to be proposed as lectotype: M. Bang 933 (K, isolectotype, E 00394848). Bolivia, Bolivian plateau.

Annual herb, 12 (--30) cm. ***Root*** simple, fibrous. ***Stems*** decumbent, with secondary stems, slightly striated, red or light green, with appressed to villous trichomes, white in colour, 2-3 mm long, denser in the upper parts (close to the inflorescence). ***Basal leaves*** absent. ***Cauline leaves*** ovolanceolate, 1.5 (--2.5) x 0.6 (--0.8) cm, acute at apex, mucronate (midvein excurrent for 0.2 mm), green, sometimes red on the abaxial side of leaf, indumentum densely villous, denser in the lower part. ***Apical leaves subtending paracladia*** *(Inflorescences)* 4-5, leaves arranged symmetrically, cordate to lanceolate, 0.5 (--1.0) x 0.5 (--1.0) cm, acuminate at apex, pale green, trichomes less dense on the adaxial side of leaf. ***Inflorescences*** globose, terminal, 0.7-1.0 (--2.0) cm in diameter, consisting of 2-5 partial florescences, white. ***Flowers*** 4.4 x 2 mm long. ***Bracts*** ovate, cymbiform, 2.6 x 1.5 mm, membranous to hyaline, white in colour, acute at apex, with visible midvein, this slightly crested. ***Bracteoles*** ovolanceolate, 4.4 x 1.5 mm, with fine membranous texture, white translucent. The bracteole with a crest extending in the upper quarter of the dorsal part, crest toothed at the entire margin, bracteoles sometimes larger than the tepals or the same size. ***Tepals*** lanceolate, narrowest at the middle part (unguiculate), membranous in texture, white, acute at apex, densely lanate, with trichomes dorsally and at the margin of all the tepals (Fig. 4-39 E). Size unequal. External 4 x 0.6 mm, intermediate 3.8 x 0.6 mm, inner 3.6 x 0.4 mm. ***Filaments*** 4.2 mm long, fused into a tube for 3.6 mm, free part 0.6 mm long. ***Filament appendages*** conspicuous, 0,4 mm long, lanceolate (the united base 0.2 mm long). ***Anthers*** oblong, 1.5 mm long, inserted between the filament appendages (Fig. 4-39 F). ***Gynoecium*** with two stigma branches of 0.8 mm length and 0.2 mm width, style 0.4 mm, ovary 0.5 mm. [voucher: Borsch & Ortuño 3755 = AC449].

Micromorphology of trichomes. Multicellular, uniseriate, on ***stems and cauline leaves*** with the first basal cells rounded, and four to eight upper cells, with firm consistence, salicose and spinous ornamentation and striate sculpture of cuticular walls; ***interlocking junctions*** conspicuous, linear scars or projections of the extreme border cells (as spines) zero angle degrees overlapping; ***on apical leaves subtending paracladia*** on the adaxial side different or similar to those of the abaxial; in the first case, trichomes short, with 2-3 thick cells, spinous ornamentation and smooth sculpture of cuticular wall, in the second case, trichomes are similar to those on stems, interlocking junctions always conspicuous (Fig. 4- 41E, F); ***on tepals*** trichomes large, with firm basal cells, the uppers with the cells collapsed, interlocking junctions not conspicuous. ***Anatomy of tepals.*** Tissues composed by elongate straight, cylindrical cells, arranged in one row, the extremes fitting perfectly, the fibre cells are closely connected with the trichomes, since they arise as the extreme tips of the fiber cells (Fig. 4- 41 C & E) [voucher Borsch & Ortuño 3755; Ortuño, Nuñez & Newman, 1217].

Taxonomic remark. The specimens close to *Gomphrena pallida* in this circumscription (see 4.3.6.1) are well resolved in the ITS tree (Chapter 3). The vouchers Borsch & Ortuño 3719 (AC432), 3755 (AC449) and 3724 (AC 435) can be determined as *G. pallida*. Their lineage is sister to G. sp. nov. (spec 2) [voucher: Wood 22662], the specimens *G. cf. pallida* [voucher: Ortuño 1217 = AC788] and *G. mizqueensis* [voucher: Borsch & Ortuño 3584 = AC455]. Morphologically, the overall appearance between these annual species is similar, but when observed in detail they have differences regarding the indumentum on tepals and bracteoles and the size in relations to the tepals. The *G. sp. nov. (spec2)* displays a clear difference with respect to *G. pallida*, with its smaller size, glabrous cauline leaves, and peculiar form of the bract.

The specimens here determined as *G. pallida* are morphologically all very similar to each other. However, is possible to detect some slight variation in the trichomes on the bracts and the shape of the more or less prominent crests (always without teeth). The most differing specimens were the voucher *Borsch & Ortuño 3719 (AC 432*), Fig. 4-40 A. and Ortuño, López & Rios 1217 (AC 788, Fig. *4-40* G); the first one with trichomes in the margin of the bract and the second with few trichomes dorsally on the bract, but the other characters are similar to *G. pallida*.

Habitat and ecology. Grow on open places in dry bushland with shale rock or with sandy slopes, together with species such as *Senegalia gilliesii* (Steud.) Seigler & Ebinger, *Athyana weinmanniifolia* (Griseb.) Radlk., *Schinopsis marginata* Engl., *Prosopis alba* Griseb, *Schinus areira* L., in the ecoregions of the Inter-Andean dry forest, Semi humid Puna, Prepuna, Tucuman-Bolivian forest, Chaco Serrano. The altitudinal range of collections is between 1207-3400 m.

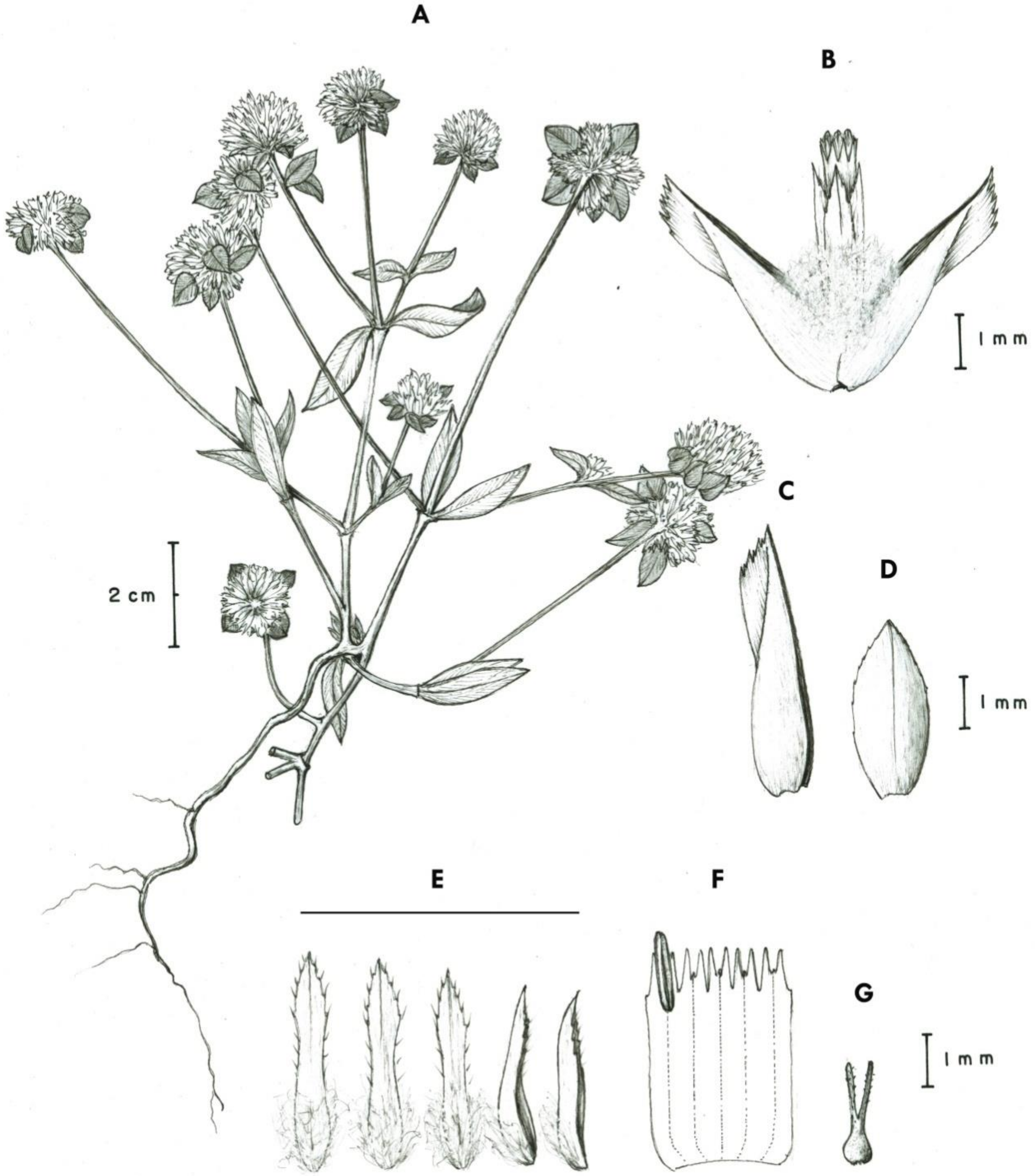


Fig. 4-39. *Gomphrena pallida* Pedersen. A) Habit. B) Flower. C) Bracteoles. D) Bract. E) Tepals. F) Detail of the androecium. G) Gynoecium [voucher: Borsch & Ortuño 3755].

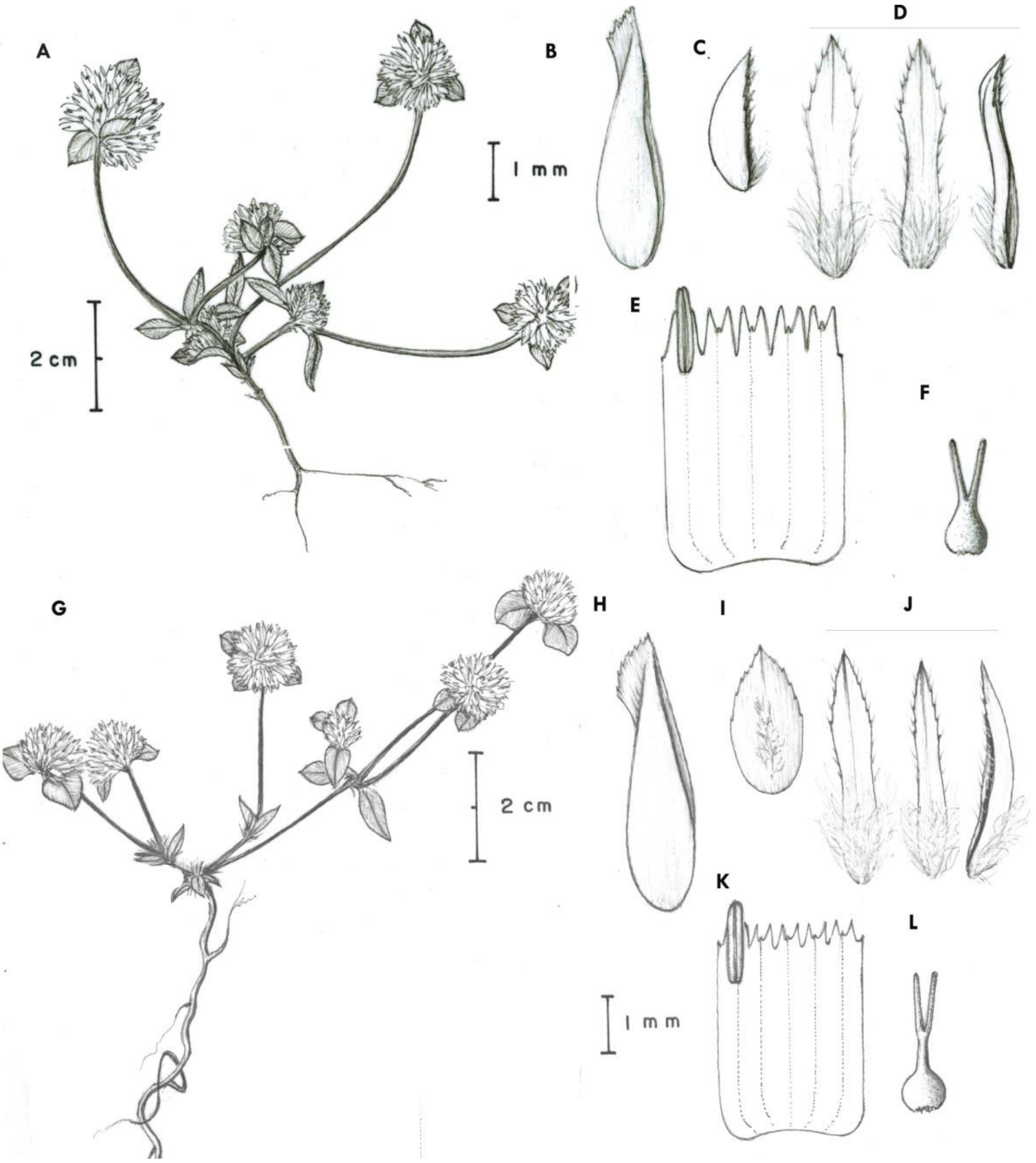


Fig. 4-40. *Gomphrena pallida* Pedersen. A) Habit. B) Bracteoles. C) Bract. D) Tepals. E) Detail of the androcium. F) Gynoecium [voucher Borsch & Ortuño 3719]. G) Habit. H) Bracteoles. I) Bract. J) Tepals. K) Detail of the androecium. L) Gynoecium [voucher: Ortuño, López & Rios 1217= AC788].

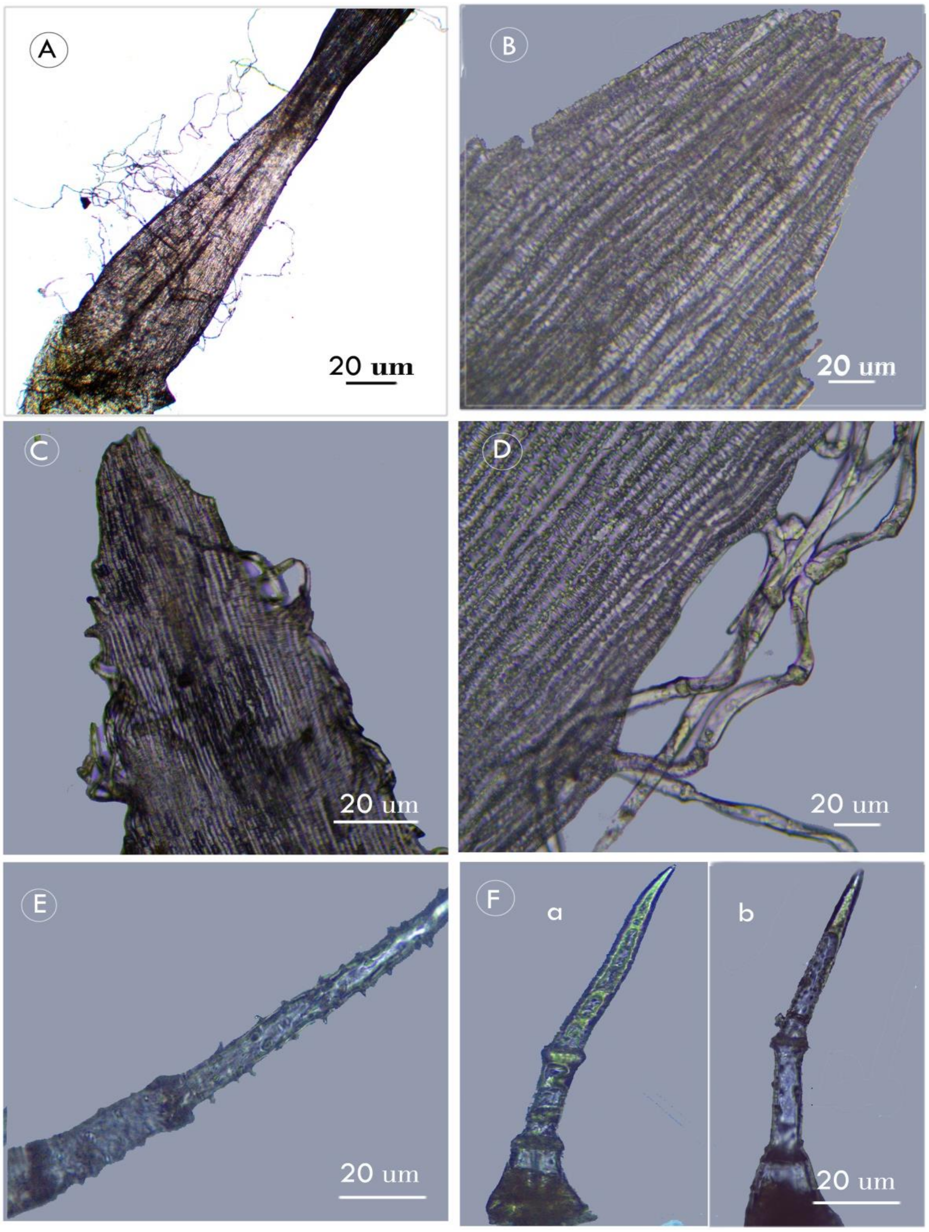


Fig. 4-41. *Gomphrena pallida* Pedersen. Tepals. A) Lanceolate, narrow in the middle part with dorsal trichomes. B) Dentate apex, tepal tissue with elongate and fibrous cells organized in one row. C) and D) Trichomes at the margin, arising of the fibrous tepals cells. [voucher: Borsch & Ortuño 3755. Trichomes of the apical leaves subtending the paracladia [voucher: Borsch & Ortuño 3755]. E) Trichomes of the abaxial part, spinous ornamentation on cuticle in upper cells. F) Trichomes of the adaxial part, a) [voucher: Borsch & Ortuño AC 3755]; b) [voucher: Ortuño, López & Rios1217].

Distribution **Bolivia**. Provinces of Mizque, Aiquile, Campero, Tapacari, Cercado (Dept. Cochabamba). Provinces of Yamparaez, Hernando. Siles. Jaime Zudañez, Oropeza, Tomina, Yotala, (Dept. Chuquisaca). Provinces Chayanta, Nor Chichas, Sud Chichas, Saavedra, (Dept. Potosí). Provinces of Arce and O'Connor (Dept. Tarija) (see Fig. 4-50).

Specimens examined for distribution assessment. ***Argentina, Jujuy***, Yavi, [-65,4618799, -22,13043], 3459 m, 20, 11, 1963, Cabrera, *A.L, 15328* (LPB). Capital, [-65,29944399, -24,18555599], 1273 m, 2, 11, 1974, *Schinini, A., 10114* (LPB). Localidad Cajas, 18, 3, 1982, *Vignale, N. D., 151* (SI). ***Bolivia***: ***Cochabamba, Mizque***, Camino de Mizque a Raykampampa. Subiendo de Tintin a Raykampampa, [-65,469333, -18,05071667], 2564 m, 3, 4, 2003, *Borsch, Th., 3591* (LPB, B). Camino de Mizque a Raykampampa, [-65,28960700, -17,952178], 2126 m, 3, 4, 2003, *Borsch, Th., 3587* (LPB, B). **Capinota**, Santivañez, [-66,24402499, -17,54979399], 2559 m, 1, 2, 1985, *Pedrotti, 52* (LBP, NY). **Campero**, Camino de Aiquile a Pasorapa, 2 km antes del poblado de Robles, [-64,8166669, -18,26666700], 1805 m, 6, 4, 2003, *Borsch, Th., 3623* (LPB, B). **Tapacarí**, Camino La Paz a Cochabamba, cerca de Cochabamba, [-66,39333, -17,64516667], 3200 m, 1, 4, 2003, *Borsch, T., 3568* (LPB, B). **Chuquisaca, Yamparáez**, 1 km de la comunidad Candelaria, [-64,8026667, -19,445], 2842 m, 13, 4, 2004, *Borsch, T., 3761* (LPB, B). A 2 km. De Tarabuco en el camino hacia Calendaria, [-64,86111099, -19,188333], 3178 m, 1, 3, 2006, *Wood, J.R.I, 22320* (LPB). **Hernando. Siles**, Heredia, [-64,12185300, -19,803514], 1207 m, 19, 11, 1988, *Murguía, O., 219*, (LPB). **Jaime Zudañez**, Río Zudañez, [-64,7833329, -18,4333], 2457 m, 29, 4, 1997, *Lara, D.,* 504 (LPB). ANMI El Palmar. Aprox. 8 km de la tranca de ingreso en dirección a la Comunidad de El Palmar, [-64.9160833, -18.7377222], 3102 m, 7, 5, 2014, *Gutiérrez, J., 2607* (LPB). Cerca poblado de Choromomo, [-64,83166667, -19,443055560], 2664 m, 12, 4, 2010, *Ortuño, T., 1217* (LPB). **Oropeza**, Camino de Potosí a Sucre sobre la carretera de asfalto, [-65,2029990, -19,2289920], 2615 m, 12, 4, 2004, *Borsch, T., 3758*, (LPB, B). Km 21 on road from Sucre to Potosi (Yotala - Puente Mendez), [-65,2344810, -19,17446899], 2615 m, 10, 3, 1996, *Wood, J.R.I, 10816* (K, B, LPB). Ca. 1/2 Km del cruce camino al señor de Maica Palamana, [-64.30385, -18.8190833], 21, 2, 2004, *Wood, J.R.I., 20212*, (LPB). Yotala, Chacaleon, [-65,26420, -19,1586], 2517 m, 2012, s/c, 6GA, (HSB). **Tomina**, Entre Villa Serrano y Tomina, en la cumbre, [-64,40916667, -19,44305556], 2665 m, 4, 3, 2006, *Wood, J.R.I., 22390* (LPB). **Potosí. Chayanta**, Ravelo Sasanta, [-65,6110670, -18,86586700], 3400 m, 0, 9, 1996, *Sallés, C., 87* (LPB). **Nor Chichas**, Camino a Vitichi Tumusla. 24,6 Km de Vitichi, [-65.55, -20.3833], 3100 m, 24, 4, 1999, *Lopéz, R., 520* (LPB). Ca. 7 km al Norte de Cotagaita, [-65,5179333, -20,0825], 3030 m, 2, 4, 2004, *Borsch, Th.,* 3724 (LPB, B). Cerca de Vitichi, [-65,518 -20,0825], 3170 m, 2, 4, 2004, *Borsch, Th., 3719* (LPB, B). **Sud Chichas**, Al Oeste-Nor-Oeste en línea recta de la comunidad de Oploca, aprox. 1.04 km, [-65,8144810, -21,336365], 3205 m, 26, 2, 2012, *Zenteno, R.F., 11470a* (LPB). Oploca, [-65,8190110, -21,33050799], 3144 m, 27, 2, 2012, *Zenteno, R.F., 11551*, (LPB). **Saavedra**, Camino de Potosí a Sucre. Retiro 3 sobre la carretera de asfalto, [-65,2455333, -19,53071667], 2983 m, 12, 4, 2004, *Borsch, Th., 3755,* (LPB, B). **Tarija**, **Aniceto Arce**, Padcaya camino de tierra a Tariquia, [-64,3972600, -21,55135999], 2094 m, 11, 4, 2003, *Borsch, T., 3651,* (LPB, B). [-64,6666670, -21,833], 2000 m, 16, 3, 1998, *Beck, St.G., 26183*, (LPB). **J. Maria Avilés**, Quebrada de Barbascuyo, [-64,84222, -21,7675], 2100 m, 21, 4, 2000, *Beck, St.G., 27237*, (LPB). **O'Connor**, [-64, 49222199, -21, 46166699], 2277 m, 10, 1, 2006, *Cervantes E., 224*, (HSB, MO).

4.3.6.2. *Gomphrena mizqueensis* Ortuño & Borsch, Novon 15(1): 183–187, f. 2, 3B, 3D, 4B, 4D. 2005.

Type: Bolivia. Cochabamba: Campero, Aiquile, camino nuevo de Raykampampa a Aiquile. a 1 hora de Aiquile, 18°11'57" S, 65° 17'28" W, 2906 m, 4 abr. 2003. T. Borsch & T. Ortuño 3614 (HT: LPB 0000447; IS: BOLV, B, K, MO).

Annual herb, 20-35 (--40) cm tall. ***Root*** simple, fibrous. ***Stem*** decumbent to erect, with tertiary stems, striate, green-red, indumentum dense, appressed to villous, trichomes near the flower often hirsute. ***Cauline leaves*** ovolanceolate, 1.8 (--2.5) x 1.7 (--2.1) cm, acute at apex, mucronate, margin entire, green on the adaxial part, light green in the abaxial side, indumentum appressed, with 1-4 mm long trichomes, light to dark brown in colour. ***Apical leaves substending paracladia*** *(inflorescences)* 4-6, leaves arranged symmetrically, cordate to lanceolate, 0.5 (--1.9) x 0.6 (--2.5) cm, acuminate at apex and mucronate (1 mm), green, generally bigger than the paracladia, indumentum appressed on the abaxial side, few hirsute trichomes on the adaxial side and the margin. ***Inflorescences*** globose to sub-globose, terminal, 0.6-1.5 (--2.5) cm in diameter, consisting of 3-6 partial florescences, white. ***Flowers*** 4-4.4 (--5) x 3 mm, 10 or more grouped along the axis forming a partial florescence. ***Bracts*** ovate to oblong, 1.6 (--2.1) x 1 (--1.2) mm, membranous to hyaline in texture, white, acuminate at apex, with prominently visible midvein, toothed for half of the upper part of the margin. ***Bracteoles*** ovate to ellipsoid, 3.4 -4.4 (--4.4) mm, menbranous to hyaline in texture, white, acuminate at apex, the bracteoles have a wide crest located in the upper half, and conspicuously toothed at the margin. Bracteoles larger than the tepals. ***Tepals*** lanceolate, narrowest at the middle, membranous-escarious in texture, translucent, prominently toothed at the apex, trichomes dorsally and at the margin of all tepals. Size unequal. External tepals 2.6-3 (--3.8) x 0.6 mm, intermediate 2.5-2.9 (--3.7) x 0.5 mm, inner 2.4-2.8 (--3.6) x 0.4 mm. ***Filaments*** 4.6 (--5.9) mm long, for the most part fused into a tube, this part 4-5 mm, free part 1mm. ***Filament appendages*** conspicuous, 0.6-0.8 mm long, lanceolate. ***Anthers*** oblong, 1-1.2 mm long (Fig. 4-42E). ***Gynoecium*** with two filiform stigma branched of 1.6 mm long, style 0.4 mm, ovary subglobose 0.4 mm. [*voucher: Borsch & Ortuño* 3584 = AC455].

Micromorphology of trichomes. Multicellular, uniseriate: ***Stems and cauline leaves***, 2-4 mm long, 1-2 short, flat basal cells, 4-8 uppers cells with firm consistence, salicose and spinous ornamentation and flat cuticule walls. ***Interlocking junctions*** thick, conspicuous, linear scars or projections of the extreme border cells (as spines) from zero angle to fourty five degrees overlapping (Fig. 4-43D); ***trichomes** on **apical leaves subtending paracladia*** on the adaxial side differing from the abaxial. In the first case trichomes short (Fig. 4-43H), with three straight, thick cells, scarcely spinous ornamentation and flat cuticule walls, in the second case similar than on stems. Interlocking junctions always conspicuous, colour varing from white to light brown. ***Trichomes** on **tepals*** trichomes large, with firm basal cells, upper cells collapsed, interlocking junctions not conspicuous. ***Anatomy of tepals.*** Tissues are composed by elongate, straight, cylindrical dermal cells, arranged in one row, the extremes fitting perfectly, the fibre cells extending into the trichomes and the dentate margin (Fig. 4-43E, F) [voucher: Borsch & Ortuño 3584].

Pollen. Spheroidal, diameter 13-14 µm. Number of apertures 30-37. Structure metarericulate, with hexagonal and pentagonal arrangement of mesporiae around apertures. Mesoporia thin, 0.3 µm. Tectum only on the distal parts and reduced in the vertical parts, few visible columellae. The transverse view of the tectum shows a thin triangular shape ending in a sharp point that is 3 times higher than the columellae; without microspines, with pointed connections [voucher: Borsch 3614].

Taxonomic remark. The predominate morphological differences are the ramose and divided stems, the indument on the stems and leave, the type of teath in the apex of tepals, and the form the androeceum (see Ortuño and Borsch, 2005).

Habitat and ecology. Locally abundant on rocky, sandy soil open places in humid ravines, steep cliffs and gullies or slopes with scattered trees and schrubs such as *Alnus acuminata* Kunth, *Kageneckia lanceolata* Ruiz & Pav., and *Dodonaea viscosa* Jacq. In the ecoregion of the Inter-Andean dry forest. The altitudinal range of collections is between 2130-3200 m.

Distribution. Endemic of Bolivia, Province Jose Carrasco, Mizque, Narciso Campero (Dept. Cochabamba), Province Charcas, (Dept. Potosí), Province Aniceto Arce (Dept. Tarija) (see Fig. 4-50).

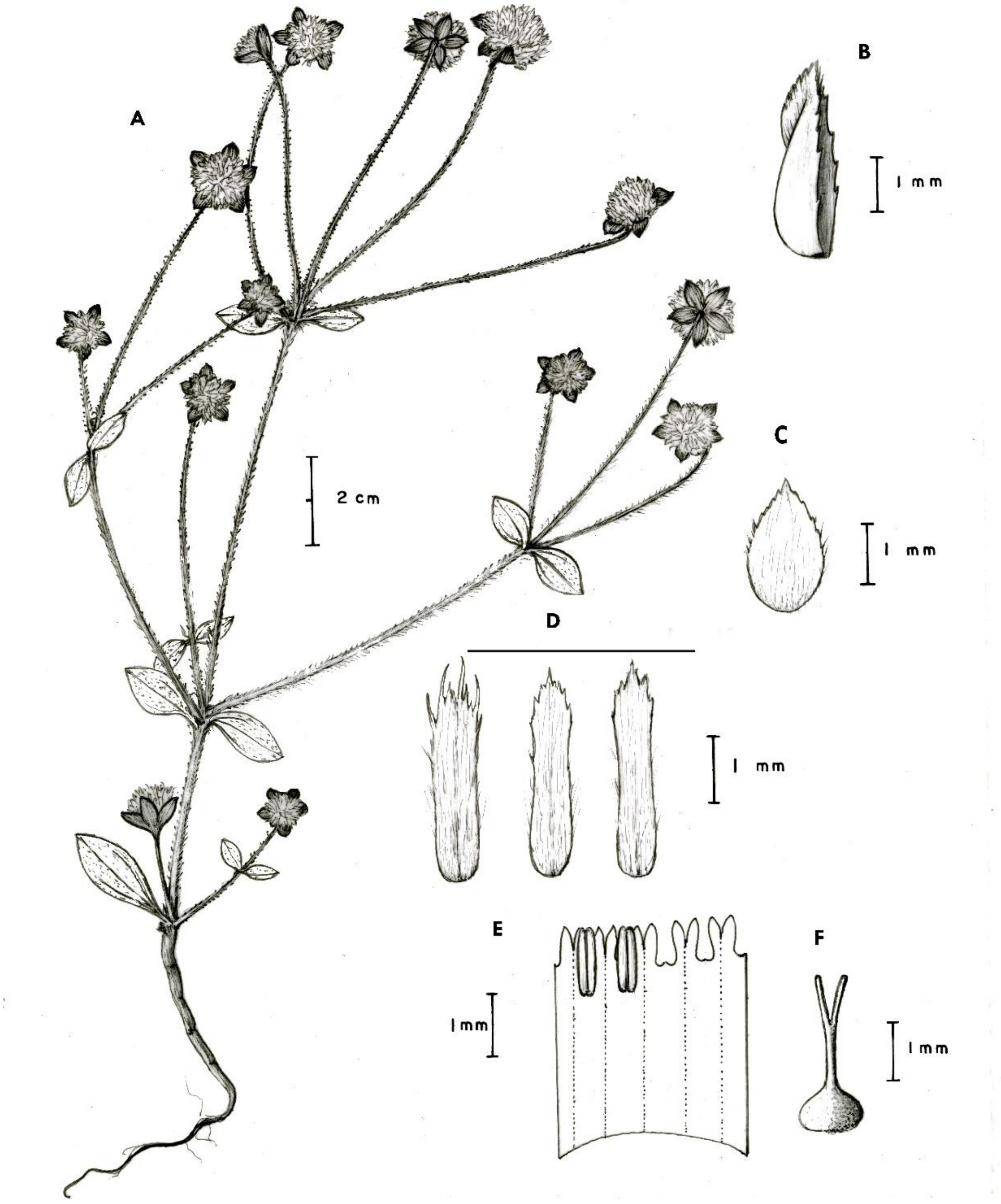


Fig. 4-42. *Gomphena mizqueensis* Ortuño & Borsch. A) Habit. B) Bracteoles. C) Bract. D) Tepals, toothed apex. E) Detail of the androecium. F) Gynoecium [voucher: Borsch & Ortuño 3584].

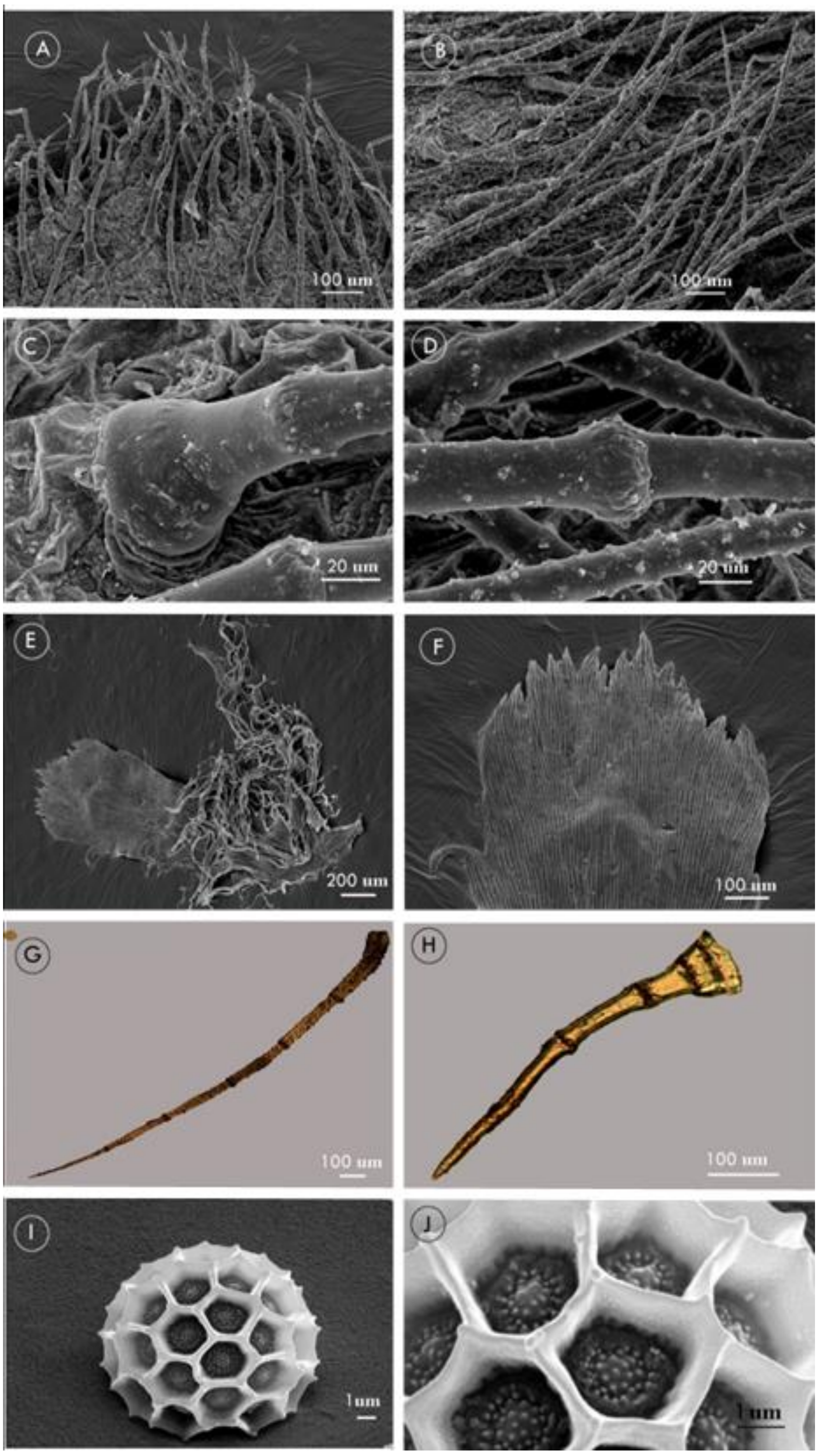


Fig. 4-43. *Gomphrena mizqueensis* Ortuño & Borsch. Cauline leave. A) Dense appresed trichomes apex leaves. B) Dense appressed trichomes in the adaxial side leave. C) Detail the basal cells. D) Detail of the interlocking junctions, scar zero and forty five degrees positions overlapping. Tepals. E) Overview of tepal and F) detail of the tepals with toothed apex dense trichomes lanate. Trichomes of the apical leaves subtending paracladia: G) From lower part. H) From upper part [voucher: Borsch 3584, the latter 3591]. I) General view of the metareticulate pollen. J) Detail of the apertures [voucher: Borsch 3614].

Specimens examined for distribution assessment. ***Bolivia, Cochabamba, José Carrasco Torrico***, 2630 m, 2, 1973, *Ceballos, A., 368*, (SI). ***Mizque***, Cumbres entre Rakaypampa y Lagunas. Camino a Lagunas, [-65,3666, -18,1666999], 3040 m, 21, 2, 1994, *Antezana, C., 796*, (BOLV, LPB). Camino de Mizque a Aiquille, segundo puente antes de llegar a Mizque, [-65,4025, -17,868333], 2579 m, 2, 4, 2003, *Borsch, T., 3584*, (LPB, BOLV).Camino de Mizque a Raykampampa. Subiendo de Tintin a Raykampampa, [-65,4693, -18,0566667], 2564 m, 3, 4, 2003, *Borsch, Th., 3591*, (B, LPB). ***Narciso Campero Leyes***, camino nuevo de Raykampampa a Aiquile. a 1 hora de Aiquile, [-65,172790, -18,115729], 2906 m, 4, 4, 2003, *Borsch, Th., 3614*, (LPB, B). ***Tapacarí***, camino La Paz a Cochabamba, cerca a Cochabamba, [-66,23603, -17,38707], 3200m, 1, 4, 2003, *Borsch, Th., 3568b*, (LPB, B). ***Potosí, Charcas***, Wila Kasa hacia las cabernas de Umajalantha, [-65,8094, -18,12472], 2935 m, 29, 1, 2012, *Huaylla, H., 3656*, (LPB).***Tarija, Aniceto Arce***, [-64,6805559, -21,957778], 2130 m, *Beck, S.G., 31619*, (LPB).

4.3.6.3. *Gomphrena sp. nov.* (*spec2a*) T. Ortuño & Borsch, [ined.]

Type: Bolivia, Dept. Potosí, Prov. Charcas. In zone of Aradia on the highest part of the road from Torotoro to San Pedro. 19°52'20" S, 66°8'59" W, 3561 m, 27. 2. 2003. *J.R.I. Wood, Huaylla, H. & M. Atahuachi 22662* (HT: LPB; IT: B, K, HSB, BOLV).

Annual herb, 3-7 cm high. ***Root*** simple, fibrous. ***Stems*** erect to decumbent, always with secondary and tertiary stems, of a striate texture, green to red, trichomes 2-3 mm long nearly cylindrical, straight, appressed to villous, scarce, light to dark brown, dense close the inflorescence. ***Basal leaves*** arranged similar to rosettes, lanceolate to ovate, 1-1.5 (--2.2) x 0.5 (--1) cm, acute at apex, fleshy and of glossy appearance, green, glabrous. ***Cauline leaves*** lanceolate to cordate, 0.5-1 (--1.5) x 0.4 (--0.5) cm, acute at apex, margin entire or lightly undulate, light to dark green marmolate; both cauline and basal leaves sometimes in the middle part with a few sparse trichomes 1.5 mm in length, or completely glabrous. ***Apical leaves subtending paracladia*** (*inflorescences*) 2-5, arranged symmetrically, lanceolate to cordate, 0.3 0.8 (--1) x 0.3-0.5 (--0.6) cm, acute to rounded at apex, mucronate (midvein excurrent for 0.2 cm), glabrous or with few trichomes, white to dark brown or black. ***Inflorescences*** globose, terminal, 0.5-0.7 (--1.1) cm in diameter, consisting of 1-5 partial florescences, with dense, dark brown trichomes at the base, trichomes 2 mm long. ***Flowers*** 2-2.5 (--3) x 1.5 mm long, 9-13 flowers forming a partial inflorescence. ***Bracts*** semifornicada cymbiform, 1.5 (--2.5) x 1.2 (--1.5) mm, membranous in texture, translucent, light to dark brown gradually changing from the base to apex, margin entire, few teeth at the apex, excurrent middle nerve (c. 2mm) (Fig. 4-44E). ***Bracteoles*** ovate, cymbiform, 1.5-2.2 (3.5) x 1 (--1.5) mm, membranous in texture, opaque white, acute at apex, the bracteole with a wide, rounded crest located in the upper half of the dorsal part, with small teeth in the margin. Bigger than the tepals. ***Tepals*** oblong lanceolate, finely membranous, white to yellow, narrowest in the middle part, irregularly toothed at the apex, the external tepals glabrous or with few trichomes in the margin, but only in the half middle basal part (fine trichomes), the inner tepals densely lanate with dorsal trichomes covering half the length of all the tepals. Sizes unequal. External tepals 1.4-1.7 (--2.5) x 0.5-0.7 mm, intermediate 1.2-1.6 (--2.4) x 0.5 (--0.6) mm, inner 1.1-1.5 (--2.2) mm. ***Filaments*** 2-2.5 (--3) mm long, fused into a tube for 1.4-1.9 (--2.4) mm, the free part 0.2 mm long. ***Filament appendages*** 0.4 mm long, rounded at the apex. ***Anthers*** oblong, 0.8 (--1.2) mm long. ***Gynoecium*** with two filiform stigma branches, of 0.5-0.6 x 0.2 mm length, style 0.2 mm long, ovary subglobose, 0.4-0.7 mm long, with only one ovule [voucher: Wood, Huaylla & Atahuachi 22662 = AC 1050].

Micromorphology of trichomes. Multicellular, uniseriate; on ***stems and cauline leaves*** one wide basal cell, the second basal cell cylindrical straight, 3-6 upper cells, the first wider, the upper thinner, with scarce spinous to granulate and salicose ornamentation, striated surface, yellow to dark brown, translucent, ***interlocking junctions*** with linear scars or projections of the extreme border cells (as spines) zero angle degrees overlapping (Fig. 4-45F); ***on apical leaves subtending paracladia*** similar to those on stems; yellow to dark brown, on ***tepals and base of the inflorescence***s the trichomes with collapsed cells, lanate. ***Anatomy of tepals.*** Tissues composed by elongate straight, cylindrical dermal cells, arranged in one row, the extremes fitting perfectly, the fibre cells marginally extending into trichomes (Fig. 4-45A) [voucher: Wood, Huaylla & Gutierrez 23269; Huaylla 3648; Wood 22662].

Taxonomic remark. The *matK- trnK* tree this clade does not resolve all the species within a sublineage (0.98PP, 73JK, 68 BS) that contains sample AC1050, *G. pallida* and perennials (Chapter 3). The marker ITS display the group of species corresponding to *G. pallida* and AC1050 (G. sp. nov. spec2a) as sisters, and this subclade again has sample AC788 and *G. mizqueensis* as successive sisters. Morphologically, *G. sp. nov. (spec 2a)* has a clear difference with respect to both species by the fleshy texture of the leaves that are glabrous, the semifornicate shape of the bract, an irregular dentate apex of tepals.

The *G. sp. nov. (spec2a)* was collected in the Semi humid Puna ecoregion between 3400 – 3500 m., and from two populations, one in Chataquila, Chuquisaca (Wood, Huaylla & Gutierrez 23263) and the other in Wila Kasa San Pedro, Toro Toro, Potosí (Wood, J.R.I, 22662). The morphology of the specimens is very similar. However, is possible to detect some difference in the sizes of the plants. In Toro Toro in general the specimens are small (2-5 cm), and the trichomes are dark (almost black).

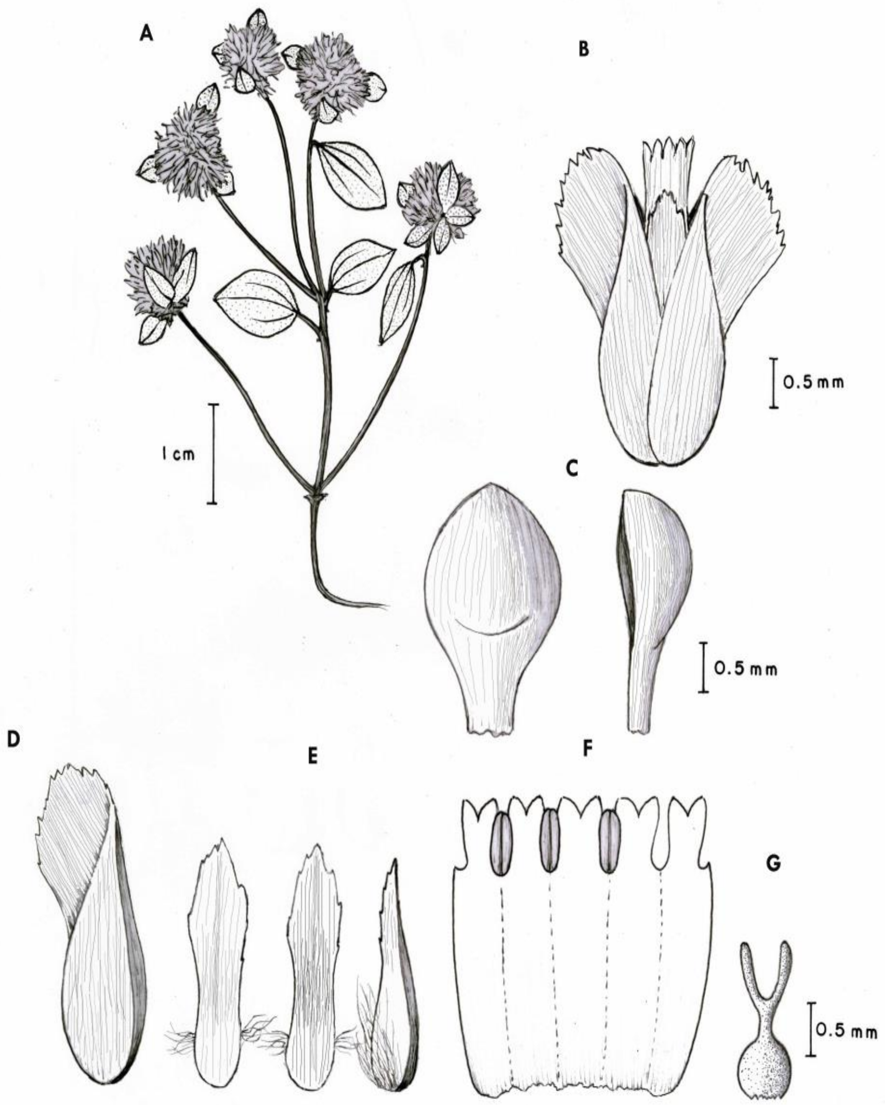


Fig. 4-44. *Gomphrena sp. nov. (spec2a)* Ortuño & Borsch. A) Habit. B) Flower with bracteoles. C) Bract, semifornicate and cymbiform in shape. D) Detail of bracteoles with crest in the upper part. E) Tepals, with trichomes on the dorsal part of the inner tepals. F) Detail of the androecium showing filament appendices laterally united and the anthers appearing in a sunken position in between. G) Gynoecium [voucher: Wood, Huaylla & Atahuachi 22662].

Habitat and ecology. Locally abundant in open moist sandy hollows. Ridges formed of soft sandstone with zones of steep cliffs and gullies with scattered trees and schrubs and other areas of open rocky hilltops with sandy hollows and boggy patches. Habitats belong to the Semi humid Puna ecoregión of southern Bolivia, where the plant has been collected between 3400-3600 m.

Distribution. Bolivia, Province Oropeza, Chataquila (Dept. Chuquisaca), Province Torotoro, in the Wila Kasa in the surroundings of San Pedro, and Marka Pagio beginning of Mila Wacana gully (Dept. Potosí) (see Fig. 4-50).

Specimens examined for distribution assessment. ***Bolivia*, *Chuquisaca*, *Oropeza*,** En la capilla de Chacatilla en el camino Punilla a Potolo, [-65,406111, -18,988611], 3496 m, 29, 3, 2005, *Wood, J.R.I, 22022*, (LPB, B, HSB). ***Potosí*, *Charcas*,** Toro Toro cerro Marka Pagio. Entrando a la quebrada Mila Wacana., [-65,858889, -18,123056], 3411m, 27, 2, 2003, *Wood, J.R.I., 19238*, (LPB, K, B). In zone of Aradia on the highest part of the road from Toro Toro to San pedro, [-65,850278, -18,127778], 3561m, 9, 2, 2007. *Wood, J.R.I, 22662,* (LPB, K. B). Wila Kasa camino hacia San Pedro, [-65,841389, -18,1315], 3625 m, 29, 1, 2012, *Huaylla, H., 3648*, (LPB, B).

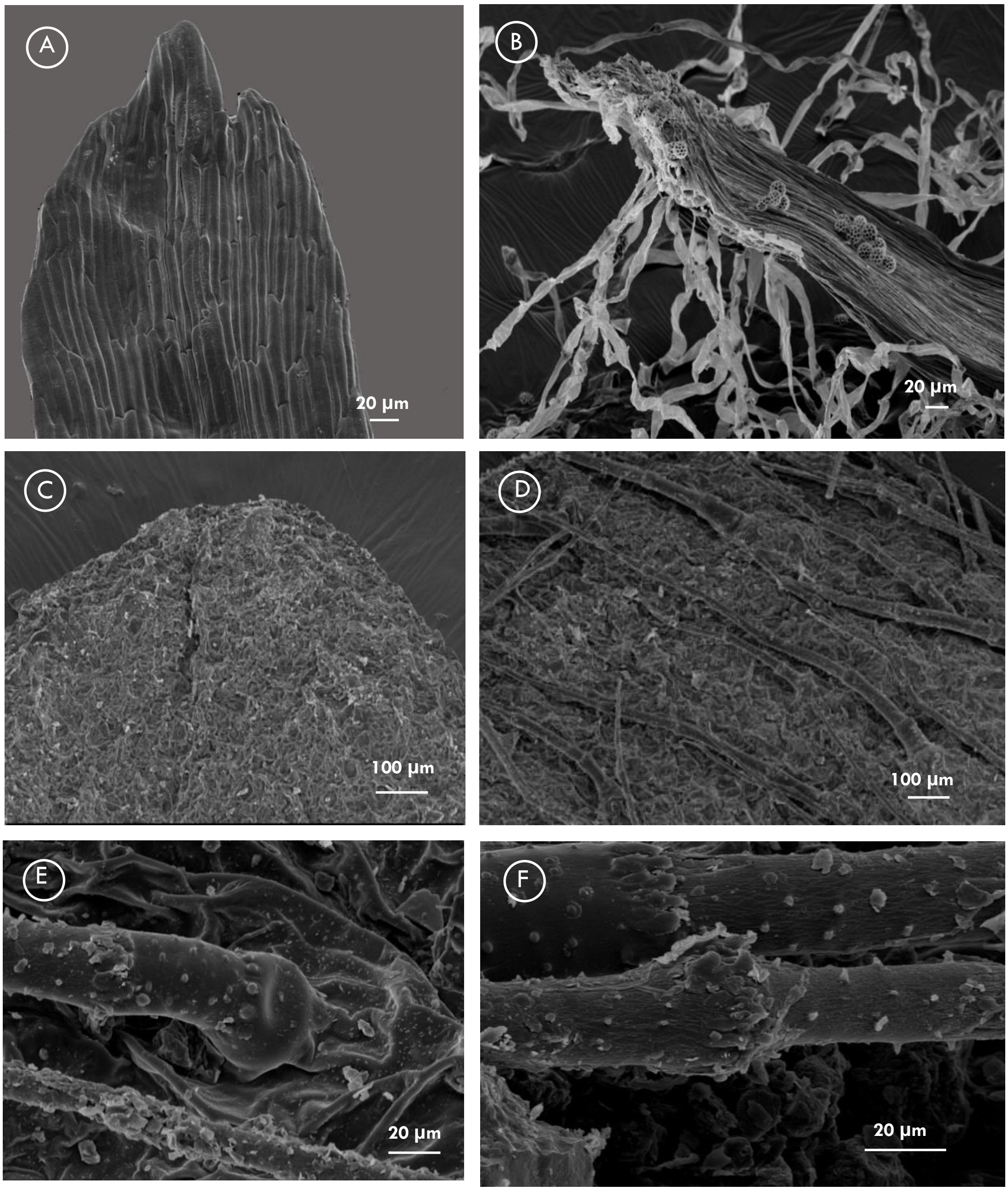


Fig. 4-45. *Gomphrena sp. nov. (spec2a)* Ortuño & Borsch. Tepals A) irregular dentate apex. B) Detail of the trichomes with collapsed cells of the inner tepals. Cauline leaves C) glabrous acute to rounded apex, D) lower part with trichomes in the main vein. Trichomes E) wide basal cells, the second cylindrical straight with granulate ornamentation F) Interlocking junctions with linear scars or projections of the extreme border cells (as spines), zero angle degrees overlapping [voucher: Wood, Huaylla & Gutierrez 23269; Huaylla 3648; Wood 22662].

4.3.6.4. *Gomphrena sp. nov. (spec 2b)* T. Ortuño & Borsch [ined.]

Type: Bolivia, Chuquisaca, Oropeza, Cerro Chataquilla, along trail following ridge top, 65ª , 24,36"W, 18ª 58'45" S, 3682 m, 28, 3, 2007, *Wood, J.R.I, 22269* (LPB, K, B, HSB)

Annual herb, 3-7 cm high. ***Root*** simple, fibrous. ***Stems*** decumbent to ascendant, always with secondary and tertiary stems, striate, green to red, trichomes 2-3 mm long, almost cylindrical, straight, villous, scarce, and light to dark brown, denser close the inflorescence. ***Basal leaves*** lanceolate and decurrent at the base, 1-1.5 (--2.2) x 0.3-0.5 (--1) cm, acute at apex, fleshy and of glossy appearance, green. ***Cauline leaves*** lanceolate to cordate, 0.5-0.7 (--1) x 0.2-0.4 (--0.9) cm, acute at apex, decurrent at base, midvein and secondary veins prominent, margin entire or slightly undulate, both cauline and basal leaves sometimes with villous indumentum only in the middle part, or completely glabrous. ***Apical leaves subtending paracladia*** *(inflorescences)* 2-3, leaves arranged symmetrically, lanceolate to cordate, 0.3 (--0.5) x 0.2 (--0.5) cm, apex acute to rounded, mucronate (midvein excurrent for 0.2 cm), glabrous or with few trichomes, these white to dark brown to black. ***Inflorescences*** globose, terminal, 0.5-0.7 (--1.1) cm in diameter, consisting of 1-5 partial florescences, with dense dark brown trichomes at the base, and 3 mm long trichomes. ***Flowers*** 1.5-3.2 (--3.5) x 1.5 mm, grouped in the axils, 9-13 flowers forming a partial inflorescence. ***Bracts*** semifornicate cymbiform, 2-2.5 (--3) x 1.2 (--2) mm, membranous in texture, translucent, gradually changing from light to dark brown from the base to the apex, margin entire, few teeth at the apex, middle nerve excurrent for c. 2mm (Fig. 4.46.C). ***Bracteoles*** ovate, cymbiform, 3 (3.5) x 1.2 (--1.5) mm, membranous in texture, opaque white, acute at apex, dorsally in the upper part for about a third midvein with a broadly winged, rounded crest, with small teeth at the margin, bigger than tepals. ***Tepals*** linear to oblong, finely membranous, white to yellow, narrowest in the middle part, irregularly toothed at the apex, the external tepals glabrous, the inner tepals with abaxial trichomes densely lanate, covering half the length of all the tepals. Sizes unequal. External tepals 1.4-1.7 (--2.5) x 0.5-0.7 mm, intermediate 1.2-1.6 (--2.4) x 0.5 (--0.6) mm, inner 1.1-1.5 (--2.2) mm long. ***Filaments*** 2-2.5 mm long, to a large part fused into a tube, fused part 1.5-2 mm long, free part 0.6 mm long. ***Filament appendages*** 0.4 mm long rounded at the apex. ***Anthers*** oblong, 0.8 (--1.2) mm, appearing inserted between two laterally fused filament appendages (Fig. 4.46 E). ***Gynoecium*** with two filiform stigma branches, 0.5-0.6 x 0.2 mm, style 0.2 mm long, ovary subglobose, 0.4-0.7 mm long, with only one ovule [voucher: Wood, Huaylla & Gutierrez 23269].

Distribution. Bolivia, Province Oropeza, Chataquila (Dept. Chuquisaca), (Fig.4-50).

Specimens examined. ***Bolivia, Chuquisaca, Oropeza,*** Cerro Chataquilla, along trail following ridge top, [-65,41, -18,979167], 3682 m, 28, 3, 2007, *Wood, J.R.I, 22269* (LPB, K, B, HSB). Cerro de Chacatilla along trail following ridge top, [-65,41, -18,979167], 3682 m, 28,3,2007, Wood, J.R.I, Huaylla & Gutierrez 23269.

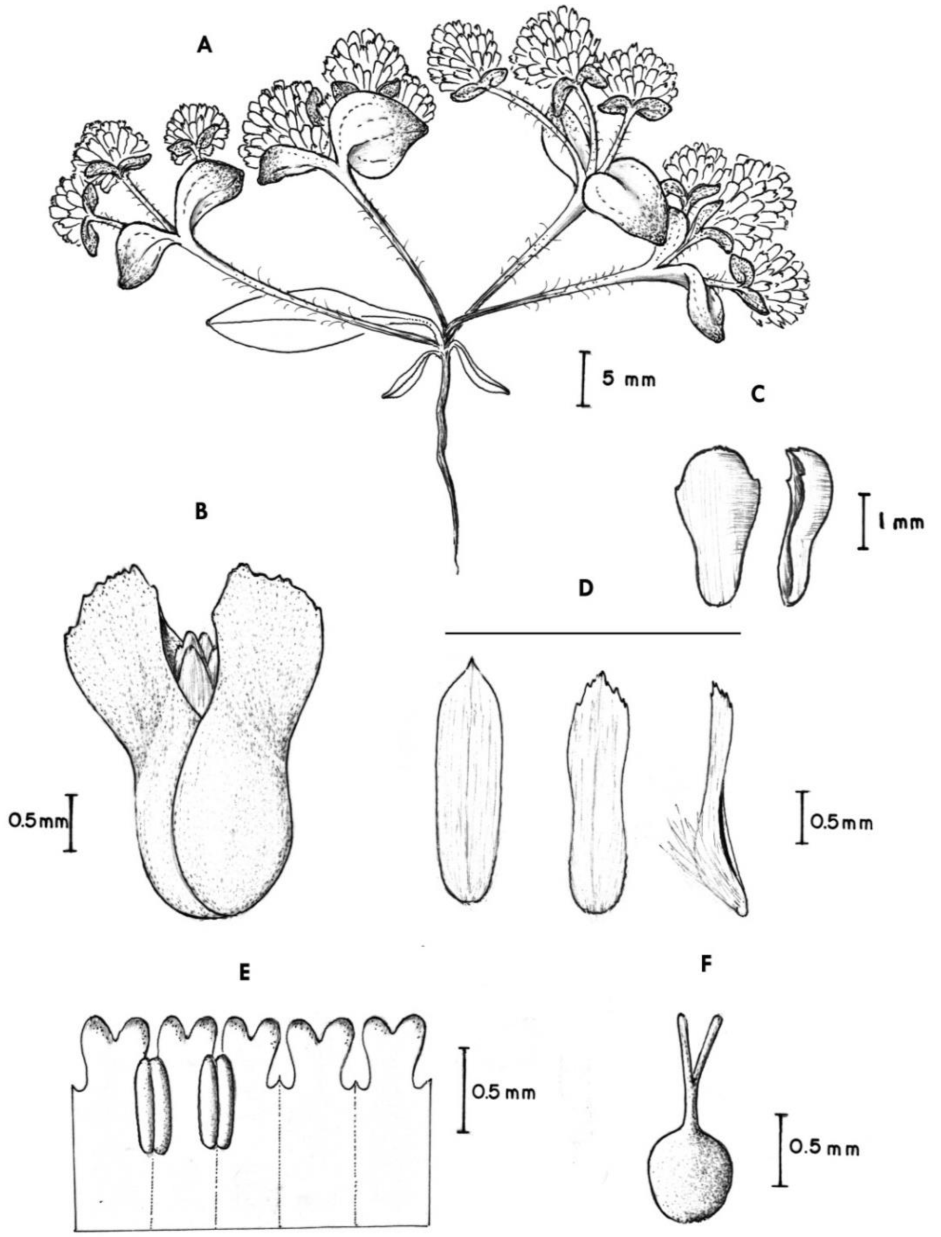


Fig. 4-46. *Gomphena* sp. nov. (Spec2 b) Ortuño & Borsch. A) Habit. B) Flower and bracteoles, C) Bract. D) Tepals, trichomes on the dorsal part of the inner tepals. E) Detail of the filament appendices of the androceum. F) Gynoecium. [*voucher: Wood, J.R. et al. 23269*].

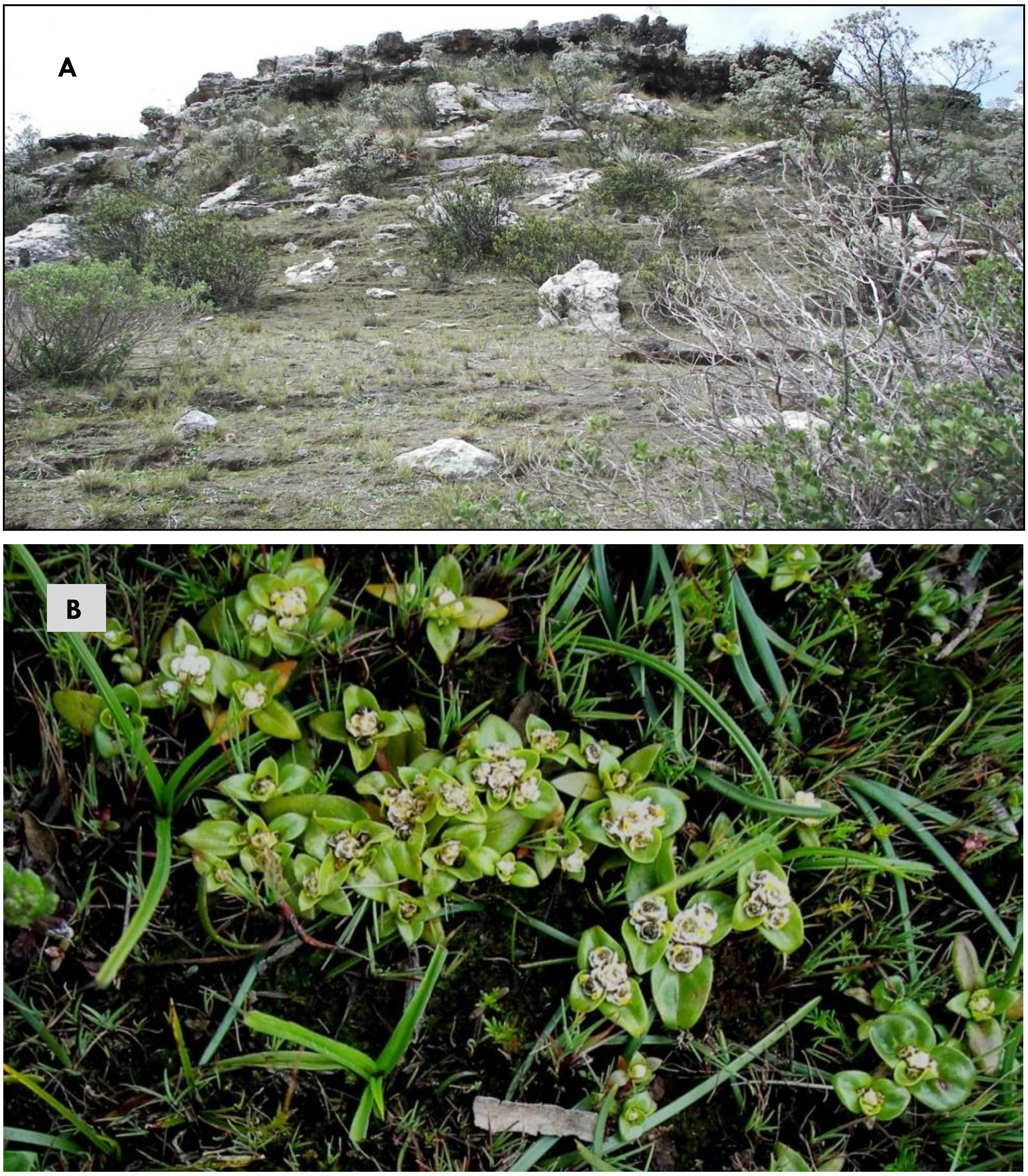


Fig. 4-47. *Gomphena spec*2 Ortuño & Borsch. A) Habitat, Wila kasa surrounding San Pedro in Toro Toro, (Dept. Potosí), sandstone ridge with bizarre rock formation and cliffs with scattered shrubs in gullies. B) Habit of *Gomphrena sp. nov. (spec*2), Photo Hibert Huaylla [voucher: Huaylla 3648].

4.3.6.5. ***Gomphrena*** *spec. nov. (Sarijchi)* Ortuño, T. & A. Lliully. [ined.]

Type: Potosi, Pocoata, localidad Sarijchi, 18°33'006" S, 65° 57'348" W, 2869 m, 31 enero. 2016. Lliully, A. & T. Ortuño *2382* (HT: LPB; IT: B).

Annual plants, 3-4 cm tall (Fig. 4-48 A). ***Root*** simple, 5-5.9 cm of long. ***Stems*** erect to ascendant, striate, reddish coulored, without trichomes at maturity. ***Cauline leaves*** ovolanceolate, 1-1.8 (--2) x 0.3-0.6 (--0.8) cm, apiculate at apex, mucronate with midvein excurrent for 0.2-0.5 mm, decurrent at base, light green, adaxial part densely covered with trichomes, abaxial part less densely and trichomes scattered, 1-4 (--5) x 0.3 (--0.7) mm, white, appressed strigose, peduncles green densely covered with large white trichomes. ***Apical leaves subtending paracladia*** *(inflorescences)* 3-5, arranged symmetrically, ovate to lanceolate, 1.5-2 (3) x 0.5 (--0.8) cm, apiculate at apex, mucronate, light green, the abaxial sideof leaf densely covered with white to light yellow, the adaxial with short hirsute trichomes (Fig. 4-48 B). ***Inflorescences*** globose, terminal, 0.5-0.8 cm in diameter, consisting of 3-5 partial florescences, white. ***Flowers*** sessile, 4 x 1.3 mm, with 9-12 flowers forming a partial florescence. ***Bracts*** ovate, cimbiform 3 (--3.3) x1 (--1.3) mm, membranous, white, with apex abruptly acute, midvein prominent, margin entire sometimes with hairs, membranous, translucent. ***Bracteoles*** lanceolate ovate, cimbiform, 4 x1.2 (--1.5) mm, laterally compressed, membranous in texture, white, with a wide winged crest from the tip to about half of the upper dorsal part, the margin dentate, with large lanate trichomes between the bracteoles and tepal. ***Tepals*** lanceolate, connate at the base, membranous, white, with lanate on the dorsal part and at the margin. Sizes unequal. External tepal 3.2-3.6 x 1-1.3 mm, intermediate 3- 3.6 x 0.5 (--0.6) mm, inner 3.2 x 0.3 mm. ***Filaments*** 2.8 mm, largely fused into a tube for 2.1 mm, free part 0.7mm long. ***Filament appendages*** conspicuous, 0.4 mm long, lanceolate, rounded in the apex, laterally united for about 0.3 mm (Fig. 4-48). ***Anthers*** oblong, 1.4 mm long, appearing inserted between two laterally fused filament appendices 5. ***Gynoecium*** with two filiform stigma branches, 1 mm long, style 0.3 mm, ovary globose 0.4 mm.

Micromorphology of trichomes. Multicellular, uniseriate; on ***stems and cauline leaves*** with one wide basal cell, the second cylindrical, straight, 3-6 upper cells with scarce spinous and salicose ornamentation, cuticle walls striated in sculpture. ***Interlocking junctions*** linear, scars arranged in parallel to the axis of the trichomes with angle zero overlapping. ***Trichomes on flowers:*** with firm to collapsed consistence, smooth cuticule walls, white. ***Trichomes on apical leaves subtending paracladia***: on abaxial surface with large trichomes similar to those on stems; on the adaxial surface trichomes with 2-3 straight cells with flat texture. ***Trichomes on tepals*** with collapsed cells, arising from the fibrous cells of the tissue of tepals. ***Anatomy of tepals***. Tissue composed of elongate, straight, cylindrical dermal cells, arranged in one row, the extremes fitting perfectly, the fibre cells extending into trichomes [voucher: Lliully & Ortuño 2016].

Taxonomic remark. One population with a high number of specimens was recently-collected (for this reason there is no molecular sequence yet). The plants are morphologically similar to the members of the annual *G. pallida* clade; similarities with *G. pallida* are the trichomes on the dorsal part and at the margin of the tepals, and the type of crest on the bracteoles. The difference among *Gomphrena sp. nov. (Sarijchi)* and *G. pallida* are the sizes of the plants the first with a short size and erect stems. The characteristic is the clear and light green colour of the cauline leaves. The inflorescence has only a few white flowers, contrary to the many found in other species of the *G. pallida* clade. It is relevant to note that the apical leaves subtending the paracladia are unique especially with respect to the colour and shape, and their sizes with respect to the inflorescence. They are much bigger than the flowers, the tissue is thin and coriaceous, the trichomes are white and in the adaxial part shorter than on the abaxial side of the leaves. The adaxial surface of the apical leaves subtending paracladia has a light green colour, the lightness is intensified through the presence of the short white trichomes. The apical leaves subtending paracladia attract small insects (Fig. 4-49 D) which are possible pollinators. Therefore it is possible to call this type of inflorescence pseudanthium, which is a composed structure that resembles a single flower (see Chapters 2 and 3).

Habitat and ecology. *Gomphrena sp. nov. (Sarijchi)* was found on bare stony soil, in the western part of the slopes bordering the Sarijchi River, a region formed by moderate and steep slopes, and rivers that cross the valley. The specific vegetation of the area consists of rocky slopes dominated by patches of *Prosopis alba* Griseb., *Schinus areira* L., *Trichocereus tacaquirensis* (Vaupel) Cárdenas ex Backeb. and *Corryocactus melanotrichus* (K. Schum.) Britton & Rose. In open areas there is a predominance of shrubs such as *Rhysolepis tucumanensis* (Hook. & Arn.) H. Rob. & A.J. and R. helianthoides (Rich.) H. Rob. & A.J. Moore. Other predominant shrubs that grow in places with higher humidity are *Baccharis linearifolia,* (Lam.) Pers., *Asclepias barjoniifolia* E. Fourn., *Buddleja tucumanensis* Griseb.. Accompanying plants in open zones communities of grasses that form macollos, are *Jarava ichu* Ruiz & Pav. and *Jarava pseudoichu* (Caro) F. Rojas. The plants were collected in remaining woody patches of Inter-Andean dry forest at 2869 m.

Distribution. Pocoata, Potosí of Potosí (see Fig. 50)

Specimens examined for distribution assessment. Bolivia, Potosí Pocoata, localidad Sarijchi, [18°33’006” S, 65° 57’348” W], 2869 m, 31. 1. 2016. *Lliully, A. & T. Ortuño,* 2382 (LPB, B).

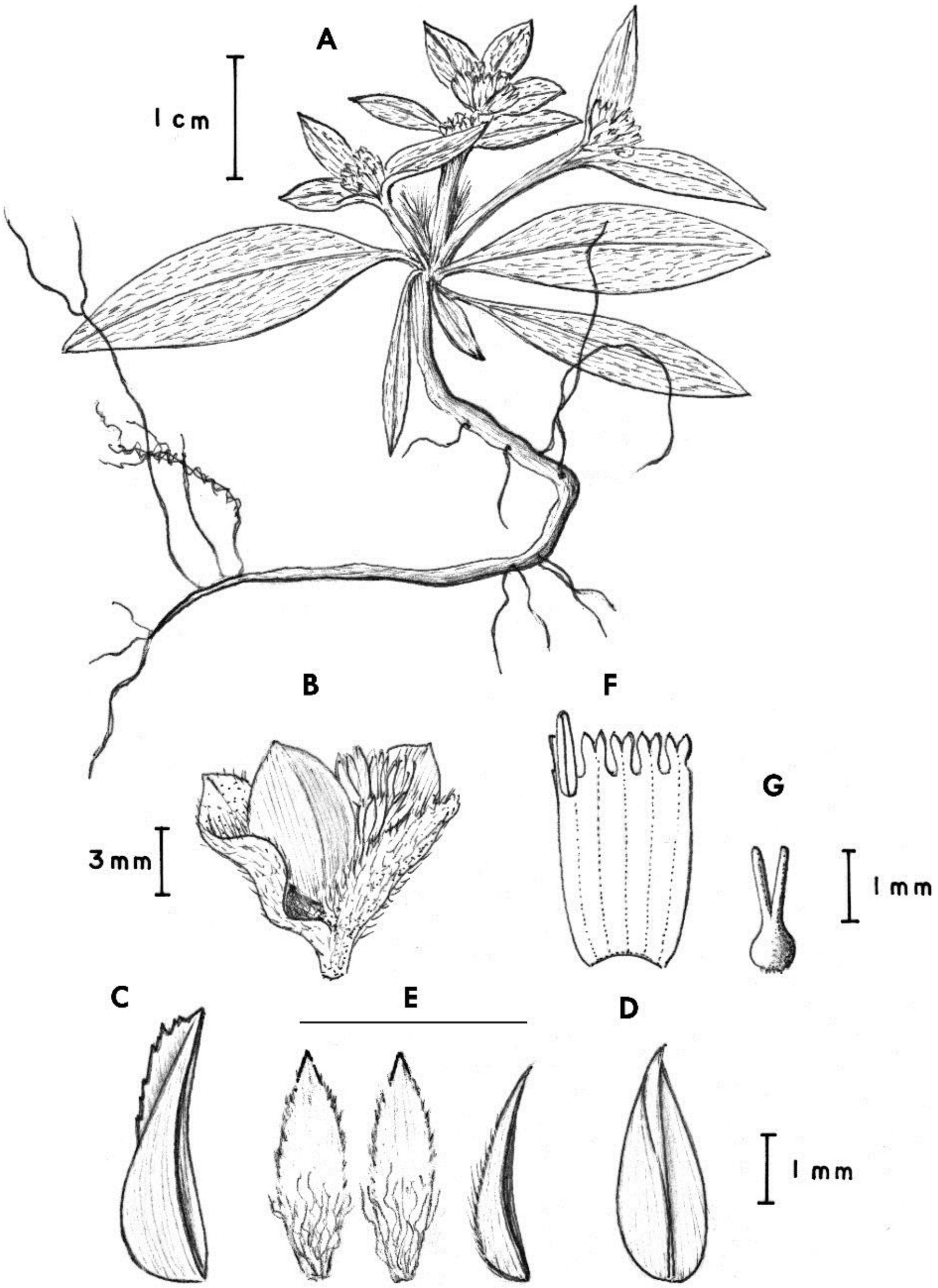


Fig. 4-48. *Gomphrena sp. nov. (sarijchi)* Ortuño & Lluilly. A) Habit. B) Flower with bracteoles. C) Bract slightly crested. D) Detail of bracteole with crest in the upper part. E) Tepals with trichomes on the dorsal part and at the margin. F) Detail of the androecium showing the almost completely fused filament tube and the lateral filament appendages. G) Gynoecium [voucher: Lluilly & Ortuño 2382].

Fig. 4-49. *Gomphrena sp. nov. (sarijchi)* A) Habitat, Sarijchi river system, in dry valley ecoregion. B & D) Detail of the inflorescence with apical leaves subtending the paracladia forming a pseudantium, C) Detail of the fibrous root - note small size of plant. E) General view of the plant. *Lliully & Ortuño* 2382 (LPB, B).

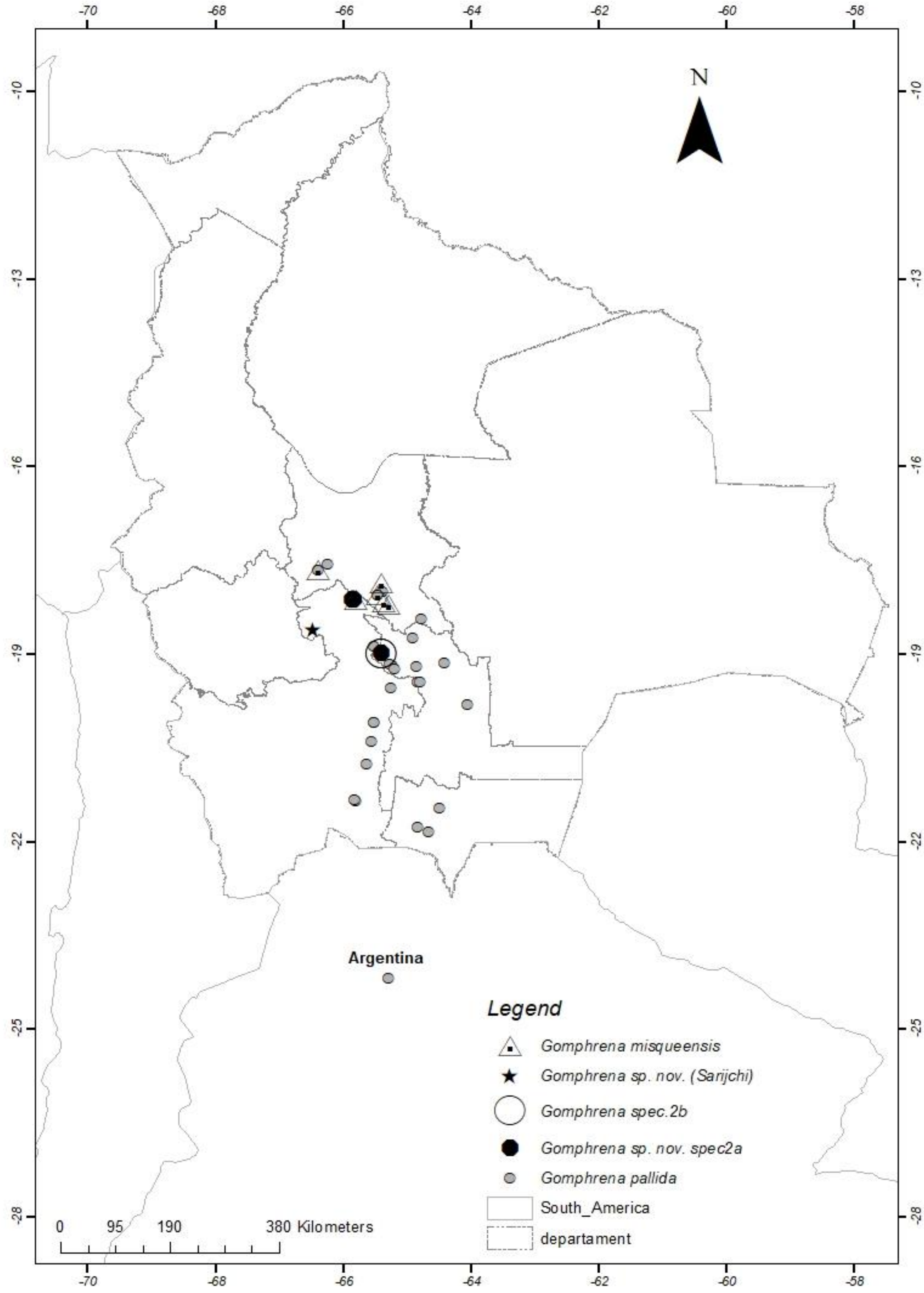


Fig. 4-50. Distribution of *G. pallida* and other annual species that are closely related.

4.3.7. Perennial taxa of the "Mostly Andean CLADE B"

Key to perennials of the mostly Andean CLADE B

1. Plants with stolons producing lateral shoots, root woody, basal leaves in loose rosette, erect, stems unbranched ....*G. sp. nov. tipo estolonifera* (Fig. 4-62)

1'. Plants with fleshy or/and woody taproot.

2. Tepals ovolanceolate without trichomes at the margin and the dorsal part, bracteoles shortly crested at the apex of the dorsal part or without crest .... *G. potosiana* (Fig. 4- 55).

2'. Plants with tepals that have trichomes at the margin and sometimes on the dorsal part.

3. Anther attached between the filament appendices.

4. Trichomes on the cauline leaves light yellow or white.

5. Bracteoles with crest extending for one fifth, toothed, bract membranous ovate, acuminate at apex, white and membranous... *G. oligocephala.* (Fig. 4-53).

5'. Bracteoles with wide crest extending for one half, abruptly widened, distally dentate, bract ovate, membranous, acute at apex. . ... *G. stellata* (Fig. 4-64)

4' Trichomes on stems close to the inflorescence and on the cauline leaves light brown, brown or dark brown.

6. Bract ovate, membranous in texture, acuminate at apex, light at base and dark brown at the apex. Indumentum on the stems and on the margin as well as on nerves of the cauline leaves appressed to villous... *G. bicolor* (Fig.4- 51).

6' Bract ovate lanceolate, membranous, acute at apex, white, indumentum hirsute on the stems, on the margin and nerves of the cauline leaves .... *G. sp. nov. (fusci2)* (Fig. 4-68).

3' Anther attached at the top of filament tube, sunken between lateral filament appendages.

7. Colour of the trichomes brown, bract and bracteoles and tepals white in colour, indumentum on the stems and margin of cauline leaves conspicuously hirsute, on apical leaves subtending the paracladia hirsute, filament tube white... *G. fuscipellita* (Fig. 4-66)

7' Colour of the trichomes light brown to dark brown, especially close to the inflorescensce. Bract and bracteoles light brown at the base and dark brown to black overall, tepals yellow to light brown in the base and becoming dark brown at the tip, filament tube dark yellow .... *G. sp. nov. (spec3)* (Fig. 4-57).

4.3.7.1. *Gomphrena bicolor* Mart., Nov. Actorum Acad. Caes. Leop. Carol. Nat. Cur. 13(1): 300 (1826). non. *G. bicolor* hort. ex Moq. DC. Prodr. 13(2): 412 (1849).
Type: Habitat in Peruvia, Haenke s.n. (HT: M 0241701).

Perennial herb, 5-10 (--15) cm (Fig. 4-51). ***Root*** a fleshy taproot, woody. ***Stems*** decumbent to erect, only with unbranched principal stems, striate, indumentum appressed, dense on the nodes, and near the inflorescence, light to dark brown and black trichomes of 1-3 mm length. ***Basal leaves*** in loose rosettes ovolanceolate, 1.4 (--2.5) x 0.4 (--0.9) cm, acute at apex, olive green, appressed indumentum above middle nerve and on margin. ***Cauline leaves*** similar than de basal leaves, 0.3 0.8 (--2) x (--0.8) cm, acute at apex, with few appressed trichomes. ***Apical leaves subtending paracladia*** *(inflorescence)* 3-5, arranged symmetrically, rounded orbicular to cordate, 0.5 (--2) x 0.4 (--1) cm, acute and mucronate at apex, hirsute at the margin, few trichomes on the blades, light to dark brown. ***Inflorescences*** terminal, 1.3-1.5 (--2.5) cm in diameter, consisting of 3-5 partial florescences. ***Flowers*** 4-5 mm long. ***Bract*** ovate, 2.2 (--3) x 1.5(--2) mm, membranous, toothed, acuminate at apex, middle nerve excurrent, light to dark brown from base to the apex, sometimes with trichomes near the apex. ***Bracteoles*** ovate to lanceolate, 4-4.2 (--5) x 1.2 (--1.5) mm, membranous, middle nerve in the dorsal part with crest extending for one fifth that is wide and toothed at the margin. ***Tepals*** lanceolate, narrowest at the middle, the apex toothed, membranous, white with trichomes on the margin, indumentum denser on dorsal part on the inner tepals, sizes unequal. External tepals, 3.4 (--5.4) x 0.7 (--0.9) mm, intemediate tepal, 3.4 (--5.3) x 0.5 (--0.8), inner tepals, 3.2 (--5.2) x 0.3 (--0.8) mm. ***Filament*** 3-5.4 (--6.2) mm, largely fused into a tube, 2-4.4 (--5.2) mm, free part 1mm long. ***Filament appendages*** conspicuous, lanceolate, 0.5-0.8 mm long, the united base sized 0.5-0.2 mm (Fig.4-51E). ***Anthers*** oblong, 1.4 (--1.5) mm, attached between filament appendages. ***Gynoecium*** with two filiform branches of 1.2 (--1.5) mm length, style 0.4 (--0.5) mm, ovary subglobose 1mm, [voucher: Borsch & Ortuño 3558=AC183 (LPB, B)].

Micromorphology of trichomes. Multicellular, uniseriate. On ***stems and cauline leaves*** 3-5 mm long, with 1-3 short basal cells, and 4-6 upper cells that are firm to flexible in consistence, ornamentation scarsely salicose to granulose on cuticule walls, sculpture with prominentl irregular striae, light to dark brown. ***Trichomes on apical leaves subtending paracladia*** with the basal cells broad and rounded, the second one straight, 2-6 upper cells with salicose ornamentation, striate sculpture of cuticule walls. All trichomes have simple interlocking junctions, which are conspicuous and broader than the remaining diameter of the cells (Fig. 4-52D). On ***Tepals*** trichomes large, with collapsed cells. ***Anatomy of tepals.*** Tissue composed by elongate straight, cylindrical dermal cells, arranged in one row, the extremes fitting perfectly, the fibre cells arising of fiber cells (Fig. 4-52E). [voucher: Borsch & Ortuño 3558 = AC183 (LPB, B)].

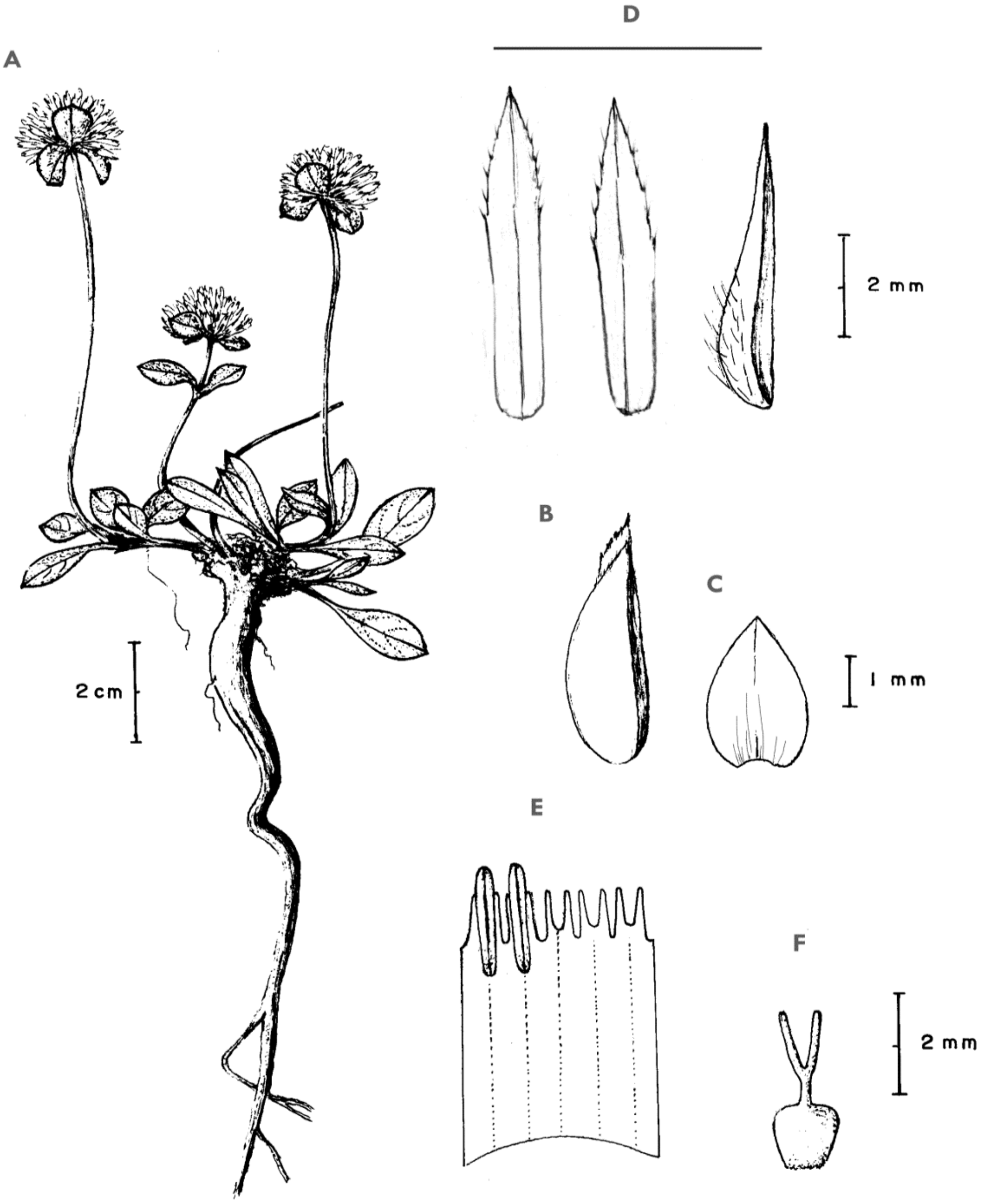


Fig. 4-51. *Gomphena bicolor* Mart. A) Habit. B) Bracteoles. C) Bract. D) Tepals, all with trichomes in the dorsal part- E) Detail of the androecium. F) Gynoecium [voucher: Borsch & Ortuño 3558 (LPB, B)].

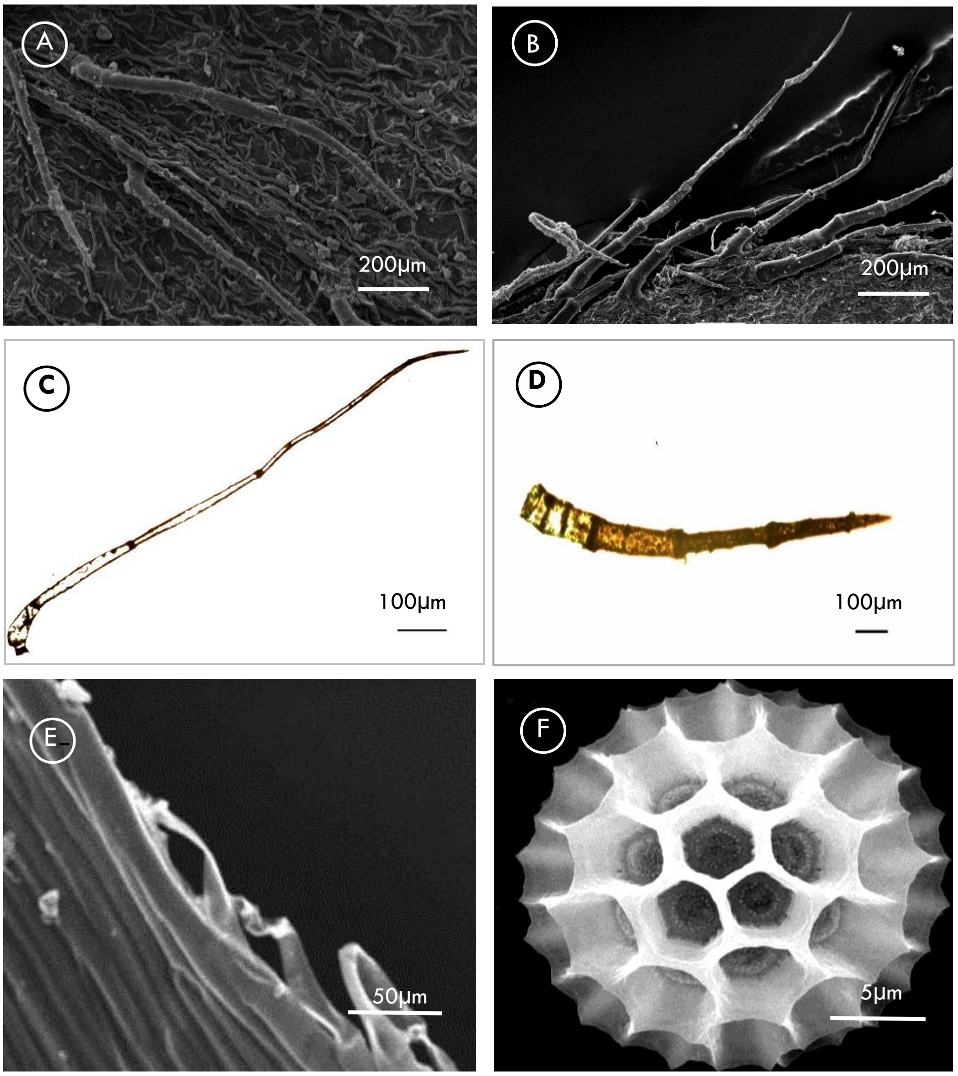


Fig. 4-52. *Gomphrena bicolor* Mart. Trichomes of cauline leaves, A) appressedon the abaxial side of the leave, B) hirsute indumentum on the margin. Trichome of apical leaves subtending paracladia, C) on abaxial side and margin, D) adaxial trichomes with three to four cells, spinous ornamentation and brown colour. E) Detail of the elongate, epidermic tepal cells, with trichomes having collapsed cells on the margin. F) SEM pollen photo of *G. bicolor* [voucher: Borsch & Ortuño 3558 (LPB, B)].

Pollen form: Spheroidal, size 22 µm. Number of apertures 40-- 52. Structure metarericulate with mostly hexagonal mesoporia around apertures with prominent, projecting corners (not microspines). Tectum with columellae in the lowest part of the mesoporium (Fig. 52F) [voucher: Borsch & Ortuño 3558 (LPB, B)].

Taxonomic remark. In the *matK-trnK* plastid tree *G. bicolor* are included in low resolved Andean clade (1 PP, 83Jk, 54BS). The *G. bicolor* subclade, including all the four specimens determined as *G. bicolor* (1PP, 100JK, 100 BS), and emerge sister of *G. pallida* clade, close to *G. potosiana* subclade clade (1 PP, 95 JK, 99 BS). The ITS nuclear marker showing a better resolution, including a *G. bicolor* in the perennial species subclade with high support (0.99PP, 99JK), grouped the tree specimens of *G. bicolor* in one subclade (0.759 PP, 63 JK). Morphologically *G. bilcolor* differenig *from G. potosiana* in the precence of trichomes in the margin tepals, the darkness colour of the bract and trichomes od the Apical leaves of the paracladia, and finally the crest of the bracteoles more big and conspicuous than in *G. potosiana*.

Habitat and ecology. Widely distributed in dry valleys, on open slopes, on sandy and rocky soil. Also on hillsides or in steep-sided river valleys, usually on areas with extensive erosion with loose, unstable soil. In dry valleys near trees such as *Polylepis subtusalbida* (Bitter) M. Kessler & Schmidt-Leb., *Alnus acuminata* Kunth, bushes as *Berberis commutata* Eichler, *Baccharis* ssp., *Escallonia resinosa* (Ruiz & Pav.) Pers., *Schinus microphylla* I.M. Johnst., *Clinopodium bolivianum* (Benth.), and herbs like *Cheilanthes* ssp, *Calceolaria* ssp., *Festuca* ssp. in the ecoregions Inter-Andean dry forest, Semi humid Puna. The plants have been collected between 1900- 3900 m.

Distribution. Restricted to Bolivia and Peru. In Bolivia in provinces: Belisario Boeto, Oropeza, (Dept. Chuquisaca). Provinces: Arani, Arque, Capinota, Cercado, José Carrasco Torrico, Narciso Campero leyes, Punata, Quillacollo, Tapacarí (Dept. Cochabamba). Province Rafael Bustillo (Dept. Potosí) (see Fig. 4- 61).

Specimens examined for distribution assessment. ***Bolivia, Chuquisaca, Belisario Boeto,*** Comunidad Huerta Mayu. Aproximadamente a 3 km de SW de la localidad de Villa Serrano. Cima del cerro Llamtha Apana., [-64,3388, -19,138888], 2468 m, 27, 2, 1994, *Serrano, M., 643*, (LPB,B, HSB). ***Oropeza***, Entre el Km 11 y Ravelo, [-65,369494000, -18,95914799], 3300 m, 19, 11, 1993, *Kiesling, R., 8426*, (LPB). Side road from Punilla north along Rio Kollpa 2 km, [-65,376111, -18,9400], 5, 4, 1997, *Wood, J.R.I., 12005*, (LPB). ***Cochabamba, Arani***, camino de Arani a Mizque. Al frente de un lago, [-65,66202854, -17,5459], 3400 m, 2, 4, 2003, *Borsch, T., 3581*, (LPB, B). Camino de Arani a Mizque. 8 Km de Arani, [-65,2219690, -17,7494489], 3115 m, 2, 4, 2003, *Borsch, T., 3580*, (LPB, B). Kewiñal, a 10 km de Arani (camino a Vacas), [-65,728071999, -17,569381], 3300 m, 24, 3, 1991, *Hensen, I., 1969*, (LPB). ***Arque***, 38 Kms al Este de Challa (camino). [-66,46992500, -17,661272], 3810 m, 31, 3, 1979, *Beck, S.G., 946*, (LPB). Camino a Oruro, 82 Km, sobre río Ballia cerca restos de *Polylepis*, [-66,488211, -17,6874220], 3500 m, 20, 11, 1991, *Ibisch, P., 621*, (LPB). Camino a Oruro, Km 86, [-66,497186, -17,698369], 3305 m, 2, 1, 1992, *Ibisch, P., 731*, (LPB). Cerca estación Chapi-Chapi, [-66,403767000, -17,819825], 3634 m, 2, 1, 1992, *Ibisch, P., 748*, (LPB). ***Capinota,*** Comunidad de Apillapampa, [-66,26666699, -17,850], 3675 m, 15, 2, 2003, *Thomas, E., 209*, (LPB). ***Cercado***, Parque Tunari, Km 15 hacia las lagunas de Wara-Wara, [-66,1308499, -

17,323172], 0, 19, 2, 1995, *Fernández, E., 312*, (BOLV, LPB). Quebrada Chaqui Mayu above the city of Cochabamba, [-66,0944444, -17,3438889], 3400 m, 15, 4, 1994, *Ritter, N., 830*, (LPB). ***José Carrasco Torrico***, Totora, ca. 2 Km S del pueblo de Totora, en el camino hacia Aiquile, [-64,121166700, -18,46816670], 1939 m, 23, 3, 2003, *Wood, J.R.I., 19427*, (USZ, LPB). ***Narciso Campero***, Camino a Aiquile, despues de la cuesta del Meadero, [-65,14513800, -17,97967600], 2080 m, 21, 11, 1993, *Kiesling, R., 8468*, (LPB). ***Punata***, Pasando San Benito, camino a Rodeo de 8 a 10 km del primer puente, [-65,858945, -17,454650], 3100 m, 11, 3, 2009, *Borsch, T., 3961*, (LPB, B). Camino Melga - Punata, Chakiqhocha, [-65,903869, -17,436539], 0, 3, 3, 1991, *Hensen, I., 1243*, (LPB). ***Quillacollo***, localidad Apote, al borde del camino Tiquipaya- Misicuni, [-66,2158060, -17,2890079], 3800 m, 2, 4, 1989, s/n, *363*, (LPB). Camino Sipe-Sipe - Lipichi, [-66,4243189, -17,666049], 0, 7, 12, 1989, *Hensen, I., 482*, (LPB). Camino Sipe-Sipe - Lipichi, [-66,4241669, -17,6658329], 3800 m, 29, 1, 1990, *Hensen, I., 540*, (LPB). Camino Sipe-Sipe - Lipichi, [-66,20765299, -17,666049], 0, 14, 2, 1990, *Hensen, I., 546*, (LPB). Highway between Cochabamba and La Paz, apromately kilometer 70, [-66,42527780, -17,68], 3510 m, 19, 2, 1995, *Ritter, N., 1581*, (LPB). Tholapujru a 13 Km aproximadamente subiendo desde la localidad de Tiquipaya, [-66,23888890, -17,2880556], 3540 m, 6, 12, 2005, *Vargas, N., 251*, (LPB, BOLV). Colcapirhua Hospital between Cochabamba and Quillacollo, [-66,2308333, -17,3916], 2600 m, 12, 3, 2003, *Wood, J.R.I., 20401*, (LPB). ***Tapacarí***, Camino La Paz a Cochabamba, 2 Km antes de Pongo, [-66,34569, -17,43025], 3801 m, 31, 3, 2003, *Borsch, T., 3558*, (LPB, B). Camino La Paz a Cochabamba, a 80 Km a Cochabamba, [-66,7839, -17,7598], 3940 m, 1, 4, 2003, *Borsch, T., 3564*, (LPB, B). Cuenca de Taquiña, [-66,23605, -17,2991993], 3628 m, 14, 1, 2012, *Huaylla, H., 3629*, (B, LPB). ***Potosí***, ***Rafael Bustillo***, Uncia 22 Kms. Hacia Pocoata, [-66,4438779, -18,606703], 3800 m, 6, 3, 1981, *Beck, S.G., 6158*, (LPB).

4.3.7.2. *Gomphrena oligocephala* J. Rémy, Ann., Sci. Nat., Bot. sér. 3(6): 350 (1846).

Type: Bolivia, laguna, ad ripas Rio Pescado. D'Orbigny 1158. (HT: P P00622673)

≡*Xeraea oligocephala* (Remy) Kuntze, Rev. Gen. Plant: 545 (1891).

Perennial herb, 10 (--22) cm. ***Root*** a fleshy, woody taproot, 5-15cm long. ***Stems*** erect, unbranched or with secondary stems, striate, green to red, with indumentum of appressed trichomes, these 1.4 -2 (--3) mm long, yellow to brown. ***Basal leaves*** rosulate, ovate lanceolate, 1.5-2 (--2.5) x 0.5-0.7 (-- 0.9) cm, middle nerve prominent, acute and mucronate (0.4 mm) at apex, indumentum appressed, white, denser in the abaxial part, similar to that on stems. ***Cauline leaves*** lanceolate, 1.5-2 x 0.9 cm, decurrent, middle nerve prominent, acute and mucronate at apex, olive green, trichomes appressed, denser on the abaxial side, white. ***Apical leaves subtending paracladia*** (inflorescences) 3-5, ovate-lanceolate, apiculate to mucronate, 1.3-1.6 (--2.5) x 0.4-0.5 (--1.5) cm, indumentum hirsute, trichomes denser on the abaxial side and the margin, appressed, less dense on the adaxial side. ***Inflorescences*** globose to subglobose, terminal, 1.5-1.8 (--2) cm in diameter, consisting of 3-6 partial florescences, indumentum densely lanate, trichomes white to ligth brown. ***Flowers*** 5.5–5.6 (--6) mm, >10 grouped on an axis forming a partial florescence. ***Bracts*** 3 x 1.2 mm, membranous in texture, ovate, acuminate at apex, irregular toothed at margin, glabrous, white, translucent. ***Bracteoles*** ovate lanceolate, 5.5 (--5.6) x 1 (--1-5) mm, membranous in texture, opaque white, with crest extending for about a fifth of the dorsal part, toothed at the margin, longer than the tepals. ***Tepals*** lanceolate narrowest in the middle, at the base connate, toothed and with hairs at the margin, trichomes on the dorsal part white. Size unequal. External tepals 5 (--5.5) x 0.8 mm, intermediate 5 (--5.3) x 0.6 mm, inner 4.8 (--5) x 0.3 mm. ***Filaments*** 4.3- 5.6 mm long, fused for the most part into a long tube, this part 3.3-4.6 mm long, free part 1 mm long. ***Filament appendages*** 0.6 mm long, lanceolate and the united base 0.4 mm long, white (Fig. 54B). ***Anthers*** 1.6 mm long, oblong, attached between the filament appendages. ***Gynoecium*** with 2 filiform branches of 1.2 -1.4 mm length, style 0.4 mm, ovary subglobose, 0.5-0.6 mm long, with only one ovule. [voucher: Borsch & Ortuño 3760 = AC251(LPB, B)].

Micromorphology of trichomes. Multicellular, uniseriate. On s***tems and cauline leaves*** with 1-3 short flat, basal cells, 4-6 upper cells firm in consistence, cuticule walls with spinous ornamentation and striate sculpture, interlocking junctions simple and thick. O*n* ***apical leaves subtending paracladia*** the trichomes on the adaxial side different from the abaxial; the adaxial with 2-3 thin short cells, spiny ornamentation, and smooth cuticule walls (Fig. 54A); on abaxial side trichomes longer, composed of 3-6 uniseriate cells, consistence firm, ornamentation granulose and cuticule walls cells with smooth sculpture. The interlocking junctions in all the trichomes conspicuous and broad in diameter, the color varying from white to brown; ***on tepals*** trichomes large, with firm basal cells, the upper with the cells collapsed, interlocking junctions not conspicuous [voucher: Borsch & Ortuño 3760 (LPB, B)]. ***Anatomy of Tepals.*** Tissues composed by elongate, straight, cylindrical dermal cells, arranged in one row, the extremes fitting perfectly, the fibre cells extending into the trichomes.

Taxonomic remark. Morphologically *Gomphrena oligocephala* differs from *G. bicolor* by the pale colour of the bract and the trichomes. They are dark brown in *G. bicolor*. The cauline leaves are more thinly lanceolate and more densely hairy in *G. oligocephala* than in *G. bicolor*.

Habitat and ecology. Frequent on open, stony plateaus to rocky places. Near to scattered *Prosopis ferox* Griseb., *Escallonia resinosa* (Ruiz & Pav.) Pers., *Schinus microphylla* I.M. Johnst., *Baccharis dracunculifolia* DC., in forest fragments of *Polylepis subtusalbida* (Bitter) M. Kessler & Schmidt-Leb, with herbs as *Nothoscordum andicola* Kunth. In the Inter-Andean dry forest, Semi humid Puna, Tucuman-Bolivian forest, Cerrado Chiquitano, collected between 400 - 3900 m

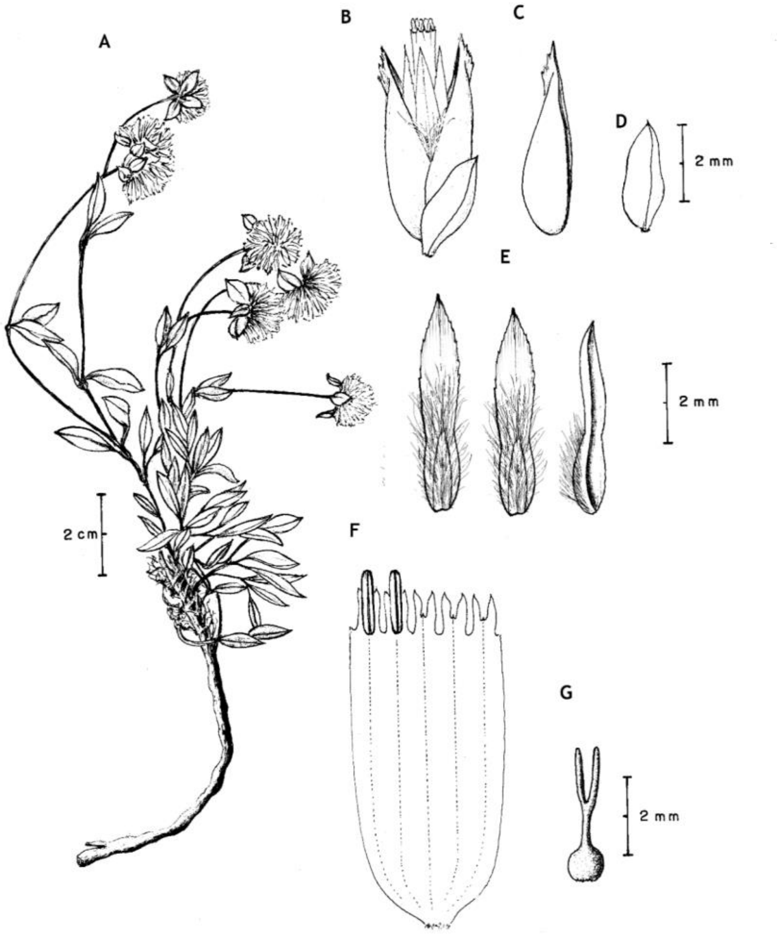
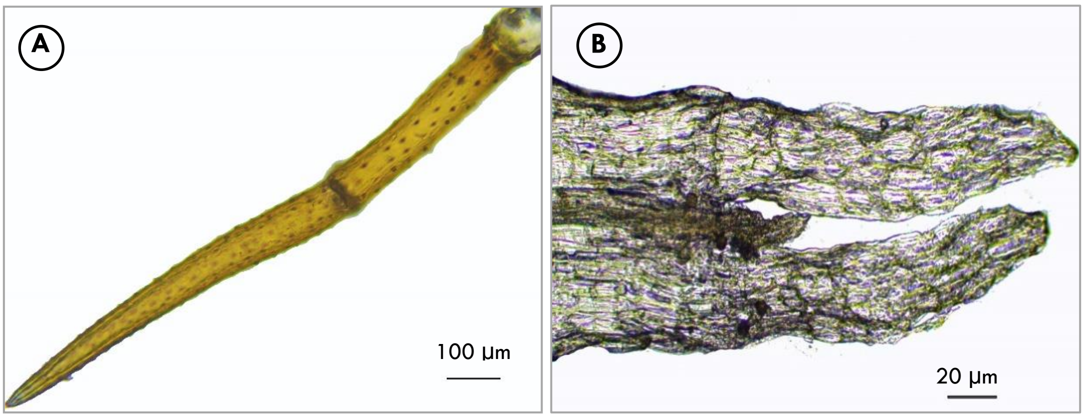


Fig. 4-53. *Gomphrena oligocephala* J. Rémy. A) Habit. B) Flower. C) Bracteoles. D) Bract. E) Tepals, all with trichomes on the margin and the dorsal part. F) Detail of the androecium with the anther positioned between the filament appendages. G) Gynoecium [voucher Borsch & Ortuño 3760].



.Fig. 4-54. *Gomphrena oligocephala* Remy. Trichomes, A) from abaxial side of leaf, two cells with spiny ornamentation and flat texture. Androecium. B) Two filament appendices, 0.6 mm long, Both photos done with light microscope [voucher: Borsch & Ortuño 3760 (LPB, B)].

<u>Distribution</u>. Endemic of Bolivia. Provinces of Oropeza and Yamparaez, (Dept. Chuquisaca). Provinces of Cercado. Mizque, Quillacollo. (Dept. Cochabamba). Province of Cornelio Savedra, (Dept. Potosí). Province of Valle Grande (Dept. Santa Cruz). Province Burnet O´Connor (Dept. Tarija) (see Fig. 4- 61).

<u>Specimens examined for distribution assessment</u>. ***Bolivia, Chuquisaca, Tomina***, Rio Pescado, valle seco entre Padilla and Monteagudo, [-64,08309, -19,607506], 1372 m, 1826, *A.C.V. d'Orbigny*, *1158*, (P). ***Oropeza,*** Cerro Obispo, [-65,343528, -18,139694], 3199 m, 5, 1, 2012, *Huaylla, H., 3621*, (LPB). Comunidad de Punilla a 25 Km de la ciudad de Sucre, Trayecto a Potolo, [-65,383222, -18,983556], 3214 m, 23, 2, 2004, *Wood, J.R.I, 20242*, (HSB, LPB). Near antenna on road from "El Tejar" (Sucre) towards Guzman in Rio Cachimayo., [-65, 283333, -19, 083333], 2898 m, 10, 1, 2003, *Wood, J.R.I, 18875,* (HSB, LPB). Tarabuco, Towards Tarabuco, [-65, 226447, -19, 082528], 2858 m, 5, 12, 1993, *Wood, J.R.I, 7691, (*K, LPB). ***Yamparáez***, 1 km de la comunidad Candelaria, [-64, 792333, -19,307], 2990 m, 13, 4, 2004, *Borsch, T., 3760*, (LPB, B). c. 5 Km from Tarabuco along road to Presto, [64°54'01", 19°03'24"], 3281m, 1, 2, 2007, *Wood, J.R.I., 22570*, (BOLV, LPB). Sucre ca. 15 kms. Hacia Tarabuco, [-65, 198764, -19, 140294], 2858 m, 7, 3, 1981*, Beck, St. G., 6216*, (LPB). ***Cochabamba, Quilllacollo***, ca. 1 km de San Miguel, [-66, 237393, -17, 295366], 3049 m, 13, 1, 2012, *Huaylla, H., 3634,* (LPB). ***Potosí, Saavedra***, Betanzos, cerro atrás del mercado municipal, [-65,45, -19,55, 3392], 14, 3, 2005, *Mendoza, M., 1502*, (LPB). ***Tarija, O'Connor***, [-64,425, -21,421667], 2670 m, 22, 2, 2006, Beck, St.G., 31687, (LPB). Límite provincia con Cercado, serranía el Cóndor, 48 km de Tarija. 3,3 km de la carretera, pasando las antenas, [-64,402222, -21,441111], 2830 m, 26, 4, 2006, *Beck, St .G., 32185*, (LPB). Camino de Villamontes a Tarija. 45 km de Entre Rios, [-64,42366667, -21,42366667], 2659 m, 10, 4, 2003, *Borsch, Th., 3646*, (LPB, B). ***Arce,***

Municipio de Padcaya Reserva Nacional de Flora y fauna Tariquia, [-64,609781, -22,000006], 3100 m, 4, 27, 2005, *Serrano, M., 6340*, (HSB). ***Santa Cruz,*** **Vallegrande,** ladera de matorral húmedo, [-64,221667, -18,723], 2385 m, 3, 12, 2011, *Parada, G.A., 3991*, (USZ, MO). 8 km al este de Pucará, [-64,133889, -18,710556], 2715 m, 22, 1, 2011, *Parada, G.A., 2917*, (USZ, MO).

4.3.7.3. *Gomphrena potosiana* Suess. & Benl., Mitt. Bot. Staatssamml. München 1:6 (1950).

Type: Bolivia, Potosí, Miraflores, 3800 m, in loco arenoso. *Cardenas* 107 (IV. 1932). Gray Herb Cambridge, Massach. (HT: GH 00037083, fragment IT: M M0241786, LIL LIL000430).

Perennial herb, 4-6 (--15) cm long. ***Root*** a fleshy, woody taproot. ***Stems*** prostrate to ascending, up to 5 cm long, usually unbranched principal stems, striate, green to red, indumentum villous, scarce, trichomes 1.3 mm of long, white. ***Cauline leaves*** ovolanceolate, 0.7 (--2.0) x 0.5 (--0.8) cm, acute-and mucronated at apex, margin entire, trichomes scattered on the blade of the leave and the margin, white. ***Apical leaves substending paracladia*** *(inflorescence)* 3-6, leaves arranged symmetrically, rounded to cordate, 0.7-1.7 (--2) x 0.2 (--0.5) mm, acute and mucronate (midvein excurrent for 0.2 mm), green, trichomes appressed, abaxial and adaxial sides nearly glabrous, densely hirsute at the base and the margin, white to light brown. ***Inflorescences*** terminal, 1-1.5 (--1.7) cm in diameter, consisting of 2-4 partial florescences. ***Flowers*** 4-5 (--6) mm long. ***Bract*** ovate, 1.8 -2.6 (--3) x1 (--2) mm, membranous in texture, acute at apex, entire or toothed at margin. ***Bracteoles*** ovate lanceolate, 3.6 -4 (--4.8) x 1 (--1.2) mm, toothed at the apex, middle nerve thick, crest absent or small and then extending for 15 % of the dorsal part, white (Fig. 55C). ***Tepals*** ovate-lanceolate, truncate, toothed at apex, glabrous, bigger than the bracteoles, size unequal (Fig.4-55E). External tepals 3.6-4.6(--5) x 0.8 mm, ntermediate tepal 3.5 – 4.4 (--4.8) x 0.6 mm, inner tepals 3.2-3.4 (--4.4) x 0.4 mm. ***Filaments*** completely fused into a tube, 3-4.2 (--5) mm long. ***Filament appendages*** conspicuous, elliptic to lanceotate, 0.6 mm long, laterally fused from two adjacent filaments, connected part below appendages 0.4 mm long. ***Anthers*** oblong, 1.3 mm long, appearing sunken between two laterally fused filament appendages (Fig. 4-55F). ***Gynocecium*** with two filiform branched stigmas of 1.3 mm length, style 0.4 mm, ovary 0.5 mm, one ovule [voucher: Borsch & Ortuño 3716 = AC249 (LPB, B)].

Micromorphology of trichomes. Multicellular, uniseriate. On ***stems and cauline leaves*** with1-2 basal cells the first one short and broadly rounded, the second straight, with granulose ornamentation close to the union point, upper cells 4-6, with firm to flexible consistence, salicose ornamentation, and striate sculpture of cuticule walls, interlocking junctions thick, conspicuous, linear scars or projections of the extreme border cells (as spines) zero angle degrees overlapping, on ***apical leaves subtending paracladia*** trichomes on the abaxial and adaxial side with very sparse indumentum, with firm to flexible consistence, spinous ornamentation, and striate sculpture of cuticule walls. ***Anatomy of tepals.*** Tissue composed by elongate strait, cylindrical dermal cells, arranged in one row, the extremes fitting perfectly (Fig.4- 56D) [voucher: Borsch & Ortuño 3716 = AC249 (LPB, B)].

Pollen*:* Spheroidal, size 17-18 µm in diameter, number of apertures 58-64. Structure metarericulate, mesoporia with prominent, aristate corners (no microspines) the surface and border undulate, tapered, building hexagons, columellae in the lower part visible (Fig.4- 56 E, F) [voucher: Borsch & Ortuño 3716 (LPB, B)].

Taxonomic remark. *G. potosiana* was described by Suessenguth and Benl. based on a specimen collected by the Bolivian botanist Martin Cardenas in a place called Miraflores in Potosí. This specimens has the tepals without trichomes, and a crest on bracteoles is nearly absent.

The specimen analysed in this work (Borsch & Ortuño 3716) was collected near the city of Potosí. In the *matK-trnK* tree this sample emerges sister to the specimes Borsch & Ortuño 3672 collected in Thomas Frias (Potosí) close to the thermal water in Miraflores. The latter specimen and specimen Borsch & Ortuño *3762* from Chuquisaca, Jaime Zudañez have some slight differences as the bracteoles are a bit bigger than the tepals with trichomes on the margin and on the dorsal part of the inner tepals. The plants may belong to this species but further investigation is needed.

Habitat and ecology. Grows in open habitats, grassland, near open forest of *Polylepis tomentella* Wedd., in rocky hillsides, or stony places near thermal waters. Other species growing in the site were *Trichocereus tarijensis* (Vaupel) Werderm., *Oreocereus* ssp., *Jarava ichu* Ruiz & Pav., *Tetraglochin cristatum* (Britton) Rothm. The species is present in the ecoregions Inter-Andean dry forest, Semi humid Puna, and Prepuna, where the plants have been collected between 3350-3900 m.

Distribution. Provinces of Jaime Zudañez and Sud Cinti (Dept. Chuquisaca). Province Antonio Quijarro, (Dept. Potosí) (see Fig.4- 61).

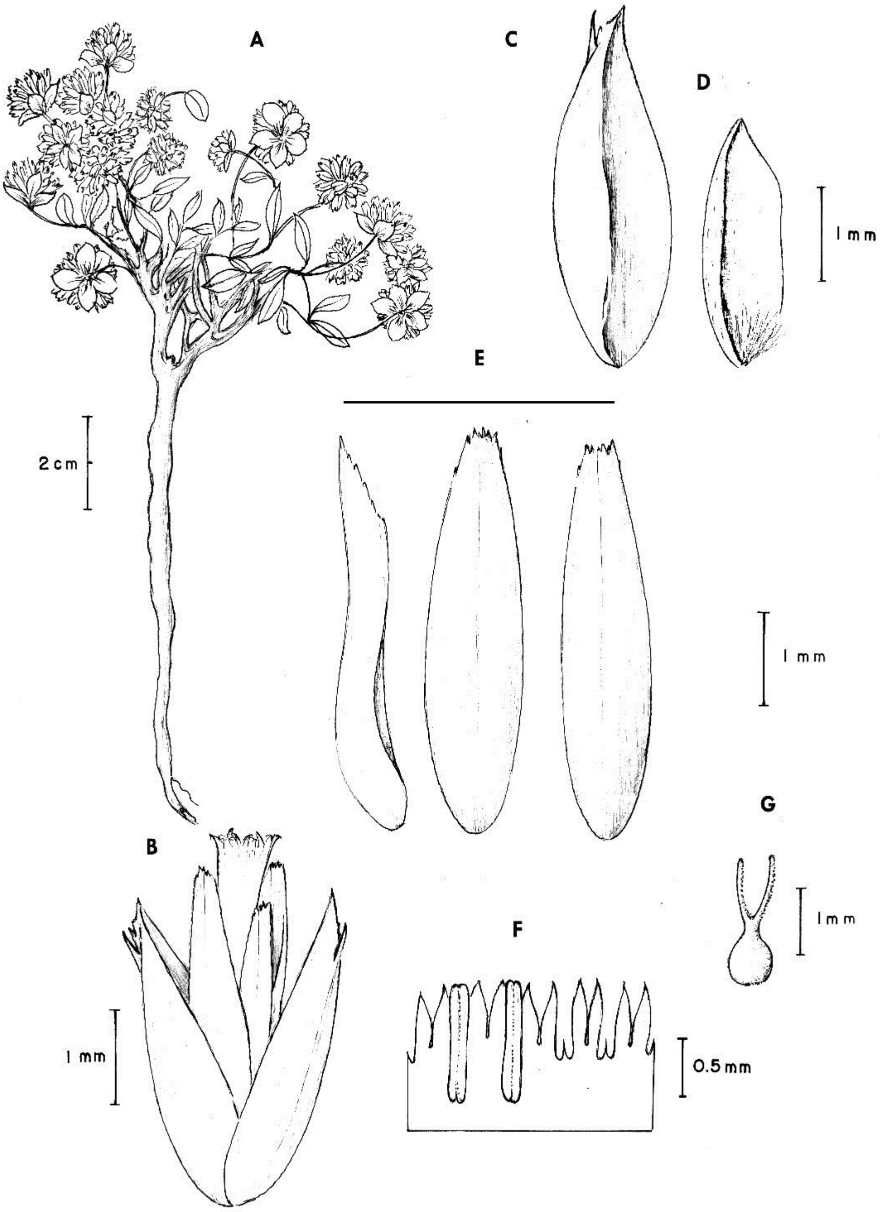


Fig. 4-55. *Gomphena potosiana* Suess. & Benl. A) Habit. B) Flower. C) Bracteoles. D) Bract. E) Tepals F) Detail of the androecium. G) Gynoecium [voucher: Borsch & Ortuño 3716 (LPB, B)].

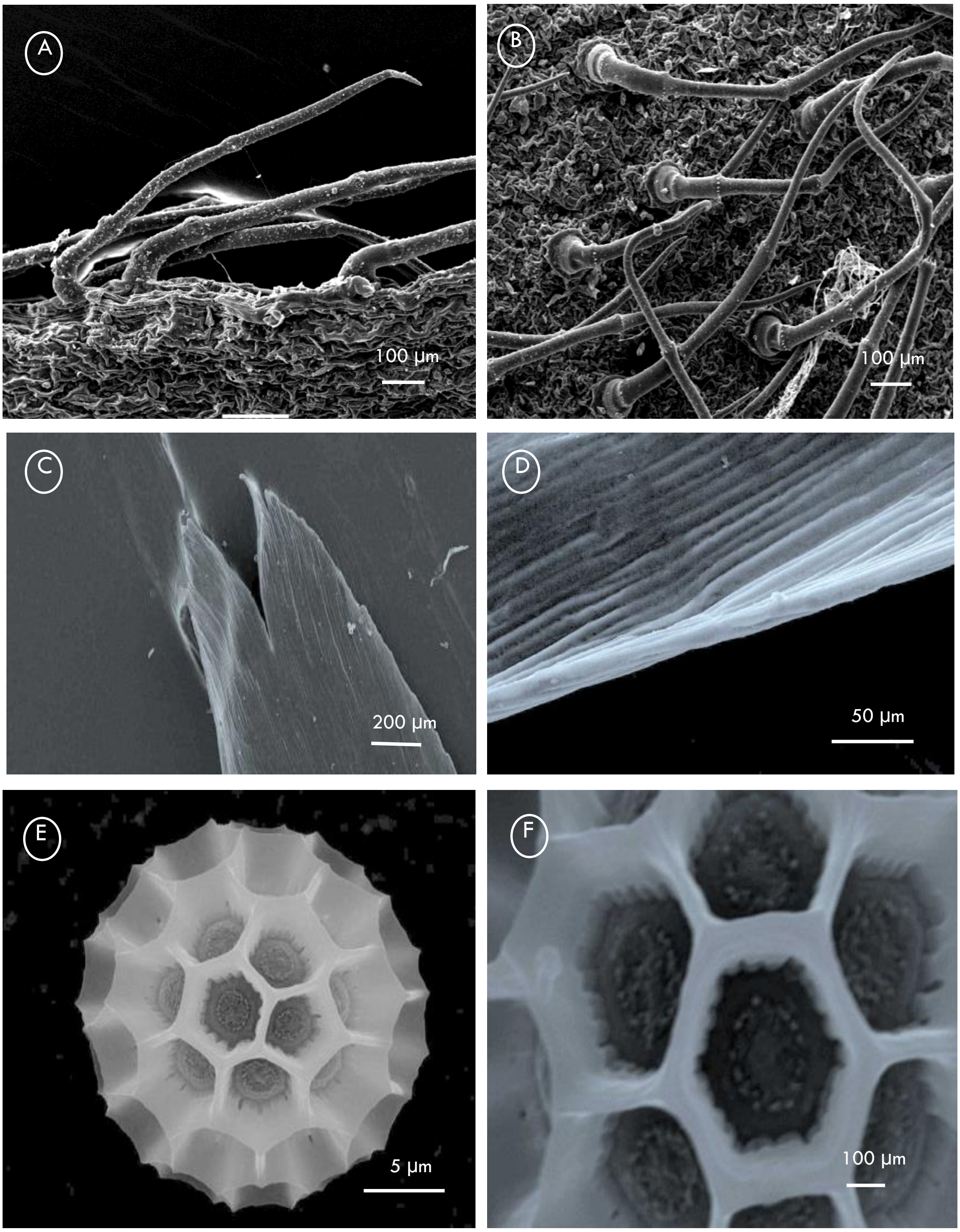


Fig. 4-56. *Gomphrena potosiana* Suess. & Benl. Trichomes of cauline leaves A) Trichomes of hirsute indumentum on the margin. B) Villous trichomes on the lower part of the leave C) and D) Detail of the tepals. E) General overview of the pollen. F) Detail of the apertures. [voucher: Borsch & Ortuño 3716 LPB, B)].

Specimens examined for distribution assessment. ***Bolivia, Chuquisaca, Jaime Zudañez**, pasando el poblado de Icla*, [-64,67383333, -19,44278333], 3458 m, 13, 4, 2004, *Borsch, T., 3762*, (LPB, B). ***Sud Cinti***, Camino de Tarija a Potosi. Cerca de Villa Abecia, [-65,12066667, -20,43566667], 3414 m, 12, 4, 2003, *Borsch, T., 3667*, (LPB, B). ***Potosí, Antonio Quijarro***, Camino de Potosi a Khucho Ingenio, 5 km antes de llegar a Khucho Ingenio, [-65,70674200, -19,852342], 3841 m, 16, 12, 1987, *Schulte, M., 79*, (LPB). Camino de Potosi a Khucho Ingenio, 5 km antes de llegar a Khucho Ingenio, [-65,706742, -19,852342], 3700 m, 16, 1, 1988, *Schulte, M., 110*, (LPB). ***Tomás Frías*** Camino de Potosí a Cucho ingenio, [-65,5703333, -19,83483333], 3900 m, 2, 4, 2004, *Borsch, T., 3716*, (LPB, B). ***Cornelio Saavedra***, Chachi Baños, Margenes de pueblo, ladera sobre cerro de donde salen aguas termales, [-65,56666, -19,616667], 3655 m, 24, 2, 2004, *Mendoza, M., 847*, (LPB, USZ).***José Maria Linares***, Comunidad de alkatuyo, Pacallo Pampa, 53 km SE de potosi, 3,3 km SW de la escuela Alkatuyo, [-65,5499, -19,883], 3560 m, 16, 3, 1993, *Marino, F., 29*, (LPB). ***Sud Chichas***, W slope of cerro Cieneguillas range 4 Km de ca, Tupiza. Ca., [-65,68333, -21,416667], 3400 m, 17, 2, 2002, *Müller, J., 9051*, (LPB). ***Tomás Frías***, Miraflores, [-65,7833329, -19,449], 3800 m, 4, 0, 1932, *Cárdenas, M., 107*, (K, GH, LIL).

Two morphologically slightly deviating samples: *G. potosiana* (type a): ***Bolivia, Chuquisaca, Jaime Zudañez***, pasando el poblado de Icla, [-64,6738333, -19,44278333], 3458 m, 13, 4, 2004, *Borsch, T., 3762*, (LPB, B). ***Potosí***, [***Tomás Frías***, -65,78866667, -19,4463333], 3356 m, 13, 4, 2003, *Borsch, T., 3672*, (LPB, B).

4.3.7.4. *Gomphrena sp. nov.* (*spec3*). Ortuño & Borsch [ined.]

Type: Bolivia, Dep. Chuquisaca, Oropeza, Cero Chataquilla, west of La Capilla, Sucre-Chaunaca, 18°58'29.49.96" S, 65°24'40.4994" W, 3699 m, 31.1.2007, *J.R.I. Wood, H. Huaylla & J. Gutierrez 22568* (HT: LPB LPB0001736; IT: B, K).

Perennial herb, 20 (--25) cm. ***Root*** a fleshy, woody taproot, up to 2.5 cm thick. ***Stems*** erect stems unbranched, striate, indumentum dense, appressed, the trichomes with 2-3 mm long, and light brown to black in colour, darker on the nodes and at the base of the inflorescence. ***Basal leaves*** sessile, lanceolate to linear, 1.3-3.5 (--7) x 0.2-0.4 (--0.7) cm, obtuse to acute at apex decurrent in the base, indumentum appressed, denser on the lower than on the upper part of leaf, latter becoming glabrous which increased age, densely hirsute at the margin, these trichomes 1.3 mm long, light to dark brown (Fig. 4-57). ***Cauline leaves*** sessile, similar in shape and indumentum to the basal leaves, 1-1.5 (--2.5) x 0.3-0.4 (--0.8) cm, acute to or mucronate (0.2 mm) at apex, middle nerve prominent. ***Apical leaves subtending paracladia*** 4-5, ovolanceolate, acute to mucronate at apex, 0.7-1 (--1.5) x 0.3- 0.4 (--0.7) cm, trichomes light brown to black, denser on the margin than on the lower part and fewer on the upper surface of leaf, the trichomes of upper surface vary from hirsute to appressed. ***Inflorescences*** globose, terminal, 1.5-2 (--2.5) cm in diameter, consisting of 3 to 5 partial inflorescences, mostly yellow and in part light or dark brown in colour. ***Flowers*** 5-7 (--10) mm, sessile, basally with dark brown trichomes. ***Bracts*** ovolanceolate, cymbiform, 2-2.5 (--3) x 1.2 (--1.5) mm, membranous in texture, light brown at the base and dark brown to black towards the apex, with irregular teeth at the margin. ***Bracteoles*** ovate lanceolate, cymbiform, 4-4.4 (--5.4) x 1.5 mm, membranous in texture, acuminate at apex, light brown at the base and becoming dark brown in the apical part, midvein extending into a crest for about a third of the dorsal part, the margin irregularly and deepely toothed. ***Tepals*** oblong-lanceolate, fine membranous, yellow to light brown at the base and becoming dark brown at the tip, acute and dentate at apex, toothed and with trichomes at margin, all the tepals with thin, twisted, erect trichomes in the dorsal part. Unequal in size, the external tepals 5-5.5 (-- 5.6) x 1-1.2 mm, the intermediate 4.9-5.4 (--5.5) x 0.5 mm, inner tepals 4.8 (--5.4) x mm. ***Filaments*** completely fused into a tube for 7.1-9.2 mm, membranous dark yellow. ***Filament appendages*** 0.6-0.8 mm long, elliptic, lanceolate, the lobes rounded at apex, two appendages of lateral filaments united base for 0.4 mm. ***Anthers*** oblong, 1.5 (--2) mm long, appearing sunken among two filament appendages (Fig. 57 E), yellow. **Gynoecium** with two filiform stigma branches of 1.1 mm length, style 0.2 mm long, ovary subglobose, 0.5 mm long [voucher: Wood, Huaylla & Gutiérrez 22568 = AC1028 (LPB, B)].

Micromorphology of trichomes: Multicellular, uniseriate; on **stems and cauline leaves** with 1-3 basal cells, first cells rounded, flat, the 4-6 upper cells with firm to flexible consistence, salicose and scarce spinous ornamentation, striate sculpture of cuticle walls, interlocking junctions conspicuous, linear, scars arranged in zero angle. ***Trichomes on apical leaves subtending paracladia*** with the lower part and margin similar than thichomes of the stems and cauline leaves (Fig. 59 A), on the upper part of the leaf variable in size, the short ones with 3-4 uppers cells and the large one with 3-6 upper cells (Fig. 59 B). The upper cells of the trichomes with the first cells rounded and the second straight and firm in consistence, sometimes the last collapsed or flexible, flat with scarce spinous ornamentation, striate sculpture of cuticule walls, interlocking junctions, conspicuous as a broad node, scars linear and arranged in an angle of zero degrees. ***Trichomes on the tepals*** arising from the margin cells of the tepals tissue, as a prolongation of the elongate cells. The trichomes on the dorsal part of tepals with firm basal cells, and the upper cells firm to flexible, collapsed and twisted, then appearing as a lanate indumentum. Interlocking junctions are conspicuous. ***Anatomy of tepals***. Tissue composed by elongate straight, cylindrical dermal cells, arranged in one row, the the extremes fitting perfectly, the fiber are close related with the trichrome, because nested or simple are the prolongation of the fiber [voucher: Wood, Huaylla & Gutierrez 22568].

Taxonomic remark. The nuclear tree (ITS) shows that the sample *G. sp. nov. (spec3)* among the perennials of the “Mostly Andean clade B”, which is well supported (0.995 PP, 99 JK). The sister group is *G. sp. nov. (stolonifera)*. The *matK-trnK* tree shows that *G. sp. nov. (spec3)* is in the same clade but within that in a broad polytomy (see Chapter 3). The principal morphological characters of *G. sp. nov. (spec3)* are the perennial life cycle, the peculiar dark brown (to golden) colour of the bract, bracteoles and tepals, that become yellow or light brown colour in the basal parts, the intense yellow colour of the filament tube and the length of the tube exceeding tepals at anthesis (see Fig. 4- 58E). Finally, the dark colour of the hirsute indumentum at the margin of the apical leaves subtending paracladia is noteworthy, which appears also on the upper side of the leaf, where the trichomes are shortly hirsute.

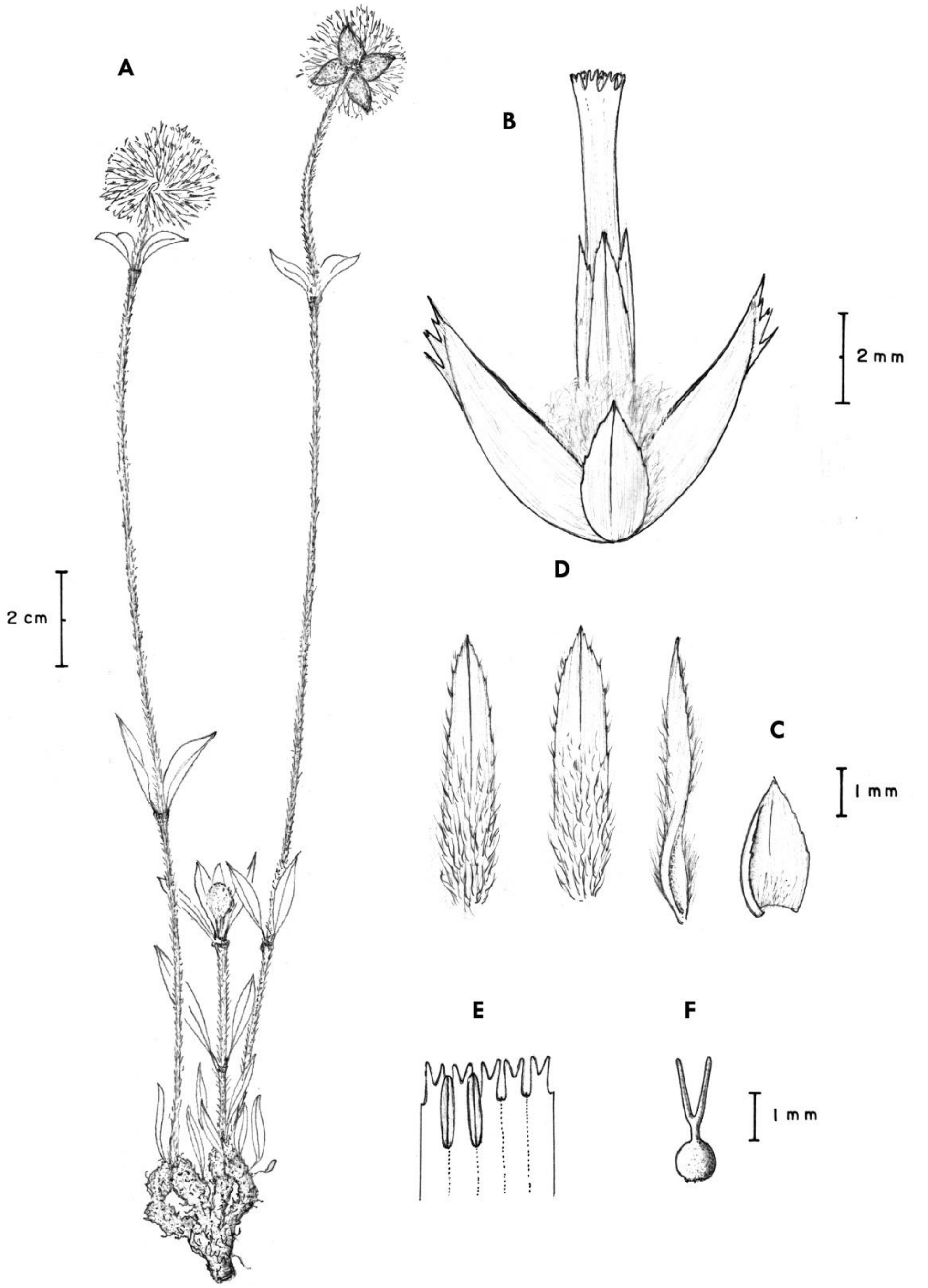


Fig. 4-57. *Gomphrena sp. nov (spec3)*. A) Habit. B) Detail of the flower with the two bracteoles. C) Bract. D) Oblong-lanceolate tepals with trichomes on the dorsal part and margin. E) Detail of the androecium. F) Gynoecium, [voucher: Wood, Huaylla & Gutierrez 22568].

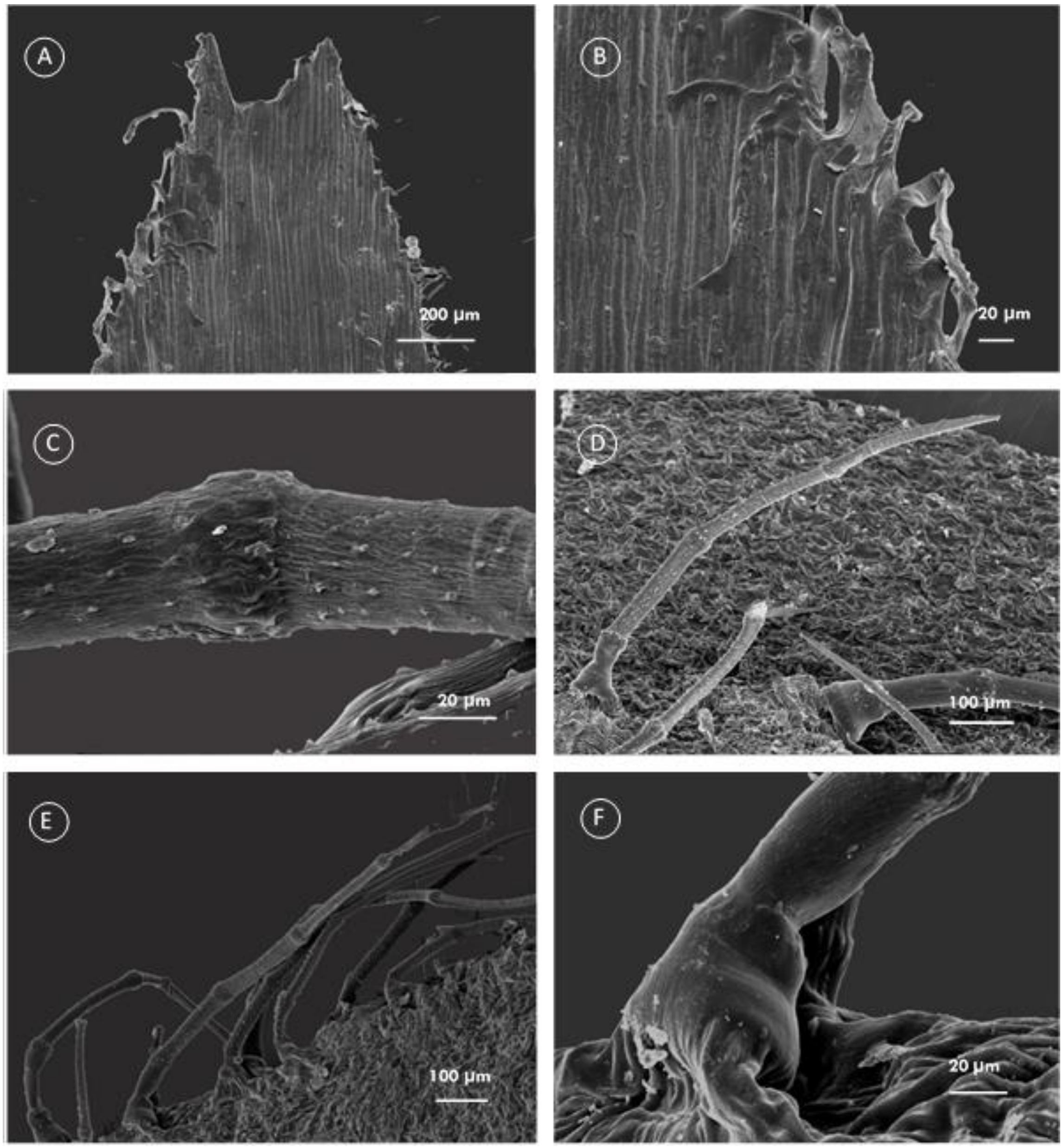


Fig. 4-58. *Gomphrena nov. sp.* (*spec3*). Tepals *A*) Detail of the apex. B) Detail of the straight and elongate form of epidermis cells, and lanate trichomes ariseing from them at the margin. Cauline leaves: C) Interlocking junctions, conspicuously broadened nodes. D) Trichomes with spinous, salicose ornamentation and striate sculpture of the cuticule walls. E) Hirsute trichomes of the margin, and firm to collapsed cells. F) Firm consistence of rounded basal cells of trichomes, [voucher: Wood, Huaylla & Gutierrez 22568].

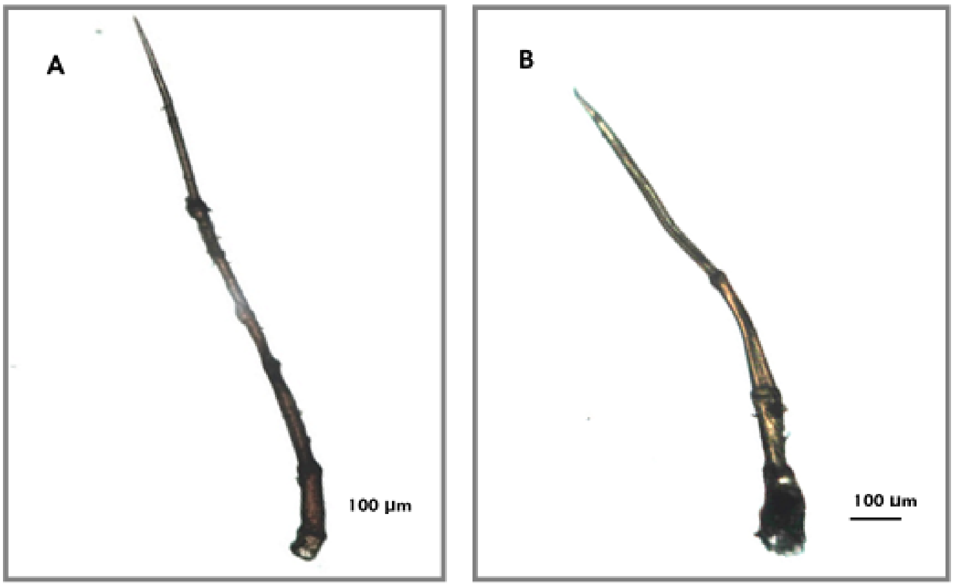


Fig. 4-59. *Gomphrena sp. nov. (spec3)*. A) Trichomes of the basal part of the apical leaves subtending paracladia with more than 4 cells, scarce spinous, salicose ornamentation, and striate sculpture of the cuticle wall. B) Adaxial or upper part of trichomes with only three cells [voucher: Wood, Huaylla & Gutierrez 22568 (LPB, B, SI)].

Habitat and ecology. Frequent on open rocky slopes, particularity in sandy runoffs. On sandstone ridges with giant boulders, rock outcrops and cliffs, the whole receiving above average cloud and rain with damp gullies and sandy run-offs. Wet Puna, in the background narrow valleys. Among relictuous forest of *Polylepis tomentella* Wedd., presence of *Ovidia sericea* C. Antezana & Z.S. Rogers, *Brachyotum microdon* (Naudin), *Orites fiebrigii* (Perkins) Diels ex Sleumer. Frequent but dispersed in the locality. In the Semi humid Puna ecoregion of southern Bolivia, where the plants have been collected between 3600-3700 m.

Distribution. Endemic to Bolivia, province Oropeza, locality Chataquila (Dept. Chuquisaca, see Fig. 4- 61).

Specimens examined for distribution assessment. ***Bolivia*, *Chuquisaca*, *Oropeza*,** Chataquila, camino a las pinturas rupestres, [-65,41125, -18,974861], 3751m, 15, 12, 2011, *Huaylla, H., 3612*, (LPB). Oropeza, Cerro chataquila, west of the capilla Sucre Chaunaca, [-65, 406389, -18, 984167], 3699 m, 31, 1, 2007, *Wood, J.R.I, 22568*, (LPB, B, K).

Fig. 4-60. *Gomphrena sp. nov. (spec3)*. A) Mountain of Chataquila, showing the rock formation where G. sp. nov. (spec3) grows. Photo Lliully, A. B) General view of the plant, photo Huaylla H. [voucher: Huaylla 3612] C) Detail of the flower, Photo: Wood, JR [voucher: Wood Huaylla & Gutierrez 22568]

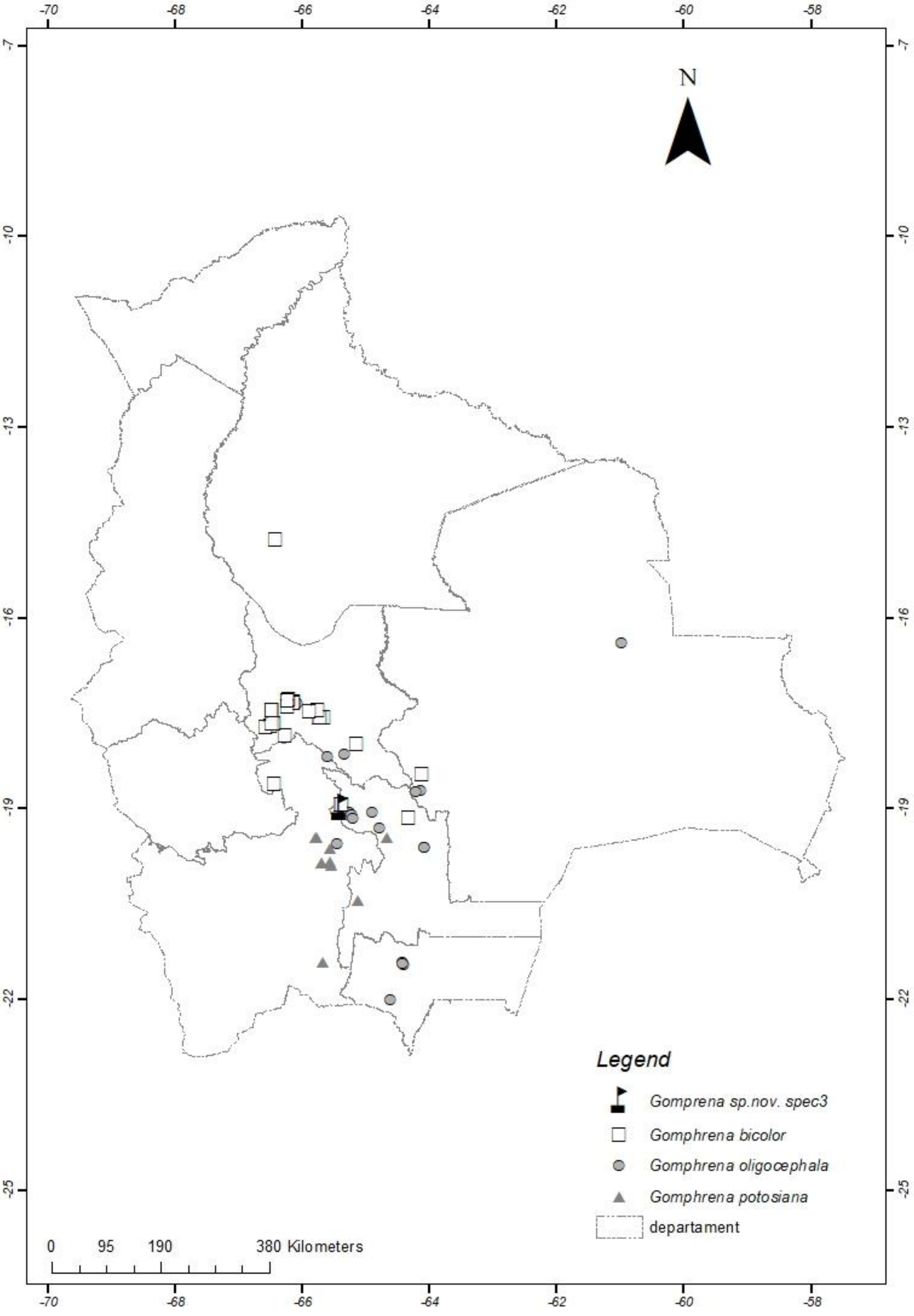


Fig. 4-61. Map of the group of perennials related to *G. pallida* in the “Mostly Andean clade B”: *G.potosiana*, *G. oligocephala*, *G. bicolor*.

4.3.7.5 ***Gomphrena sp. nov.*** *(stolonifera)* Ortuño & Borsch [ined.].

Type: Cochabamba, Provincia Mizque, Camino de Raykampampa a Molinero por el camino viejo hasta la cumbre, 18°09'41364",65°12'19.548", 2870 m, 4 abril 2003. *Borsch T. & T. Ortuño, 3610* (HT: LPB LPB0001718, B).

Perennial, herb. 12-14 (--20) cm long. **Root** a fleshy, woody stolon, the mainly root up to 0.5 m, individual plants arising as lateral shoots (Fig. 4-62). ***Stems*** erect unbranched, striate, trichomes 1-2 mm long, appressed, multicellular, light to dark brown. ***Basal leaves*** arranged in rosettes, ovate lanceolate, 2.5 (--4) x 0.4 (--1) cm, acute and mucronate at apex, trichomes appressed, denser at the margin, few on both sides of the leaves. ***Cauline leaves*** ovate to elliptical, 2 (--2.8) x 0.2 (--0.5) cm, sometimes more than two leaves growing in the same node, usually smaller than the main two opposite leaves. ***Apical leaves subtending paracladia*** *(inflorescence)* 3-6, arranged symmetrically, ovolanceolate, 0.8-1 (--1.5) x 0.3-0.7 (--1) cm, apiculate and mucronate at apex, villous on the abaxial side, densely hirsute at the margin, less dense on the adaxial side, trichomes light to dark brown. ***Inflorescence*** terminal, 1.5-1.7 (--2) in diameter, consisting of 3-6 partial florescences, with firm dark trichomes at the base. ***Flowers*** 4-5 (--6.2) mm long, white. ***Bracts*** ovate, lanceolate, 3-3.2 (--3.6) x 1-1.2 mm, membranous in texture, acute at apex, margin toothed and sometimes with trichomes at the margin, opaque, light brown in the base, dark brown at the apex, middle nerve with a short crest at the apex without teeth. ***Bracteoles*** ovate to lanceolate, 4.5-5 x 1.4 mm, membranous, translucent, the middle nerve dorsally with a toothed crest for one third to two trirds. ***Tepals*** ovolanceolate, membranous in texture, with trichomes at the margin, unequal in size, external tepals 3.1-5 (--5,6) x 0.6 (--0.8), intermediate tepal 3-4.8 (--5.3)x0.6 mm, the inner tepals is 2.8-4.5 (--5.2) x 0.5 mm, white, connate at the base, fine membranous, trichomes in the margin see (Fig.4-62 E). ***Filaments*** 4.4-6 (--6.4) mm, largely fused into a tube, 3.4-4.4 (--5) mm, membranous, light brown, the free part 1 mm long. ***Filament appendages*** conspicuous 0.6-0.8 mm long, lanceolate. ***Anthers*** 1.2 mm long, oblong. ***Gynoeceum*** with 2 filiform branches, stigma 1.2 mm long, style 0.4 mm, ovary subglobose 0.5-0.6 mm [voucher: Borsch & Ortuño 3610 = AC185 (LPB)].

Micromorphology of trichomes. Multicellular, uniseriate. On ***stems and cauline leaves*** 3-5 mm long, with 1-3 short, flat, thin basal cells, the 4-6 upper cells firm to flexible, with scarce spinous ornamentation, prominently irregularly striated sculpture of cuticule walls. ***Trichomes on apical leaves subtending paracladia*** on the adaxial side of the leaf different than on the abaxial, in the first case trichomes short with one broad, white basal cell, and 2-4 thin upper cells, with spinous ornamentations, smooth cuticule walls, light to dark brown in colour, on the abaxial side similar than on stems, more dark brown. All types of the trichomes with simple ***interlocking junctions*** that are conspicuous and broader than the diameter in the remaining part of the cells. On ***tepals*** with collapsed cells, white.

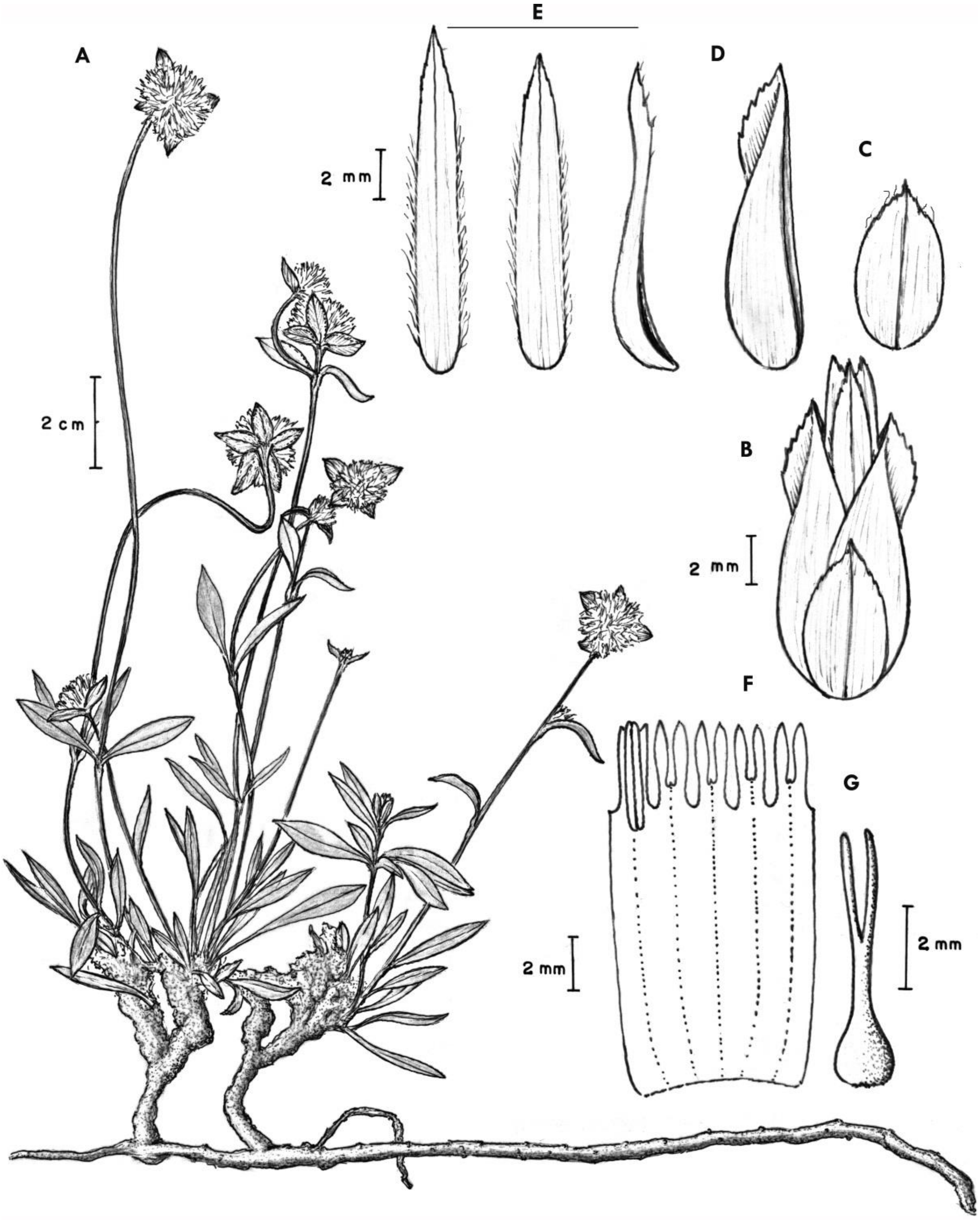


Fig. 4-62. *Gomphrena sp nov. (stolonifera)* Ortuño & Borsch. A) Habit. B) Flower. C) Bract. D) Bracteoles. E) Tepals, trichomes on the margin of the tepals. F) Detail of the androecium. G) Gynoecium. [voucher: Borsch & Ortuño 3610].

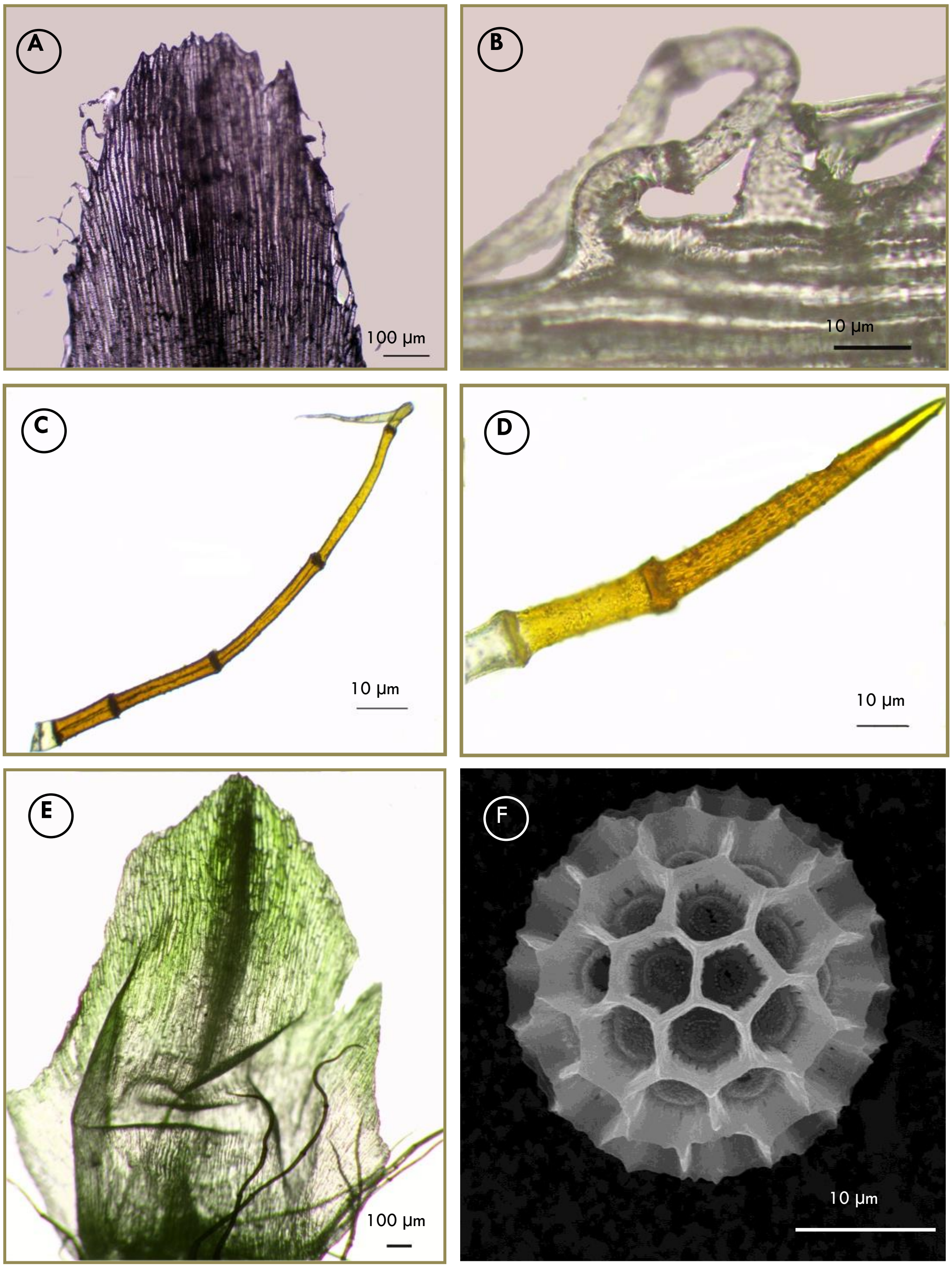


Fig. 4-63. *Gomphrena sp nov. (stolonifera)* Ortuño & Borsch. A) Detail of the epidermis cells of tepal. B) Trichomes with collapsed cells from the margin of tepals. Trichome of apical leave subtending paracladia. C) Abaxial trichome with 4-6 upper cells of firm consistence, scarce spinous ornametation and smooth sculpture of cuticule walls. D) Trichome from uppers part, with 1-4 light to dark brown cells. E) Bract, cimbiform, light to dark brown in colour, dark trichomes from the internal base. F) Pollen. Metareticulate, with narrow mesosporia and the columellae visible in the lower part. [voucher: Borsch & Ortuño 3610].

Anatomy of tepals. Tissue composed by elongate, strait, cylindrical dermal cells, arranged in one row, the extremes fitting perfectly. ***Pollen.*** Form spheroidal, 26 μm in diameter. Number of apertures 40-52. Structure: metarericulate with mostly hexagonal meshes with prominent, projecting corners (not microspines). Mesoporia narrow, tapering distally, tectum reduced laterally with columellae visible lower than the middle of the mesoporium. [voucher: Borsch, T & T. Ortuño 3610 (LPB,B)].

Taxonomic remark: The principal difference of *G. sp. nov. (stolonifera)* to other species in the Mostly Andean clade B is the stoloniferous root type; others are the disposition of the basal leaves, with sometimes additional small cauline leaves growing in the axils of normal cauline leaves on the stems.

Habitat and ecology. Frequent on open slopes, stony, steep hillsides on sandstone, with scattered *Polylepis* sp. or *Podocarpus* sp. Forest patches and herbaceous vegetation such as grasses, *Jarava ichu* Ruiz & Pavon, *Deyeuxia* sp., *Muhlenbergia* sp. and herbs of the families Commelinaceae and Gentianaceae. The habitats belong to the ecoregions of the Inter-Andean dry forest, bordering with the Tucumano forest, where the plant has been collected at elevations between 2200- 3000 m.

Distribution. Endemic of Bolivia, Province of Mizque (Dept. Cochabamba). Province of Oropeza and Valle Grande (Dept. Santa Cruz) (see Fig.4- 71).

Specimens examined for distribution assessment. ***Bolivia*, *Chuquisaca*, *Oropeza***, Chaunaca, alongside road following aqueduct from c. 1 Km, [-65, 423056, -18,995], 3060 m, 31, 1, 2007, *Wood, J.R.I, 22558*, (LPB). Pasando el poblado de Punilla, [-65,3835, -18,9445], 3055 m, 14, 4, 2004, *Borsch, Th., 3766*, (LPB, B). **Cochabamba, Mizque**, camino de Raykampampa a Molinero por el camino viejo hasta la cumbre. [-65,382222, -18,23555556], 2870 m, 4, 4, 2003, *Borsch, Th., 3610*, (LPB, B). **Santa Cruz, Vallegrande,** Pueblo de Guadalupe, ca. 5,5 km de la represa, hacia los cerros pasando por la estancia Collamarca a la cima,[-64,110833, -18,566389], 2261 m, 18, 1, 2003, *Mendoza, M, 431*, USZ.

4.3.7.6. ***Gomphrena stellata*** T. Ortuño & Borsch, Kew Bull. 61(4): 566. 2007.

Type: Bolivia, Chuquisaca, B. Boeto, km 51.5 on road from Villa Serrano to Valle grande, below Nuevo Mundo. 3 Abril, 2003, J.R.I. Wood, A. Carretero & M. Mercado 19600 (HT: LPB 000448; IT HSB, BOLV, K).

Subshrub, 30-40 cm (Fig. 4-64A). ***Root*** a fleshy taproot woody with nodes. ***Stems*** erect to ascending, unbranched or with secondary stems, branches striate, scarcely pubescent in the upper parts, with dense appressed, white, 0.4--1.2 mm long trichomes, becoming woody and glabrous in the second year, somewhat thickened at nodes. ***Cauline leaves*** obovate-lanceolate, 1.0-4 (--4.5) x 0.2-0.3 (--0.5) cm, tapering and amplexicaule at base, mucronate and midvein excurrent for ca. 0.4 mm as a spine, subglabrous, trichomes only few and scattered, of the same morphology as on stems. ***Apical leaves subtending paracladia*** (inflorescences) 4-5 (--6), conspicuous, ovate-lanceolate, 1.2- 1.5 x 0.6 cm, acute and mucronate with midvein excurrent for ca. 0.2 mm at apex, slightly fleshy in texture, similar to cauline leaves, variable in length within a single inflorescence. ***Inflorescence*** terminal, 0.7-1.1 cm in diameter, composed of 3-5 (--6) partial florescences. ***Flowers*** 3.5-4 (--4.5) mm. ***Bracts***, ovate, 1.6 x 1.2 mm, acute at apex, upper part of margin with simple trichomes (c. 1 mm long). ***Bracteoles*** ovate to lanceolate, 1-2 (--3.5) x 1.5 mm, for about their half with a dorsal crest that is then narrowly extending to the base of the bracteole. ***Tepals*** oblong lanceolate, membranous to scarious at maturity, the apex and upper lateral parts hyaline, abruptly acute at apex. The tepals with trichomes 0.4-0.5 mm long, in the margin and dorsal part. Size unequal, external tepals 3.5- 3.6 x 0.7-0.8 mm, intermediate tepals 3.4- 3.5 x 0.6 mm, inner 3.4-3.5 x 0.4 mm (Fig. 4-64 E). ***Filaments*** 3.2-3.8 mm, largely fused into a tube, 2.2 - 2.8 mm long, free part 1mm long. Filament appendages conspicuous ca. 0.5 mm, elliptical, united part 0.4-0.5 mm long. ***Anthers*** 1.1 - 1.8 mm long.***Gynoecium*** with 2 filiform branches c. 0.6 mm ling, stigma 0.5 – 0.4 mm, style distinct, ovary subglobose 0.5-0.4 mm [voucher: Wood, Carretero & Mercado 19600 (LPB, USZ , B, K)].

Micromorphology of trichomes. Multicellular, uniseriate: On ***stems and cauline leaves*** with 1-3 different basal cells, the first rounded, the 4-6 upper cells firm to flexible in consistence, with granulate to spiny ornamentation, striate sculpture of cuticule walls. ***Interlocking junctions*** conspicuous. On ***apical leaves subtending paracladia*** similar than on stems but trichomes more fine on the upper part. On ***tepals*** trichomes on the margin and the dorsal part with with 5-6 collapsed upper cells (Fig.4-65D). ***Anatomy of tepals***. Tissues are composed by elongate strait, cylindrical dermal cells, arranged in one row, the extremes fitting perfectly, trichomes of dentate margin arise from fibre cells [voucher: Wood, Carretero & Mercado 19600].

<u>Taxonomic remark</u>. This species was described (Ortuno and Borsch, 2007), but is so far not yet included in the molecular tree. The morphological characteristics apparently are similar to the specimens of the Andean clade B, because the plants have trichomes on the margin of tepals, and the morphology of the androeceum with is a mostly fused tube with the anther attached between two conspicuous filament appendages, as well as the type of the crest of the bracteoles.

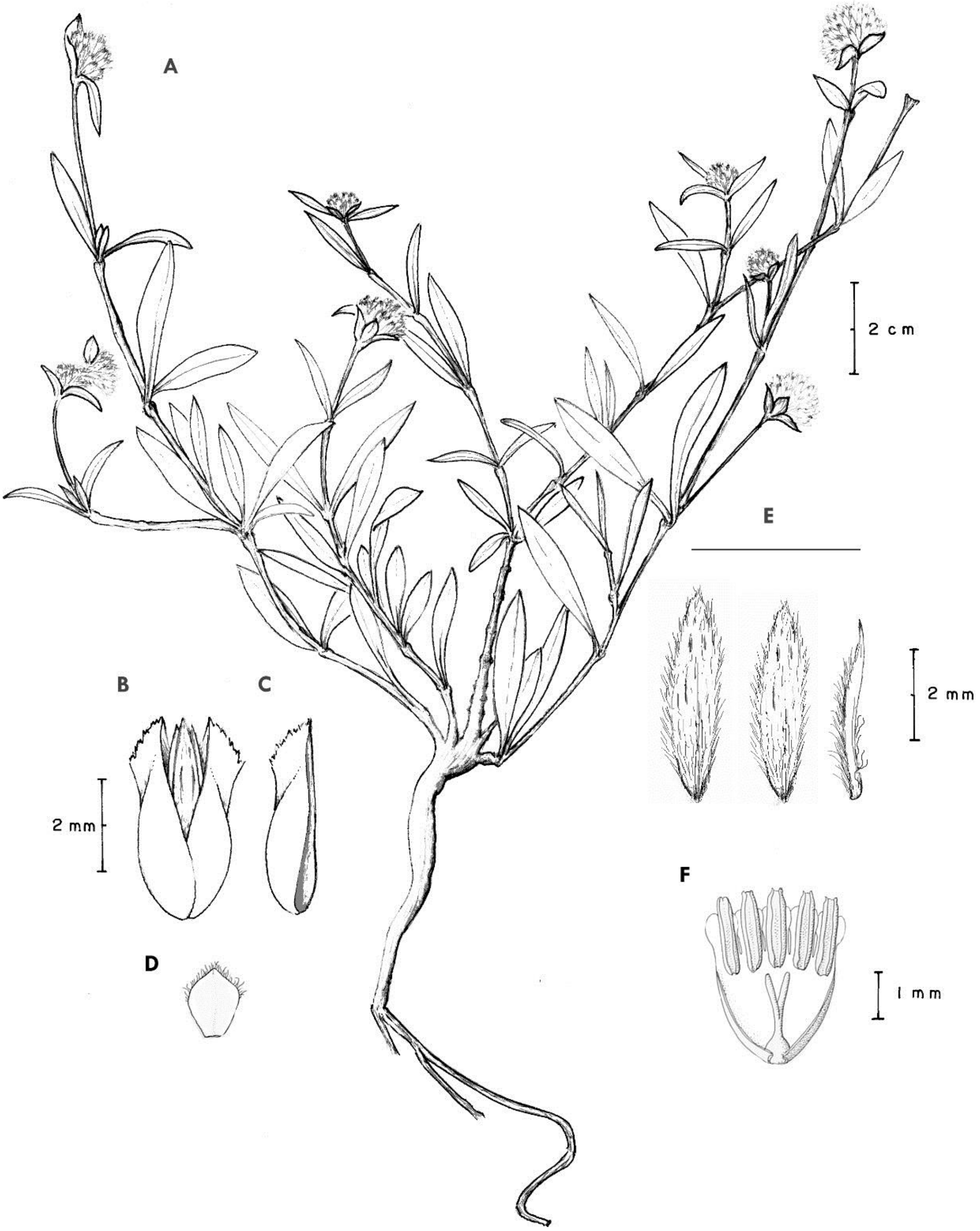


Fig.4-64. *Gomphena stellata* T. Ortuño & Borsch. A) Habit. B) Flowers. C). Bracteoles. D) Bract E) Tepals. F) Detail of the androecium with anther appearing between the filament appendages. [Wood, Carretero & Mercado 19600 (LPB, USZ , B, K)].

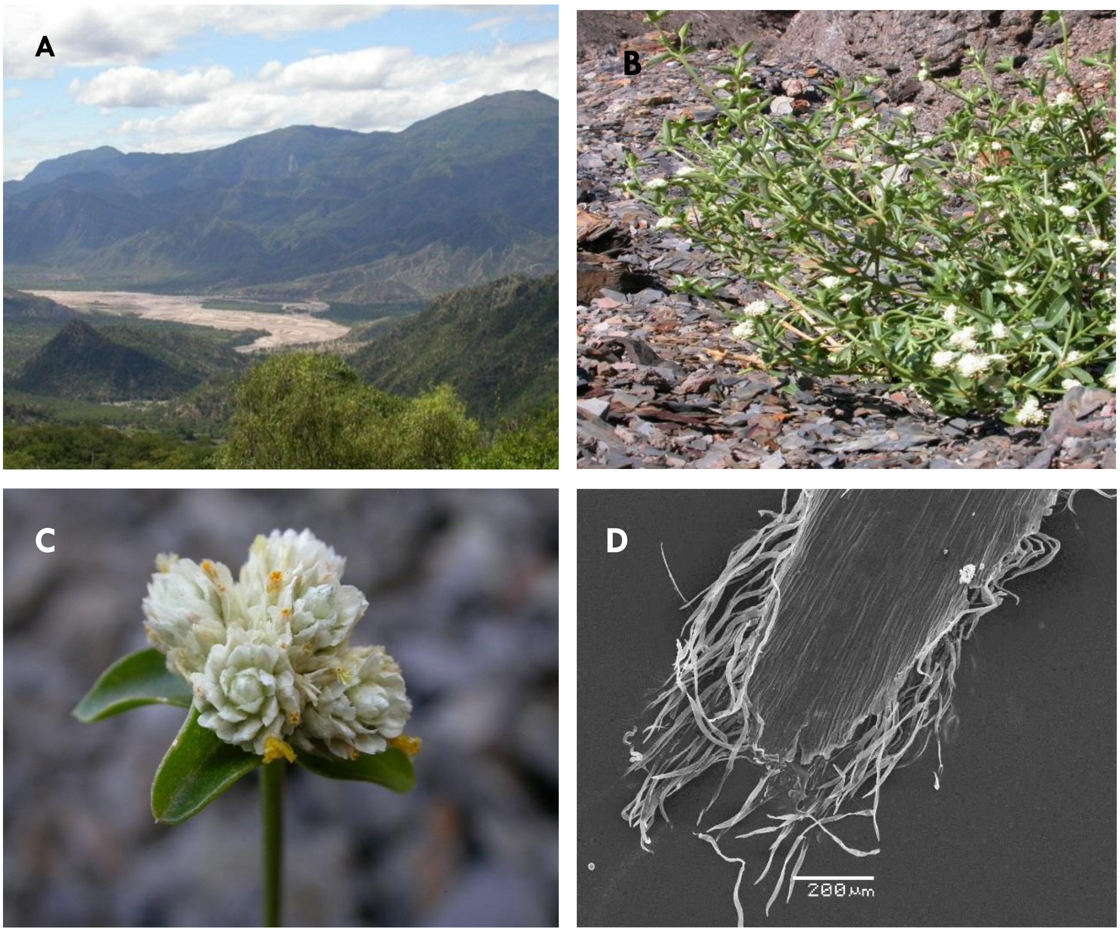


Fig. 4-65. *Gomphrena stellata* Ortuño & Borsch. A) Rio Grande, Chuquisaca. Photo Loza, N. B) Habit of the plants. C) Detail of the inflorescence with the apical leaves subtented inflorescence mucronate. Photos: Wood, J.R. D) Detail of the tepals apex with trichomes.

Habitat and ecology. This species is growing in the Chaco Serrano or dry valley ecoregion. This area has close relations with the Cerrado and paranense sharing many species, and the vegetation is characterized by the presence of xeric elements much of them spiny species of trees and Cactaceae such as *Schinopsis marginata* Engl., *Cardenasiodendron brachyosterum* (Loes.) F.A. Barkley, *Espostoa guentheri,* etc. This ecoregion belongs to the Central Andes, which were upraised during the Andean uplift in the Tertiary. These dry valleys constitute ecosystems of high plant diversity and endemism due to their isolation. In the dry valley system of the Río Grande, a number of endemic species occur such as *Salvia graciliramulosa* Epling & Játiva (*Lamiaceae*), *Espostoa guentheri* (Kupper) Buxb. (*Cactaceae*), *Funastrum rupicola* Goyder, (*Apocynaceae*) and *Myrocarpus emarginatus* A. L. B. Sartori & A. M. G. Azevedo (*Leguminosae*), (Navarro et al. 2002). However, looking at the distribution of *G. stellata* in the Chaco Serrano ecoregion, it is likely that the new species is restricted to the Río Grande valley system, where the plant has been collected between 1100-1400 m. Currently this species is cataloged as EN in the "Red book of the flora of Bolivia- Andean zone" [Ortuño, T., et al. 2012].

Distribution. Endemic to Bolivia. Province of Vallegrande (Dept. Santa Cruz). Province Belisario Boeto (Dept. Chuquisaca) (see Fig. 4- 71).

Specimens examined for distribution assessment. ***Bolivia, Santa Cruz, Vallegrande*** 1 Km arriba al E del puente de Santa Rosa en el camino a Pucara, [64°17,59', 18°42,49'], 1185 m, 6, 3, 2005, *Wood, J.R.I, 21808,* (USZ, LPB). Pueblo de Guadalupe, ca. 5,5 km de la represa, hacia los cerros pasando por la estancia Collamarca a la cima, [-64,110833, -18,566389], 226 m, 1, 18, 1, 2003, Mendoza, M, 431, (USZ). ***Chuquisaca, Boeto,*** 51.5 Km en el camino de Serrano hacia Valle Grande, pasando la comunidad de Nuevo mundo,[-64,305458, -18,850778], 1394, 3, 4, 2003, *Wood, J.R.I, 19600*, (HSB).

4.3.7.7. *Gomphrena fuscipellita* Ortuño & Borsch, Novon 15(1): 183–187. 2005.

Type: Bolivia. Cochabamba: Mizque, Tintin, camino de Mizque a Raykampampa, ladera exposición este, con pendiente de 35°, estacionalmente húmeda. 18°09'95" S, 65° 25'98" W, 2870 m, 3 abr. 2003, T. Borsch & T. Ortuño, 3594 (HT: LPB0000446; IT: BOLV, B, K, MO).

Perennial herb 12 (--30) cm. ***Root*** a fleshy taproot, woody. ***Stems*** prostrate to decumbent, secondary and tertiary branches short, light and pale yellowish-green, with dense and long hirsute indumentum of 2-4 mm long trichomes, light brown to yellow in colour. ***Cauline leaves*** ovate to elliptic, 1-2.3 (--2.8) x 0.5-1.5 (--1.8) cm, acute at apex, with densely appressed indumentum on both sides of leaves and hirsute at margin, brown (Fig. 4-66 B). ***Apical leaves subtending paracladia*** (*inflorescence*) 4-5, leaves located symmetrically at the base of each paracladium, ovate to cordate, 0.5-0.8 (--1.3) x 0.3-0.7 (--1) cm, acute at apex, margin entire, densely appressed trichomes on the abaxial leaf side, hirsute in the adaxial and at margin. ***Inflorescence*** globose and terminal, 1-1.4 (--2.5) cm in diameter, consisting of 3-5 partial florescences, white. ***Flowers*** 4-4.6 mm. ***Bracts*** ovate to lanceolate, 2.0 (--2.2) x 0.9 (--1) mm, membranous, white hyaline, acute at apex, margin entire, middle nerve excurrent. ***Bracteoles*** lanceolate, 4-4.9 (--5) x 1.1 mm, membranous white and hyaline, acuminate apex, with prominent middle nerve. The bracteole owns a crest extending for the half of the upper dorsal part, is winged and toothed. Bracteoles longer than the tepals. ***Tepals*** lanceolate, membranous hyaline and white, trichomes on the margin, toothed at the apex. Size unequal, external tepals 4 - 4.2 (--4-6) mm, intermediate tepals 3.9-4.1 (--4.5) mm, inner tepals, 3.8 - 4 (--4.4) mm. ***Filaments*** 3.1- 5 mm, largely fused into a tube, 2.1-4 mm long, free part 1mm long. ***Filament appendages*** conspicuous, 0.5 mm long. ***Anthers*** oblong, 1-1.4 mm long, positioned between the free lobes of the filament appendages. ***Gynoecium*** with 2 filiform branches, stigma of 1.1 mm, style 0.7 mm, ovary subglobose 0.5 mm. [voucher Borsch, T. & Ortuño, T. 3594 = AC138 (LPB, B, K, BOLV)].

Micromorphology of trichomes. Multicellular, uniseriate: On ***stems and cauline leaves*** with 1-2 flat basal cells, the first rounded, the second straight, the 4-6 upper cells of firm consistence, salicose to scarcely spinous in ornamentation, striate cuticule wall, ***interlocking junctions*** conspicuous, linear scars or projections of the extreme border cells small spines, zero angle degree overlapping; on ***apical leaves subtending paracladia*** on adaxial side with 2-3 thin, long cells, scarcely spinous or without ornamentation, cuticule walls flat, on abaxial side of leaf with large trichomes of 3-6 firm cells, similar than on cauline leaves and stems; on ***tepals*** with large trichomes with firm basal cells and collapsed upper cells. ***Anatomy of tepals.*** Tissue composed by elongate, strait, cylindrical dermal cells, arranged in one row, the extremes fitting perfectly [voucher: Borsch & Ortuño 3594].

Pollen. Spheroidal, 14.4--16.0 µm in diameter, number of apertures 34-44. Structure metareticulate, mesoporia in hexagonal, heptagonal, and pentagonal meshes, with prominent, aristate corners, tectum only in the distal parts and reduced in the vertical parts, columellae free; in transverse view the tectum with a thin triangular shape ending in a sharp point, 3 times higher than the columellae. [voucher: Borsch & Ortuño 3594].

Taxonomic remark. The phylogenetic analysis of the ITS marker shows that *G. fuscipellita* is included in among the perennial species of the Mostly Andean Clade B. The chloroplastidial tree (*matK-trnK*) is less resolved than the ITS tree, grouping all this species in a clade (1PP, 84BS, 95JK) that is internally not resolved, and including *G. fuscipellita*, *G. pallida*, *G. mizqueensis*, *G. oligocephala* (1PP, 100BS, 100JK; see chapter 3). The morphological characteristics of *G. fuscipellita* are the hirsute indumentum, the colour and density of trichomes in the stems and leaves, the prostrate stems, which are divided dichotomously, and finally the position of the anther on a mostly fused filament tube between two filament appendices.

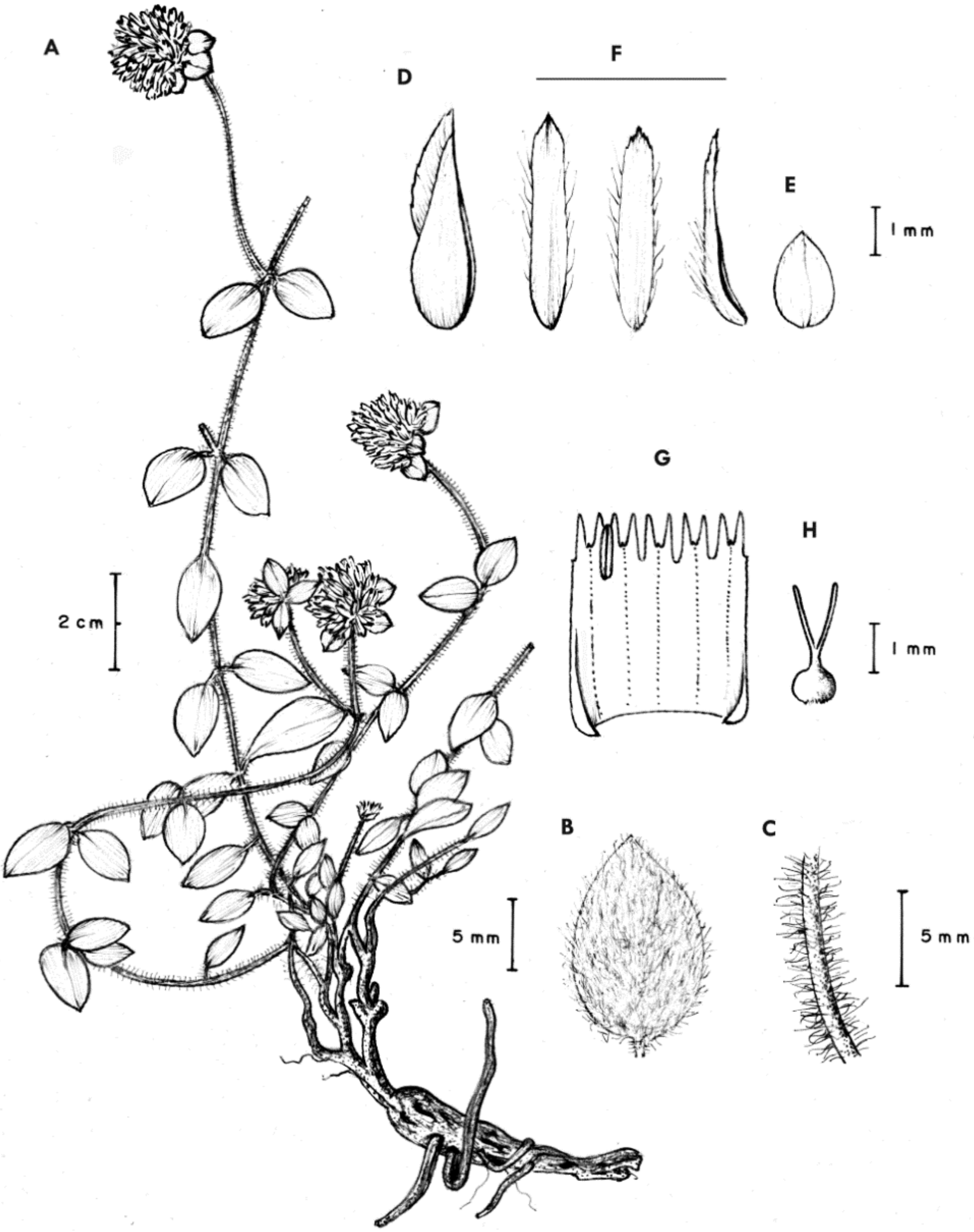


Fig. 4-66. *Gomphrena fuscipellita* Ortuño & Borsch. A) Habit. B) Detail of hirsute indumentum of leaves C) Hirsute indument of stems, D) Bracteoles, E) Tepals. F) Bract. G) Detail of androecium, with the anther inserted between two filament appendices. H) Gynoecium [voucher: Borsch & Ortuño 3594].

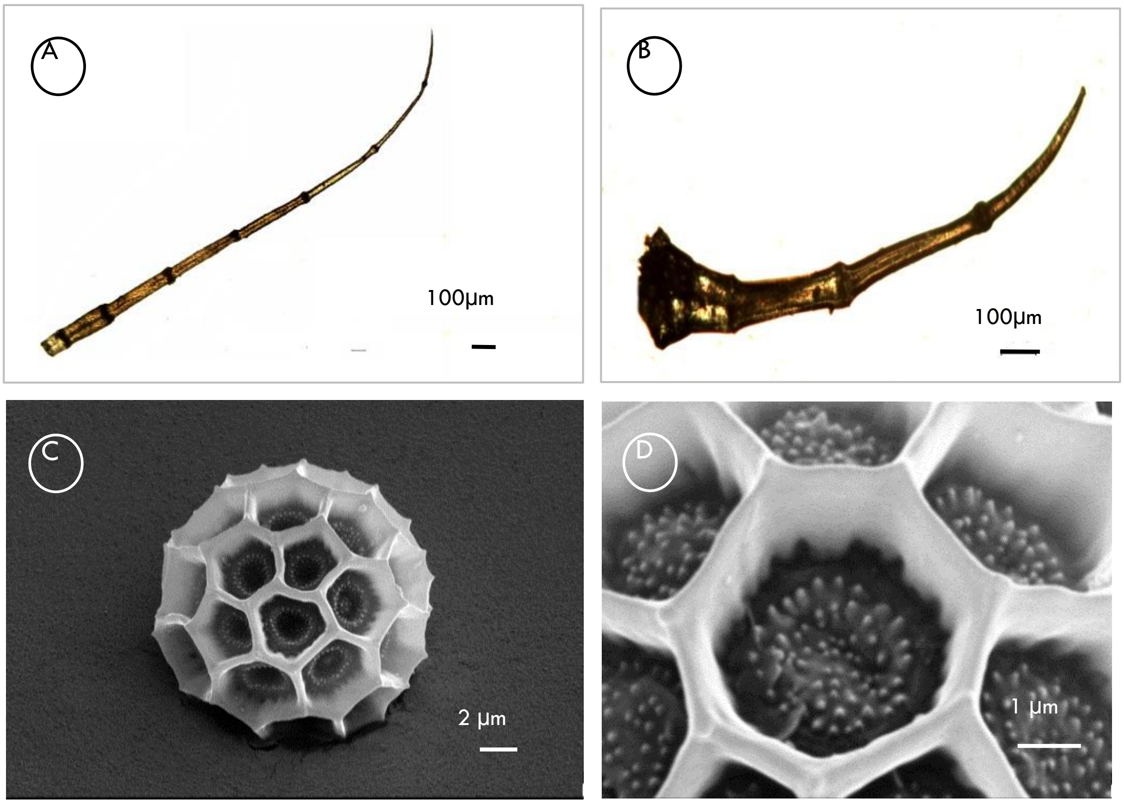


Fig. 4-67. *Gomphrena fuscipellita* Ortuño & Borsch. Trichomes of the apical leaves subtending paracladia. A) From lower part, with more than 4 cells. B) From upper part with 3-4 cells. C) General overview of the pollen. D) Detail of the aperture [voucher: Borsch & Ortuño 3594].

Habitat and ecology. *Gomphrena fuscipellita* grows on eastern slopes, with slopes varying from 25° to 45° above or near rocky outcrops, in soils with shales and slates, which are sandy, somewhat argillaceous and reddish, shallow, slightly acidic and with little organic matter. Sometimes in shrub land with *Dodonaea viscosa* Jack and *Acanthostyles buniifolius* (Hook. ex Arn.) R.M. King & H. Rob. (Tollita), *Croton* spp.. Mostly the vegetation is composed of *Salvia* spp., *Lepechinia* spp., *Baccharis latifolia* (Ruiz & Pav.), *Baccharis tola* Phil., *Jarava ichu* Ruiz & Pav., *Chersodoma* spp., *Puya* spp., and has open places with mosses and lichens as well as ferns *Cheilantes pruinata* Kaulf., *Pellaea ternifolia* (Cav.), and *Sellaginella ssp.*, *Stevia samaipatensis* B.L. Rob. The majority of the reviewed *G. fuscipellita* specimens comes from the transition of the Inter-Andean dry forest, the Semi humid Puna, Tucuman-Bolivian forest, where the plants have been collected between 2280 to 3400 m.

Distribution. Endemic to Bolivia, province of Jaime Zudañez (Dept. Chuquisaca), province Mizque (Dept. Cochabamba), provinces Charcas, Rafael Bustillo (Dept. Potosí), province Aniceto Arce (Dept. Tarija) (see Fig.4- 71).

Specimens examined for distribution assessment. ***Bolivia, Chuquisaca, Jaime Zudañez***, ANMI El Palmar, along road from Presto to El Rodeo., [-64,897778, -18,799167], 2943 m, 1, 2, 2007, *Wood, J.R.I., 22576*, (B). ***Cochabamba, Mizque***, Camino de Mizque a Raykampampa. Subiendo de Tintin a Raykampampa, [-65,3609, -18,111265], 2870 m, 3, 4, 2003, *Borsch, T., 3594*, (LPB, B). Camino Raykapampa a Molinero por el camino viejo, [-65,383332, -18,233332], 2935 m, 4, 4, 2003, *Borsch, T., 3608*, (LPB, B). Raqaypampa, localidad Kollpana, [-65,702731, -18,004308], 2860 m, 10, 4, 1992, *Gutiérrez, E., 57*, (BOLV, LPB). Localidad de Ramadero, [-65,383927, -17,905913], 2280 m, 14, 3, 1994, *Lopez, A., 381*, (BOLV, LPB). Camino de herradura de Molineros hacia Botijas, [-65,43888889, -18,218333], 2700 m, 24, 1, 1994, *Lopez, A., 151*, (BOLV, LPB). Cantón Molinero, Rakaypampa, [-65,371578, -18,2621220], 2792 m, 11, 1, 1987, *Sigle, M., 237*, (LPB). ***Potosí***, **Charcas**, Cerro Manka Paqui, entrando a la quebrada Mula Wacana, [-65,858889, -18,1230559], 3411 m, 27, 2, 2003, *Wood, J.R.I., 19239*, (BOLV). **Chayanta**, Pocoata. Pacotanca ayllu Jilawi y Jila Quellana, [-66,2036669, -18,780306], 3674 m, 4, 2, 2016, *Lliully, A. & Ortuño,T, 2470*, (LPB). **Rafael Bustillo**, Uncía. Localidad Kara kucho. Al lado de la carretera Uncía a Chayanta, [-66,49550, -18,44020], 3891 m, 26, 1, 2016, *Jiménez, I., s/n*, (LPB). Kara kucho. Al lado de la carretera Uncía a Chayanta, [-66,4955, -18,4402], 3891 m, 26, 1, 2016, *Jiménez, I., IJ-7205*, (LPB). Kara kara ayllu Laime/Pucara, [-66,4689439, -18,596806], 3763 m, 25, 1, 2016, *Lliully, A., 2275*, (LPB). Llallagua. Localidad Sencoma ayllu Laime/ Puraca, [-66,5213059, -18,749889], 4288 m, 26, 1, 2016, *Jiménez, I., s/n*, (LPB). ***Tarija***, **Aniceto Arce**, El Carmen, [-64,841389, -22,0294440], 2600 m, 12, 2, 2006, *Zenteno-R, F., 3723*, (LPB).

4.3.7.8. *Gomphrena* to be tested for a separate entity close to *G. fuscipellita* (nov. spec. ?)

Possible type: Bolivia. Potosí, Pocoata, Pocotanga, Jilawi Qullana, 18°46'49.102"; 66°12'13.201", 3074 m, 4. Feb. 2016, 3074 m, Ladera SE-NO, Lluilly, A. & T. Ortuño, 2470 (HT: LPB).

Perennial herb, 3.5 -5 (--7) cm. ***Root*** a fleshy, taproot, woody. ***Stems*** fleshy, 4-7 cm, decumbent to erect, with secondary and tertiary stems, indumentum densely hirsute with trichomes of white to dark brown colour. ***Cauline leaves*** rounded to ovate, 0.5-0.7 (--1.3) x 0.3-0.5 (--0.9), acute at apex, with densely hirsute indumentum on the nerves on both sides of leaves, and hirsute also on the margin. ***Apical leaves subtending paracladia*** *(inflorescence)* 2-5, leaves of different sizes subtending each paracladium, orbicular, cordate to ovocordate, 0.5-0.8 (--1.3) x 0.3-0.7 (--1) cm, rounted at apex, margin entire, densely hirsute on the abaxial nerves and with short trichomes on the adaxial side of leaf or glabrous. ***Inflorescences*** terminal, 0.5 (--1.5) cm in diameter, consisting of 1-5 partial florescences, white. ***Flowers*** 4-4.2 mm. ***Bracts*** ovate to lanceolate, 2.2 x1.5 mm, membranous to white hyaline, acute at apex, margin entire, middle nerve excurrent. ***Bracteoles*** lanceolate, 4 mm, membranous to hyaline, white, acuminate at apex. The bracteole owns a crest located in about one third of the upper distal dorsal part, which is winged and toothed. Bracteoles smaller than the tepals. ***Tepals*** ovolanceolate, membranous to hyaline and white, toothed at the apex, trichomes short at margin and the dorsal part of the inner tepals. (Fig. 68D) Size unequal, external tepals 4.2 mm, intermediate tepals 4.1 mm, inner 4 mm. ***Filaments*** 2.2 mm, largely fused into a tube, fused part 1.6 mm long (Fig. 4-68E), free part 0.6 mm long. ***Filament appendages*** conspicuous, 0.4 mm long lanceolate, free part below 0.2 mm. ***Anthers*** oblong, 1-1.4 mm long, positioned between the free of the filament appendages. ***Gynoecium*** with 2 filiform stigma branches of 1 mm, style 0.6 mm, ovary subglobose 0.4 mm. [voucher: Lluilly & Ortuño, 2470 (LPB)].

Micromorphology of trichomes. Multicellular, uniseriate. On ***stems and cauline leaves*** with 1-2 basal cells, the first rounded the second straight, and 4-6 upper cells of firm consistence, spinous ornamentation and striated cuticule walls, ***interlocking junctions*** conspicuous, linear scars or projections of the extreme border cells (as spines) zero angle degrees overlapping; on ***apical leaves subtending paracladia*** on adaxial side with thin 2-3 long cells, without ornamentation, and flat cuticule walls, on abaxial side of leaf with large trichomes with 3-6 firm cells, similar than on cauline leaves and stems; on ***tepals*** trichomes large, with firm basal cells and collapsed upper cells. ***Anatomy of tepals.*** Tissue composed by elongate straight, cylindrical dermal cells, arranged in one row, the extremes fitting perfectly [voucher: Huaylla 3653]

Taxonomic remark. *Gomphrena fuscipellita* was described based on a specimen from Inter Andean dry valley (ca. 1500-300 m; Ortuño and Borsch, 2005). During the last years the number of collections of similar plants has been increasing on much high altitudes (3600-4200 m), and the plants appear a bit different (*Gomphrena sp. nov. (fusci2)??*) from the dry valley populations because they are in smaller size, the trichomes are darker, the shape of cauline leaves and apical leaves subtending the paracladia is more cordate or subcordate. Also the tepals have short trichomes on the margin but only few on the basal part, dense on the inner tepals. The question is if these are just habitat modifications as a consequence of the environmental conditions at higher altitudes or genetically different populations that belong to a different species. It will be important to include these specimens from higher altitudes into the molecular phylogenetic analyses.

Habitat and ecology. Occurs on steep slopes (45^a) with rock outcrops, with eroded soil, or soil with high percentage of rocks. Plants are often is surrounded by scrubs as *Baccharis tola* Phil., *Adesmia spinosissima* Meyen ex Vogel, and grasses as *Jarava ichu* Ruiz & Pav. or *Festuca orthophylla* Pilg. The ecoregion is the Semi humid Puna, where the plants have been collected between 3600-4300 m.

Distribution. Endemic to Bolivia, province of Charcas, Colquechaca and Pocoata (Dept. Potosí), province of Challapata, locality of Qaaqchaca and Wankarani (Dept. Oruro) (see Fig. 4-71).

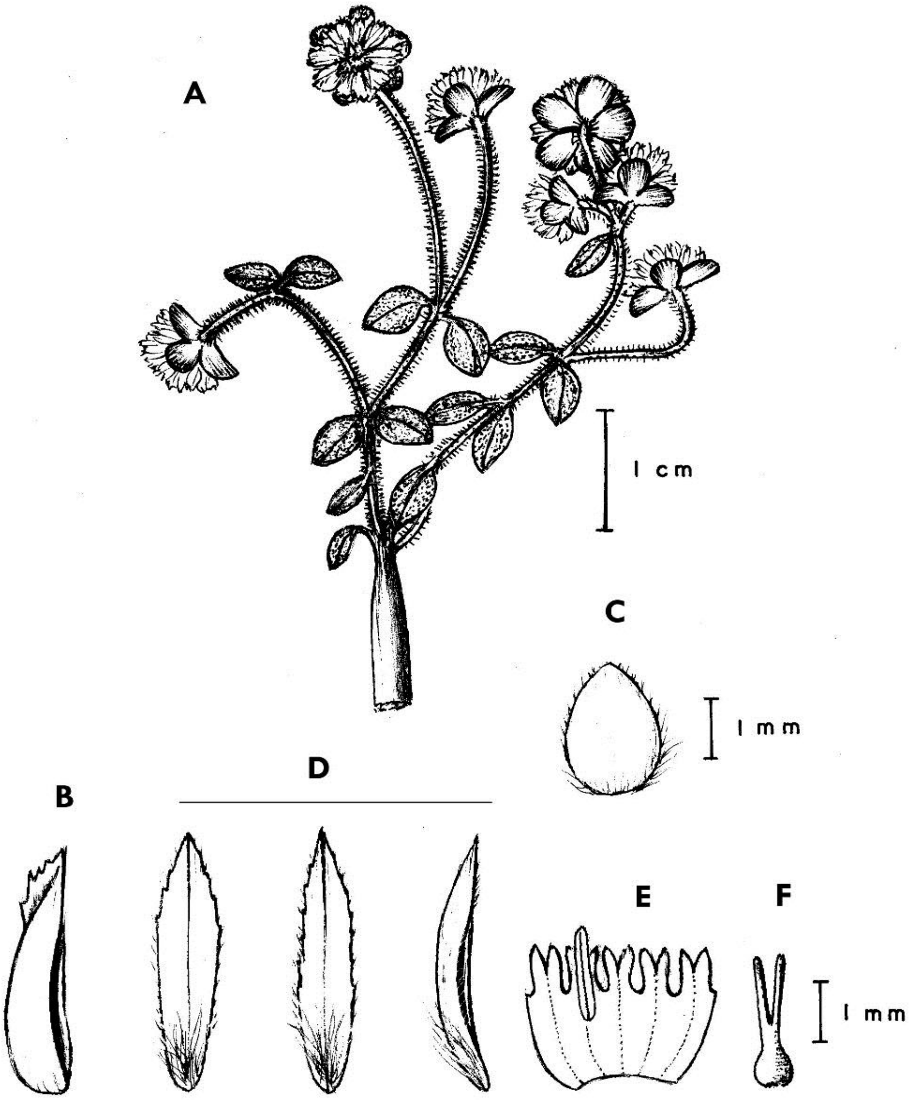


Fig. 4-68. *Gomphrena sp. nov. (fuscipellita 2)*. A) Habit. B) Bracteoles. C) Tepals. D) Bract. E) Detail of the androecium. F) Gynoecium [voucher: Lliully & Ortuño 2470].

Specimens examined for distribution assessment. ***Bolivia***. ***Potosí***, ***Charcas***, *Toro Toro*, [-65,8413888, -18,13138889], 3625 m, 17, 12, 2011, *Ortuño, T., 1670*, (LPB). Ciudad del Ita [-65,8413888, -18,13138889] 3625 m, 17, 12, 2011, *Ortuño, T., 1663*, (LPB). Ciudad del Ita, [-65,8413888, -18,13138889], 3625 m, 17, 12, 2011, *Ortuño, T., 1664*, (LPB). Ciudad del Ita, [-65,8413888, -18,13138889], 3625 m, 17, 12, 2011, *Ortuño, T., 1665*, (LPB). Ciudad del Ita, [-65,8413888, -18,13138889], 3625 m, 17, 12, 2011, *Ortuño, T., 1666*, (LPB). Ciudad del Ita, [-65,8413888, -18,13138889], 3625 m, 17, 12, 2011, *Ortuño, T., 1667*, (LPB).

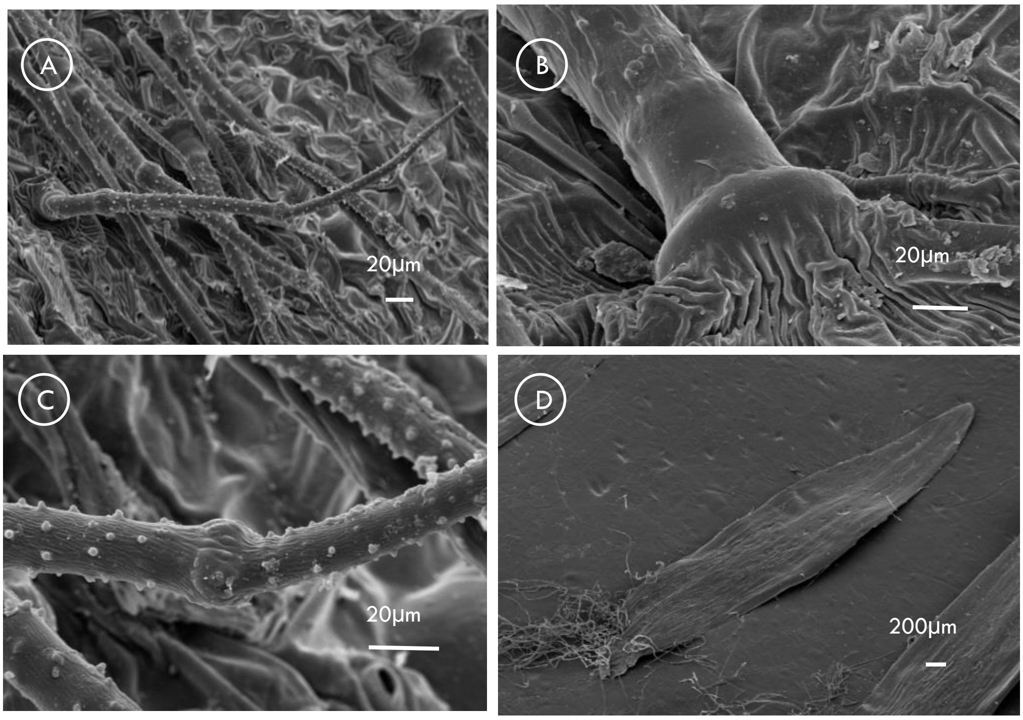


Fig. 4-69. *Gomphrena sp. nov. (fusci2)*. *A*) Densely appressed trichomes at apex of leaves. Trichomes: B) Detail of the basal cells. C) Detail of the interlocking junctions. Tepals. D) Overview of the tepal with lanate trichomes in the basal part, tepals otherwise glabrous.

Ciudad del Ita, [-65,50289, -18,075340], 3625 m, 17, 12, 2011, *Ortuño, T., 1668*, (LPB). Ciudad del Ita, [-65,7189, -18,219], 3625 m, 17, 12, 2011, *Ortuño, T., 1669*, (LPB). Vila Kasa camino hacia San Pedro, [-65,841389, -18,1313889], 3625 m, 29, 1, 2012, *Huaylla, H., 3646*, (LPB). Vila Kasa camino hacia San Pedro, [-65,841389, -18,131388], 3625 m, 29, 1, 2012, *Huaylla, H., 3647*, (LPB). VilaKasa camino hacia San Pedro, [-65,851249, -18,125278], 3650 m, 29, 1, 2012, *Huaylla, H., 3653*, (LPB). **Colquechaca**, Sarijchi a Colquechaca, Suni medio Jatun Ayllu Pocoata, [-65.9124479, -18.624], 4356 m., 1, 3, 2016. *Zenteno, F. 16345* (LPB). **Pocoata**, Jilawi y Jila Qullana, Chaupiraña superior, [-66.203667,-18.78], 3674 m. 4, 2, 2016. *Lliully, A. & Ortuño 2470* (LPB). Uncia, Kara Kara, Suni inferior, [-66.420349,-18.46], 4800 m. 26, 1, 2016. *Zenteno, 16115* (LPB). ***Oruro***, ***Challapata***, Cuchini Chaupiraña superior, Qaaqchaca, [-66420349, -1878], 3900m 5, 3, 2016, *Zenteno, 17221* (LPB). Chaupiraña superior, [-66420349, -1878], 3900m, 5, 3, 2016, *Zenteno, 17224* (LPB). Challapata, Wankarani, [-66.449258, -187093], 3900 m, 1, 3, 2016. *Zenteno*, *16943* (LPB).

Fig. 4-70. *Gomphrena sp. nov. (fusci2*). A) Habitat in Potosí, camino de Sarijchi a Colquechaca, Pocoata. Voucher: Zenteno 16345 B) Detail of the decumbent to erect stems habit. C) Inflorescence with orbicular to cordate asymmetrical apical leaves subtending the paracladia [Voucher Zenteno 16345]. D) Specimens from Potosi, Charcas growing on the rock outcrops, [voucher: Huaylla 3653].

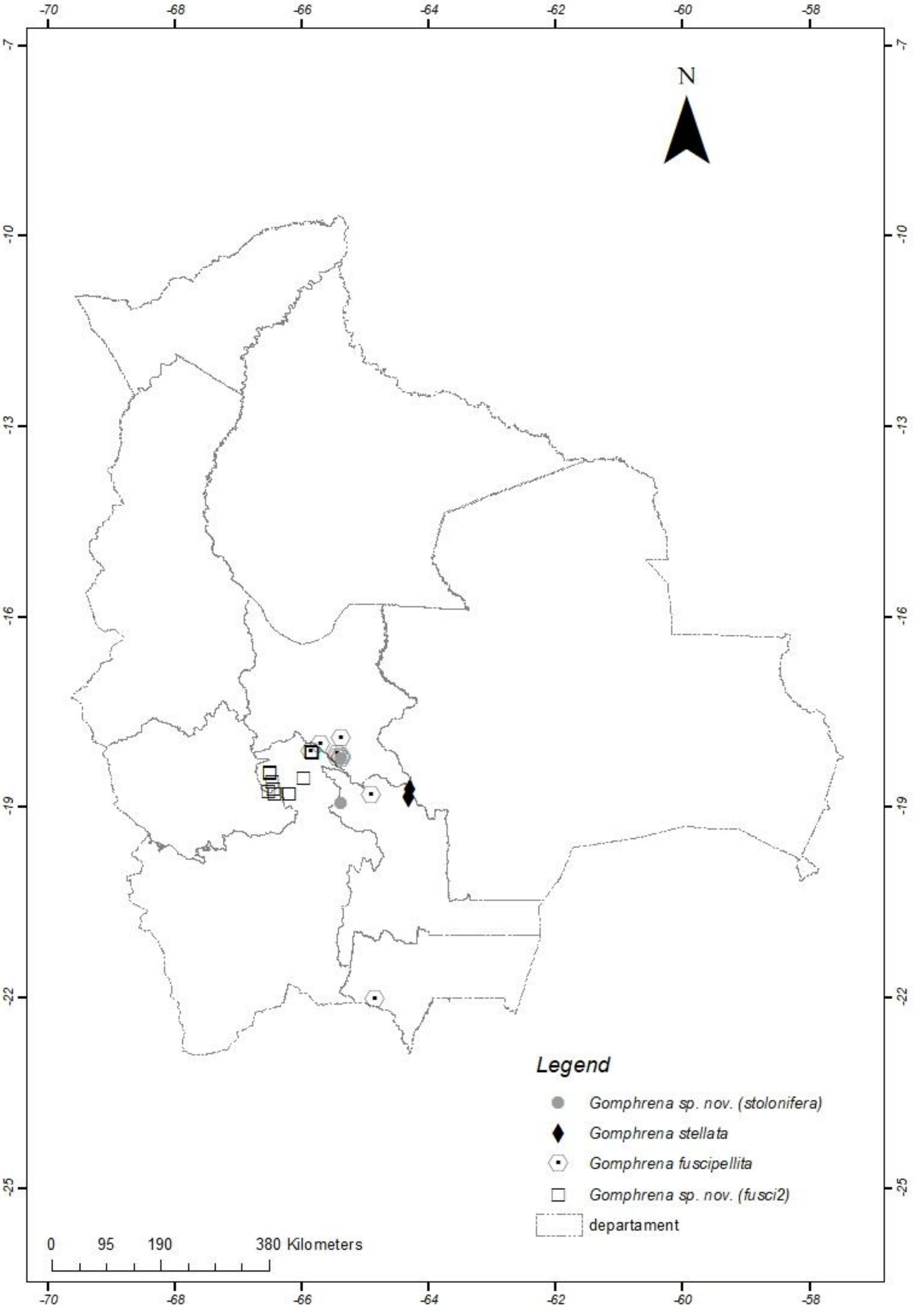


Fig. 4-71. Maps of group the species the perennials G. pallida clade: *G. fuscipellita*, *G. stellata*, *G. sp. nov.* (stolonifera), *G. sp. nov.* (fusci 2).

4.3.8. Gomphrena meyeniana CLADE

The phylogenetic analyses show that *G. meyeniana* and allies are monophyletic with high support from the nuclear (ITS; 1PP, 100JK) and plastidial markers (*matK*-*trnK*) and (1.00 PP, 100 BS, 100JK; see chapter 3). However, in both trees the Gomphrena meyeniana clade is internally poorly resolved. There is a bit more resolution in ITS but node support values are very low. Also, as observed in the pherograms of ITS, there were multiple copies with many polymorphic sites indicating hybridization. Therefore, the molecular data that are available in this thesis do not yet support any conclusion on species limits in the *G. meyeniana* clade. To clarify and arrive to a consistent conclusion, it is necessary to do deeper studies including population genetics.

The treatment here is based on the comparison of morphological characters. What is clear is that there is a morphological separation between the specimens that present leaves on the stem and those that do not, which correspond to the varieties of G. *meyeniana* var. *flaccida* and G. *meyeniana* var. *meyeniana,* respectively. Here the varieties published in Pedersen (1990) are simply used. However, deeper studies may show a clearer separation at different levels of species.

The species *Gomphrena meyeniana* has been historically treated to include several varieties based on comparison of morphological characters realized by other authors (Stuchlik´s, 1913; Sussenguth, 1934; Holzhammer, 1956; Pedersen, 1976). The most recent key was published by Pedersen (1990), which appears to be consistent with the variation observed in the Bolivian and apparently clear differences between the varieties. In the key provided here, some of the characters used also Pedersen (1990) are used, but these are complemented by other features or defined a bit differently (shapes etc.) to be coherent with characters observed in the examination of the specimens (see below). An Important remark is that there are apparently no differences in the trichomes between the species or varieties, other than among *G. pallida* and relatives, for example.

To clarify this pattern of differences, it is necessary to revise a major set of samples from Peru, Chile and Argentina. However, the species is mainly distributed in the Andes of Bolivia. Currently, there is an important data set of samples of this species housed at different herbaria from Bolivia (LPB, BOLV, USZ), which is useful to have a better idea about this taxon, and to better understand how the numerous mountain may act as barriers, and altitudinal gradients (including the climate) could have influenced the variation of some characters.

Key to Gomphrena meyeniana CLADE

1. Terminal inflorescence on stems without cauline leaves (2).

2. Tepals all glabrous ……………………………..……*G. meyeniana var. meyeniana* (Fig. 4-72)

2'.Tepals with indumentum in the dorsal part (3)

3. All the tepals with lanate indumentum in dorsal part ……………..….G. *meyeniana* var. *genuina*

3'. Only the inner tepals with indumentum in the dorsal part ……..…..G-*meyeniana* var. *conwayi*

1'. Terminal inflorescence on stems with cauline leaves. Tepals all with indumentum in the dorsal part in all the tepals or only in the inner (4)

4. Stems decumbent to ascendant, flaccid, cauline leaves ovolanceolate
…………….……………………………………………*G. meyeniana* var. *flaccida* (Fig. 4- 72)

5. Only the inner tepals with indumentum in the dorsal part.
……………………………………………………………...*G. meyeniana var. levitepala* (Fig. 4- 76)

4'. Stems erect, firm consistence, cauline leaves lanceolate to lineal
………………………………………………………………*G- meyeniana caulecent* (Fig. 4-77)

4.3.8.1. *Gomphrena meyeniana* Walp., Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19 (Suppl. 1): 404. 1843.

Type: Peru, in planitie circa Tissaloman, 4572 m. Laguna de Titicaca, FL Apriili. IV, 1831, Meyen s/n (LT: B100673185, ITLT: F F0BN00325). Lectotype designated by Bena 2017.

≡ *Gomphrena meyeniana* var. *aureiflora* Stuchl., Beih. Bot. Centralbl., Abt. 2. 30(2): 406. 1913 Fedde, Rep. Spec. Nov. 12: 521. 1913.-Argentina (GCI)

= *Gomphrena acaulis* Remy., Ann. Sci. Nat., Bot. ser. 3, 6 (3): 350. 1846. Type: Bolivia, Coteaux des monts de los Laguna de Potosí, Orbigny, A. d' 1479 (HT: P P006 23703, IT P00623705).

Perennial herb. ***Root*** a fleshy, woody taproot. ***Stems*** *acaule* 4-5 (-8) cm long, the acaule stems develop near the surface, are covered with many large uniseriate trichomes protecting the buds, in the lateral part with adventitious roots that help to fix the plant in the soil, stems red to green, with densely lanate trichomes, 1-3 mm long, white. ***Basal leaves*** ovolanceolate, in rosettes, 1.5- 2.5 (--3) x 0.3-0.5(--0.8) cm, acute at apex, 2.5-3.5 cm, petiolate, decurrent, trichomes similar to the stems, colour white or light brown. ***Cauline leaves*** absent (Fig.4-72A). ***Apical leaves subtending paracladia*** (inflorescences) 5-6, leaves arranged symmetrically, ovolanceolate, 0.5-1 x 0.3-0.4 cm, acute at apex, green-olive, dense indumentum on the abaxial side of the leaf and on the margin (similar to the stems), glabrous on the adaxial side of leaf, white in colour. ***Inflorescences*** globose, terminal, 0.9-1.4 (--2.5) cm in diameter, consisting of 1-5 partial florescences. ***Flowers*** 4.5 (--5) mm long. ***Bracts*** ovate-lanceolate, 1.8 (--2.5) x 1.5 (--2) mm, membranous in texture, translucent white or light brown, acute at apex, dentate in the margin.

Bracteoles ovate-lanceolate, 3.8 (--4) x 2 mm, membranous, light yellow, rounded to acute at apex, tepals bigger than the bracteoles. ***Tepals*** spatulate to lanceolate, membranous in texture, white or light yellow, rounded at apex, few teeth at the apex, tepals glabrous (Fig. 4-472). Size unequal, external tepals 6.0 x1-1.3 mm, intermediate tepal 5.9 x1-1.3 mm, inner tepals 5.8 x 0.6 mm. ***Filaments*** 4 (--4.6 mm) mm long, mostly fused into a 3.8-4.2 mm long tube, yellow, free part 0.4 mm long, broad and abruptly obtuse terminally. ***Filament appendages*** lacking. ***Anthers*** oblong, 1 mm long. ***Gynoecium*** with two filiform stigma branches, of 0.8 mm length, style 0.4 mm, ovary 0.8-1 mm, one ovule [voucher: Borsch & Ortuño, 3954 = AC785].

Micromorphology of trichomes. Multicellular, uniseriate. On ***stems and cauline leaves*** firm, smooth and without ornamentations, striate, with 1-2 basal cells, 4-6 upper cells cells firm to collapsed or flexible, striate cuticule walls. ***Interlocking junctions*** conspicuous, linear, scars arranged in parallel to the trichomes, zero degrees overlapping; on ***apical leaves subtending paracladia*** similar than on the stems; on ***tepals*** in dorsal part, 2(--3) mm, firm, rounded shape in the 1-2 basal cells, the upper cells with collapsed cells, flexible, without ornamentation, flat in sculpture, and interlocking junctions simple, glabrous. [voucher: Borsch & Ortuño 3955= AC449].

Taxonomic remark. According to Pedersen (1990), *Gomphrena meyeniana* is an extremely variable species. Following the key built by Pedersen (1990), and testing the possibility to use it to distinguish some varieties (also observed in field work), the morphological characters observed seem to fit. Important are different patterns based on the presence or absence and disposition of cauline leaves, and the indumentum of the tepals. The principal characteristics of G. *meyeniana* var. *meyeniana* are the leaves that grow directly from the node, without stems and that all the tepals are glabrous.

Habitat and ecology. Occurs in high mountain peaks with steep rock falls below cliffs, on steep stony open slopes or hillsides, sometimes on open places or protected near rock or among other plants. Often together with small herbs, grasses (e.g. *Jarava ichu* Ruiz & Pav) and shrubs (e.g. *Baccharis boliviensis* (Wedd.) Cabrera) or among *Polylepis* ssp. trees. This taxon is found in a wide latitudinal range in the wet (or humid) Puna, Semi humid Puna, High Andean vegetation from Cordillera Oriental, nival and subnival floors, Dry Puna, Desertic Puna regions where the plants are collected between 3400 - 4800 m.

Distribution. Occurs in Northern Argentina: provinces of Catamarca, Jujuy, Salta. Perú: Cuzco, Puno, Tacna. Chile: Tarapacá. Bolivia: Prov. Jaime Zudañez (Dept. Chuquisaca), provinces of Cercado, Arque, Ayopaya, Mizque, Quillacollo, Tapacarí (.Dept. Cochabamba). Provinces of Rafael Bustillo, Tomas Frías, Sud Chichas (Dept. Potosí). Provinces of. Eduardo Avaroa, Ladislao Cabrera, Sajama, (Dept. Oruro), Provinces of Prov. Cercado (Dept. Cochabamba). Murillo, Aroma, Bautista Saavedra, Ingavi, Loayza, Los Andes, Omasuyos, Pacajes (Dept La Paz) (see Fig. 4-79).

Specimens examined for distribution assessment. ***Argentina, Catamarca***, Andalgalá, Común La Hoyada, [-66,4, -27,3667], 3100 m, 20, 2, 1916, *Jörgensen, P., 1106*, (DB_Tropicos). Minas Capillitas, Refugio del Minero. [-66,389, -27,3825], 3050 m, 16, 2, 2010, *Zuloaga, F.O., 11900*, (SI). ***Jujuy,*** Humahuaca, 22 km de Humahuaca hacia Palca de Asparazo, [-65,149825, -23,165075], 3900 m, *Hunziker, J., 10413*, (SI). Tilcara, Quebrada de Guasamayo, [-66,40, -27,3667], 2600 m, 13, 2, 1980, *Cabrera, A.L., 273*, (DB_Tropicos).

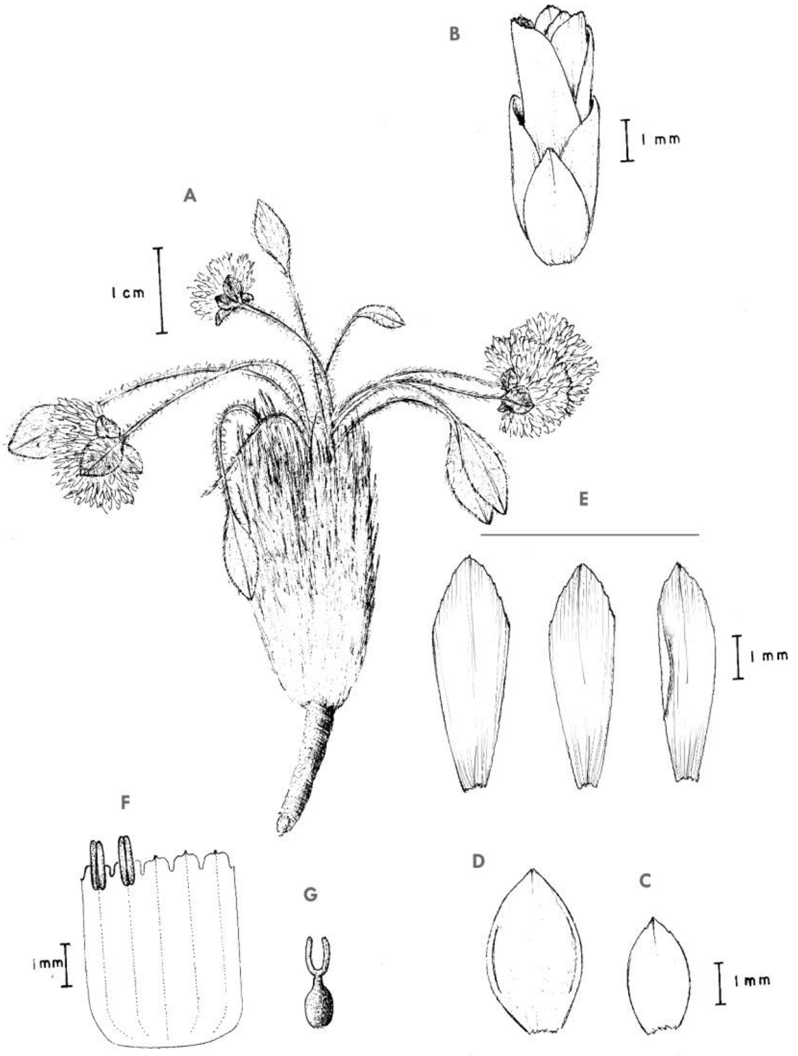


Fig. 4-72. *G. meyeniana* Walp., all the tepals glabrous. A) Habit. B) Flowers. C) Bract. D) Bracteoles. E) Tepals. F) Detail of the androecium. G) Gynoecium [voucher: Borsch & Ortuño 3954 = AC785]

Quebrada de Ventura, [-65,36, -23,5667], 3221 m, *Cabrera, A.L., 13995*, (LPB, Tropicos).

Yavi. Camino de Yavi a Santa Victoria, [-65.2821666667, -22.2193], 3934 m, 4, 4, 2004, *Borsch, T., 3726*, (LPB, B). ***Bolivia, Chuquisaca, Jaime Zudañez***, 1-2 km west of highest point on road from Icla to Azurduy crossing cordillera de los Sombreros, [-64,6380, -19,56], 3900 m, 14, 12, 2002, *Wood, J.R.I., 18632*, (LPB). ***Cochabamba, Tiraque,*** sobre el camino a kaspicancha a

Santa Rosa, [-65,66666, -17,38], 4011 m, 16, 3, 2004, *Wood, J.R.I., 20424*, (LPB). ***Arque***, 6 km E de Challa (camino). 10° SE, [-66,5994443, -17,723], 4240 m, 31, 3, 1979, *Beck, S.G., 969*, (LPB). ***Ayopaya***, Independencia 28 Km hacia Kami, [-66,805313, -17,208546], 3650 m, 11, 5, 1988, *Beck, S.G., 14617*, (LPB, LL, CTES). Villuni, Independencia, [-66,8127180, -17,347317], 3935 m, 31, 1, 2006, *Quisbert, H, 4*, (BOLV, LPB). Bosque abierto de *Polylepis*, Sapanani alto, Pacha Wasa, [-66,075556, -17,33416], 3900 m, 7, 4, 1991, *Hensen, I., 2322*, (LPB). ***Chapare***, Parque Tunari, [-66,145,- 17.3172222], 3700 m, 23, 3, 1991, *Hensen, I., 990*, (LPB). ***Quillacollo***, camino Sipe-Sipe a Kami cuenca del valle de Cochabamba, [-66,487778 -17,4416667], 3800 m, 23, 4, 1989, *Beck, S.G., 18053*, (LPB, SI). Camino Sipe-Sipe - Lipichi, [-66,484444, -17,4444], 3800 m, 29, 1, 1990, *Hensen, I., 525*, (LPB). On road from Quillacollo to Cerro Tunari, [-66,3405, -17,2683], 3900 m, 27, 1, 1996, *Wood, J.R.I., 10474*, (LPB). Pasando la comunidad de San Miguel, [-66,332, -17,271417], 3989 m, 13, 1, 2012, *Huaylla, H., 3627*, (LPB). ***Tapacarí***, Comunidad de Japo (Km 125 Cbba-Oruro), Jacha Kaima Irana, [-66,76, -17,692778], 4200 m, 21, 3, 1996, *Pestalozzi, H.U., 854*, (LPB). Caluyo, al lado del cerco, al E de Japo K'asa (km 125 en la carretera Cbba-Oruro), [-66,775, -17,68], 4160 m, 24, 1, 1995, *Pestalozzi, H.U., 267*, (LPB). Phia kala, Aynoka de quinua, 3 km al E de Japo K'asa (km 125 enla carretera Cbba-Oruro), [-66,775, -17,68], 4200 m, 25, 1, 1995, *Pestalozzi, H.U., 301*, (LPB). Camino de La Paz a Cochabamba, cerca a la Comunidad "Japo", [-66,783388, -17,701104], 4266 m, 9, 3, 2009, *Borsch, T., 3952*, (LPB, B). Camino de La Paz a Cochabamba, cerca a la Comunidad "Japo", [-66,7833, -17,70110], 4266 m, 9, 3, 2009, *Borsch, T., 3953*, (LPB, B). Camino de La Paz a Cochabamba, cerca a la Comunidad "Japo", [-66,783, -17,701104], 4266 m, 9, 3, 2009, *Borsch, T., 3954*, (LPB, B). ***La Paz***, ***Aroma***, Huaraco, [-67,625, -17,3588889], 3900 m, 4, 1, 1982, *Fisel, U., U-113*, (LPB). Taparasi, Comunidad Taparasi, a 40 km de la carretera Oruro - La Paz., [-69,6341667, -17,1419444], 3900 m, 13, 3, 2003, *Muriel, L., 269*, (LPB). ***Franz Tamayo***, Ulla-Ulla. Cerca de la Estación Experimental, [-69,2933, -14,95805], 4410 m, 9, 1, 1983, *Menhofer, X., X-1790*, (LPB, DB_Tropicos). ***Ingavi***, Granja de CORDEPAZ en Huacullani, [-68,7361, -16,4525], 3950 m, 7, 2, 1979, *Beck, S.G., 333*, (LPB). Comunidad Tacaca. Presente en cerro Callejas Grande, [-68,833507, -16,666768], 4500 m, 17, 4, 1988, *Hensen, I., 111*, (LPB). Cantón Jesús de Machaca, comunidad Titicani-Tacaca. A 20 km de Guaqui. Cerro Vilin Pata, [-68,8341, -16,683], 4100 m, 15, 3, 1989, *Villavicencio, L., 132*, (LPB. J). ***Bautista Saavedra***, Amarete, [-68,989722, -15,234444], 3900 m, 4, 2, 1980, *Feuerer, T., 8411e*, (LPB). *Charazani*, Sacanogon, [-68,9941, -15,1768], 24, 3, 1992, *Gutte, P., G 22*, (LPB). ***Loayza***, Municipio de Luribay, comunidad Tumi entrando por la carretera hacia arriba de la comunidad, [-67,719443, -17,151667], 4100 m, 8, 1, 2011, *Beck, S.G., 33453*, (LPB). Municipio de Calroma, Asiento Araca, Cerro Rosario, [-67,54, -16,80], 4000 m, 10, 4, 2004, *Beck, S.G., 29341*, (LPB). Asiento Araca, a 2 km hacia Cairoma, [-67,549, -16,80], 3932 m, 2, 5, 2004, *García, M.C., CR1*, (LPB). Río Jiskha Choque Khota which leads down from Cerro Huatia Khota. Ca. 4 km SE from Viloco, [-67,483, -16,89], 4300 m, 7, 12, 1987, *Lewis, M., 871318*, (MO, LPB). ***Los Andes***, 40 km NO linea recta de La Paz, [-68,3572221, -16,21583], 4280 m, 25, 1, 1981, *Beck, S.G., 4305*, (LPB). Zona Chiripaca-Batallas, del proyecto de riego. Pampa de Karhuiza y alrededores, [-68,5142, -16,28119], 3900 m, 15, 2, 1987, *Beck, S.G., 12869*, (LPB). Hichukkota. Sobre pediente un poco seca por encima de las vegas, [-68,3977778, -16,1983333], 4155 m, 27, 2, 1985, *Ostria, C., 298*, (LPB). ***Manco Kapac***, Copacabana, Lago Titicaca, [-69,083, -16,166667], 3835 m, 2, 2, 1957, *Cañigueral, J., 258*, (LPB). ***Murillo***, Al NO de La Paz, unos 6 km arriba del Lago Challapata, [-68,008055, -16,3919], 4450 m, 28, 12, 1990, *Beck, S.G., 17899*, (LPB). Ca. 15 km al NNE de La Paz. Pie del nevado Chacaltaya, [-68,16861, -16,39166], 4500 m, 27, 3, 1983, *Beck, S.G., 9140*, (LPB). La Paz, Alto, 5 km. Hacia Chacaltaya. 3-5° NO, [-68,1664166, -16,465847], 4200 m, 7, 3, 1980, *Beck, S.G., 2928*, (LPB). La Paz, Calacoto. 17 km hacia el SE por Collana, [-67,98083, -16,62361], 4160 m, 11, 1, 1981, *Beck, S.G., 4296*, (LPB). La Paz, El Alto (tranca), 39 km hacia el SSE, vía Sapahaqui. 40° S, [-68,0602777, -16,8661], 4200 m, 30, 1, 1983, *Beck, S.G., 9109*, (LPB). Calacoto, 60 km hacia el nevado Illimani. Panguyo. 20° N, [-67,8016, -16,6883], 4250 m, 19, 1, 1983, *Beck, S.G., 9088*, (LPB). Chacaltaya, [-68,166685, -16,36939], 4550 m, 2, 3, 1983, *de Avila, D.K., 16*, (LPB). Jacha Toloko aprox. 21 km de la ciudad de La Paz, camino a Yungas, [-68,0166, -16,35], 4600 m, 19, 3, 1987, *Estenssoro, S., 240*, (LPB), Siete lagunas, [-68,13, -16,416667], 4200 m, 22, 2, 1986, *García, E., 770*, (LPB). 2 km de la Tranca de Chuquiaguillo en direccion a los Yungas, en la Serrania Cuchilla Chuquiaguillo, cerca del desarenador de SAMAPA, [-68,0836, -16,440277], 4135 m, 28, 12, 1988, *Liberman, M., 2383*, (LPB). En las nacientes del Valle Hampatur-Irpavi. En los alrededores de la laguna Ajuan-Kkota, [-68,0011, -16,381], 4600 m, 6, 4, 1985, *Liberman, M., 884*, (LPB). Cabecera de valle de La Paz, Putupampa, [-68,00 -16,5167], 4500 m, 7, 1, 1995, *Lopez, R., 105*, (LPB). Ceja El Alto hacia Zongo, [-68,1679, -16,4684], 25, 4, 1985, *Moraes, M., 134*, (LPB). 2.7 km SW of pass at head of Valle del Zongo, [-68,15, -16,30], 4600 m, 15, 3, 1984, *Solomon, J.C., 11794*, (LPB). 4.8 km al noreste del autopista por el camino subiendo el Valle del Río Kaluyo (margen norte de La Paz), [-68,13, -16,41666], 4100 m, 28, 2, 1987, *Solomon, J.C., 16203*, (LPB). Ceja de El Alto, 5.8 km N of the La Paz-Tiquina Road on the road to Milluni, [-68,150, -16,433], 4200 m, 25, 4, 1985, *Solomon, J.C., 13400*, (DB_Tropicos, LPB). Camino a Alto Chacaltaya. Entrando 200m hacia el camino de la Comperativa Minera Kellguani, [-68,15611, -16,432221], 4320 m, 21, 12, 1986, *Valenzuela, E., 903*, (LPB). Pata-Pampa. 2,5 Km del desvio, [-68,088, -16,37249], 4440 m, 21, 12, 1986, *Valenzuela, E., 934*, (LPB). ***Pacajes***, Caquiaviri; cerro 0,5 km E of town, [-68,59, -17,0166], 4250 m, 13, 3, 1983, *Johns, T., 83-118*, (LPB). Vichaya, 2 km E on road to Caquiaviri, [-68,76, -17,1166667], 3800 m, 7, 2, 1983, *Johns, T., 83-36*, (LPB). Caquiaviri, cerro 0.5 km E of town, [-68,59, -17,016667], 4250 m, 13, 3, 1983, *Johns, T.*, 83118, (LPB). ***Oruro***, ***Cercado***, Quilquani, camino de La Paz a Cochabamba, cruce de Quilquani. 1 km a Caihuasi. 17 km al cruce Caracollo, [-67,010, -17,6611], 3900 m, 31, 3, 2003, *Borsch, T., 3557*, (LPB). ***Challapata,*** Tirani, Pucara [-66.33267, -19.0441], 4800m, 26.2.3016, 7, *Zenteno F. 16717* (LPB). Tirani, Pucara [-66.458127, -19.0441], 3900-4800, 23.2.2016. Zenteno, F. 16559 (LPB). ***Ladislao Cabrera***, W de Salinas de G. de Mendoza. Borde del Salar de Coipasa, [-67,895, -19,5481], 3550 m, 1, 3, 1986, *Beck, S.G., 11821*, (LPB). De Salinas de G. Mendoza hacia el Oeste via Iswaya, [-67,78, -19,6275], 3800 m, 1, 3, 1986, *Beck, S.G., 11798*, (LPB). De Salinas de G. Mendoza hacia el Oeste via Iswaya, [-67,785, -19,6236111], 3750 m, 1, 3, 1986, *Beck, S.G., 11809*, (LPB). ***Bolivar***, Entre provincia Bolivar y Oruro, [-66,76027, -17,98], 4250 m, 7, 2, 1992, *Ibisch, P., 1056*, (LPB). ***Sajama***. Unos 4 km del pueblo, subiendo el valle del río Sururia, [-69,0, 18,166667], 4550 m, 10, 4, 1995, *Beck, S.G., 22355*, (LPB).Lado Sur del nevado Sajama, en estepa de gramíneas y arbustos, [-68,8686, -18,279722], 4350 m, 8, 5, 1981, *Liberman, M., 353*, (LPB). Nevado de Sajama. Al sur del Nevado Sajama (sur del cerro Jasasuni). [-68,83, -18,262933], 4450 m, 18, 3, 1984, *Liberman, M., 820*, (LPB. DB_Tropicos, CTES, MO, NY, K. Cerca a las aguas termales, [-68,73257, -17,885], 4070 m, 0, 4, 2011, *Ortuño, T., 1373*, (LPB). Cerca a las aguas termales, [-68,732, -17,885589], 3950 m, 4, 2011, *Ortuño, T., 1374*, (LPB). ***Potosí***, ***Antonio Quijarro***, Vilacollo, camino al lago K'asilla, [-68,0869110, -20,626581], 4500 m, 22, 12, 2005, *Condo, K.S., 10*, (LPB). ***Rafael Bustillo***, Uncia, Suni, Chulluncani, [-66.431291,-18.9225], Zenteno, 16173 (LPB) Uncia. Localidad Chulluncani, ayllu Aymaya, [-66,564943, -18,5697], 4225 m, 27, 1, 2016, *Jiménez, I., s/n*, (LPB). Uncia. Localidad Chulluncani, ayllu Aymaya, [-66,5649, -18,569721], 4225 m, 27, 1, 2016, *Jiménez, I., s/n*, (LPB). Uncia. Localidad Kara kucho, Karacha, [-66,499167, -18,439527], 3900 m, 26, 1, 2016, *Lliully, A., s/n*, (LPB). Uncia. Localidad Sencoma, ayllu Laime/Pucraca, [-66,52622, -18,753527], 4239 m, 23, 1, 2016, *Lliully, A., AL 2237*, (LPB). ***Potosí***, ***Sud Chichas***. Wakawañusca, al nor-oeste en línea recta de Salo aprox. 11.71 km, [-65,8591, -21,20916], 3990 m, 6, 3, 2012, *Beck, S.G., 33933*, (LPB). Summit region of cerro Cieneguillas, 4 km de Tupiza, [-65,683, -21,39], 3600 m, 17, 11, 2002, *Müller, J., 9072*, (LPB). Abra Blanca, al nor-este en línea recta de la ciudad de Tupiza aprox. 4.14 km, [-65,68361, -21,4155], 3496 m, 8, 3, 2012, *Zenteno-R, F., 11913*, (LPB). Al oeste-nor-oeste en línea recta de Chilco aprox. 11.93 km, [-66,266389, -21,3597], 4197 m, 10, 3, 2012, *Zenteno-R, F., 12021*, (LPB). Al oeste-nor-oeste en línea recta de Chilco aprox. 7.88 km, [-66,231, -21,3738], 4024 m, 10, 3, 2012, *Zenteno-R, F., 12011*, (LPB). Cieneguillas, al nor-este en línea recta de la ciudad de Tupiza aprox. 4.97 km, [-65,678, -21,411389], 3586 m, 8, 3, 2012, *Zenteno-R, F., 11923*, (LPB). Wakawañusca, al nor-oeste en linea recta de Salo aprox. 11.35 km, [-65,8575, -21,212], 3945 m, 6, 3, 2012, *Zenteno-R, F., 11863*, (LPB). ***Tomás Frías***, serranía del Khare-Khare, arriba de la ciudad de Potosí, a orillas de la laguna Chalaviri, [-65,721389, -19,610833], 4400 m, 20, 2, 1988, *Schulte, M., 156*, (LPB). On S side of summit between Laguna Mazuni and Laguna Ulistia, Cordillera Kari Kari, [-65,70231, -19,611657], 4700 m, 20, 3, 1999, *Wood, J.R.I., 14721*, (LPB). ***Tarija***, ***Eustaquio Méndez***, Iscayachi 16 km. Hacia Cienaguillas, Camargo, [-65,015833, -21,3580556], 3500 m, 12, 11, 1993, *Beck, S.G., 22121*, (LPB). Iscayachi 16 Kms hacia Cieneguillas, Camargo, [-65,02121, -21,357942], 3500 m, 12, 11, 1993, *Beck, S.G., 22120*, (LPB). Iscayachi 18 Kms hacia Cieneguillas, via Potosí, [-65,025, -21,3633], 3450 m, 9, 11, 1993, *Beck, S.G., 22038*, (LPB). ***José María Aviléz***. Bajando del abra de Turcamarca hacia Antigal, [-65, -21,80], 4000 m, 22, 4, 2000, *Beck, S.G., 27380*, (LPB).

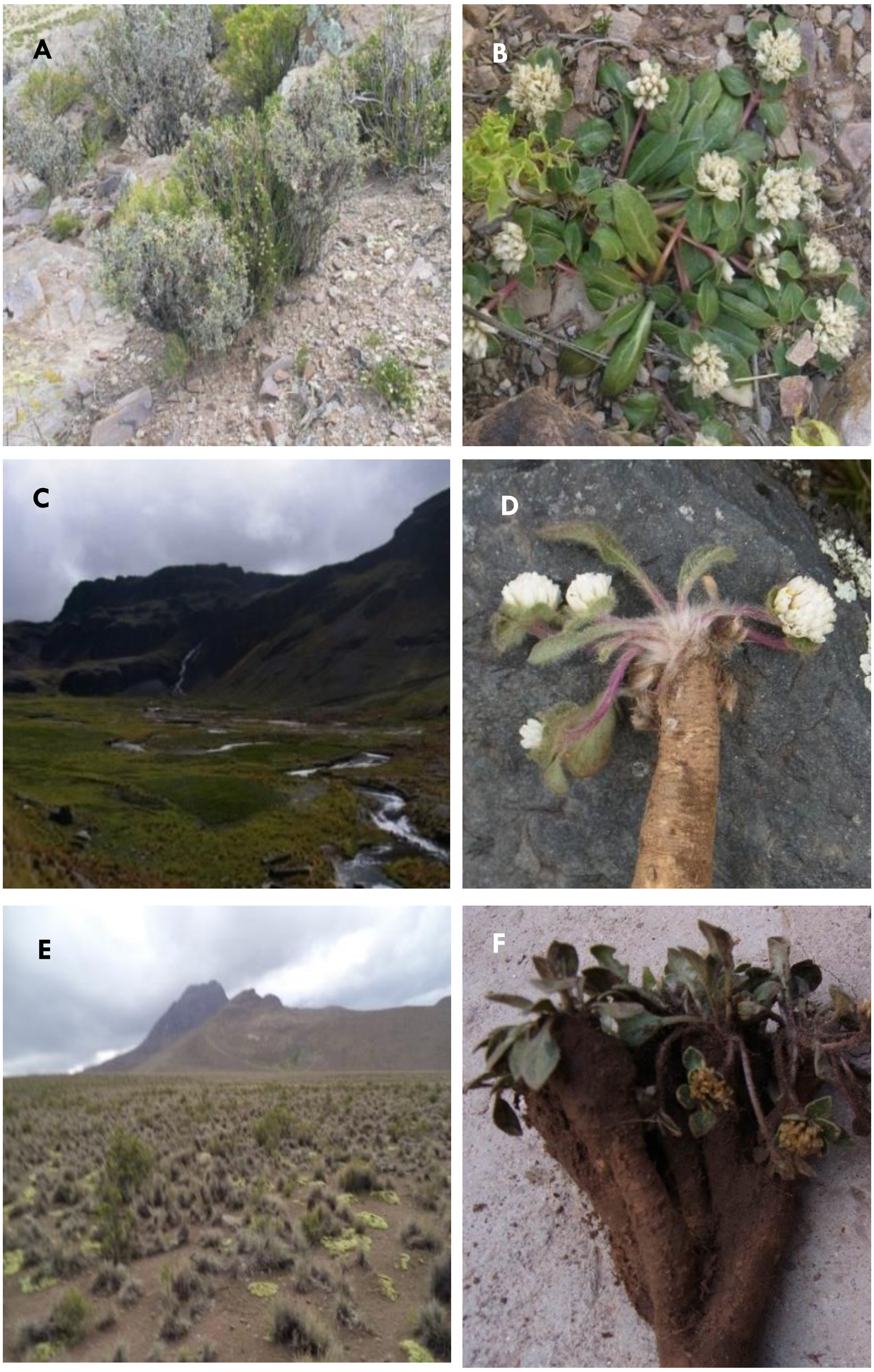


Fig. 4-73. *Gomphrena meyeniana* Walp. Habit A) Province of Mendez (Dept. Tarija). B) *G. meyeniana* var. *flaccida*. C) Province of Murillo, Loc. Hampaturi Loc. (Dept. La Paz). D) *G. meyeniana var. meyeniana,* detail of the acaule stem, not divided, only one axe. E) Province of Bustillo, municipality of Chayanta, locality of Chucarasi, (Dept. Potosi). F) *G. meyeniana* var. *meyeniana*, detail of acaule stems with many branches. [voucher: Zenteno & Moya 16235], photo of landscape F. Zenteno.

4.3.8.2. *Gomphrena meyeniana* var. *flaccida* Pedersen

Gomphrena meyeniana var. *flaccida* fa. *flaccida* Pedersen, Bull. Mus. Natl. Hist. Nat., B, Adansonia ser. 4, 12 (1): 82. 1990.

Type: Argentina, Province Jujuy, Detp Tilcara, Quebrada de Guasamayo 2600-2800 m, 13.2. 1980 A.L. Cabrera et al. 31577, (HT. SI).

Perennial herb, 2.5 (--8) cm long. ***Root*** a fleshy, woody taproot. ***Stems*** *acaule* 8 cm long, the acaule stems develop near the surface, covered with many large uniseriate trichomes protecting the buds, in the lateral with adventitious roots that help to fix the plant to the soil. ***Stems*** decumbent and ascending, individual branches 2.5 (--8) cm long, with dense villous and lanate trichomes, 1-3 mm long, white. ***Basal leaves*** ovolanceolate, in rosettes, 3-5 x 0.4-0.5 cm, acute at apex, trichomes similar to the stems, white or light brown. ***Cauline leaves*** ovate lanceolate, 1.4 x 0.4-0.5 cm, obtuse at apex, opposite, densely villous to lanate, on both sizes of leaf. ***Apical leaves subtending paracladia*** (inflorescences) 5-6, leaves arranged symmetrically, ovate to orbicular, 0.6- x 0.4-0.5 cm, acute at apex, green olive, density of trichomes in the adaxial and abaxial side leaf similar, (and trichomes similar to the stems). ***Inflorescences*** globose, terminal, 1.1 (--1.3) cm in diameter, consisting of 1-5 partial florescences. ***Flowers*** 5 mm long. ***Bracts*** ovolanceolate, 3.5 x 2.2 mm, membranous in texture, translucent, white light yellow, rounded at apex, dentate at the margin. ***Bracteoles*** ovolanceolate, 3.8 x 2 mm, membranous, light yellow, rounded to acute at apex. Tepals bigger than the bracteoles. ***Tepals*** spatulate-lanceolate, membranous in texture, white or light yellow, rounded at apex, with few theeth in the apex and at margin, all the tepals with trichomes dorsally. Size unequal. External 5.3 x1.5 mm, intermediate tepals 5.2 x1.5 mm, inner tepals. 5 x 2 mm. ***Filaments*** fused into a yellow tube almost completely, 4 mm long, free part 1 mm. ***Filament appendages*** inconspicuous, 0.6 mm long, rounded (united base 0.3 mm). ***Anthers*** oblong, 0.8 mm long, inserted at the apex of each individual filament appendix. ***Gynoecium*** with two filiform stigma branches, of 0.9 mm length, style 0.2 mm, ovary 0.8 mm [voucher Borsch & Ortuño 3663 = AC492].

Pollen. Size ~21.9 μm. Pore number 52-58. Pores ~4.5 μm in diameter, pore membrane with ektexinous bodies, widely arranged in a mosaic like a pattern. Mesosporia forming hexagons or pentagons, at corner with projections like microspines. ***Tectum***: A strong distal band, columnellae visible around a pore, in a row with varying distances to each other and ~1.2 μm high. *Microspines*: about ~0.6 μm high, in the corners of the pentagon's/hexagons [voucher: Borsch, Ortuño & Lopéz 3726].

Habitat and ecology. Occurs in the open places between scrubs such as *Baccharis boliviensis* (Wedd.) Cabrera, *Tetraglochin cristatum* (Britton) Rothm, and grasses (Tholar) such as *Jarava ichu* Ruiz & Pav., close to columnar Cactaceae such as *Trichocereus atacamensis* (Phil.), W.T. Marshall &

T.M. Bock, and trees such as *Prosopis ferox* Griseb., in the ecoregions wet (or humid) Puna, Semi humid Puna, Desertic Puna, where the plants were collected between 3200-4300 m.

Distribution. South of Bolivia. Province Jose Maria Avilés, Eustaquio Mendez (Dept. Tarija). Province tapacarí (Dept. Cochabamba). Province Omasuyo (Dept. La Paz) (see Fig. 4-78).

Specimens examined for distribution assessment. ***Bolivia, Tarija, José María Avilés*** Cerca Passajes, [-65,08666667, -21,741111], 3260 m, 29, 1, 1986, *Bastian, E., 638*, (LPB). Laguna Chica cerca de Copacabana, Laguna Tajzara, [-65,0833329, -21,85], 3750 m, 6, 3, 1998, *Beck, S.G., 23652*, (LPB). Laguna Chica cerca de Copacabana, Laguna Tajzara, [-65,083332, -21,85], 3750, 6, 3, 1998, *Beck, S.G., 23682*, (LPB). Laguna Chica cerca de Copacabana, Laguna Tajzara, [-65,133, -21,93], 3785 m, 6, 3, 1998, *Beck, S.G., 23716*, (LPB). Municipio de Yuncharà, Pampa Salitre arriba de Rupasca, [-65,31, -21,916667], 3660 m, 16, 4, 2000, *Beck, S.G., 26942*, (LPB). Pampa de Tajzara, Arenales, [-65,033, -21,83], 3820 m, 18, 4, 2000, *Beck, S.G., 27078*, (LPB). Salida de Tojo hacia Copacabana. Arenales en la pampa de Tajzara, pampa de Tajzara Pozuelos, [-65,133, -21,80], 3700 m, 17, 4, 2000, *Beck, S.G., 27010*, (LPB). Cerro Pastillas y Abra Yunchara, [-65,150, -21,8], 4000 m, 8, 3, 1998, *Beck, S.G., 23769*, (LPB). ***Eustaquio Méndez***, Iscayachi 16 Kms hacia Cieneguillas, Camargo, [-65,0212, -21,35794], 3500 m, 12, 11, 1993, *Beck, S.G., 22121*, (LPB). Cantón Paycho, [-65,003333, -21,2586111], 3200 m, 1, 3, 1991, *García, E., 2507*, (LPB). Pasando la cuesta de Sama. Camino de Tarija a Potosi, [-65,0196667, -21,3598333], 3530 m, 11, 4, 2003, *Borsch, T., 3663*, (LPB, B). **Cochabamba, *Tapacarí***, Camino La Paz a Cochabamba, cerca de Pongo, [-66,5265, -17,7055], 4100 m, 1, 4, 2003, *Borsch, T., 3561*, (LPB). Camino de La Paz a Cochabamba, cerca a la Comunidad "Japo", [-66,783, -17,701104], 4266 m, 9, 3, 2009, *Borsch, T., 3955*, (LPB, B). ***La Paz, Omasuyos,*** Cantón Huarina, Comunidad de Moco Moco, [-68,633, -16,199], 3870 m, 24, 1, 1997, *Loza de la Cruz, F., 71*, (LPB).

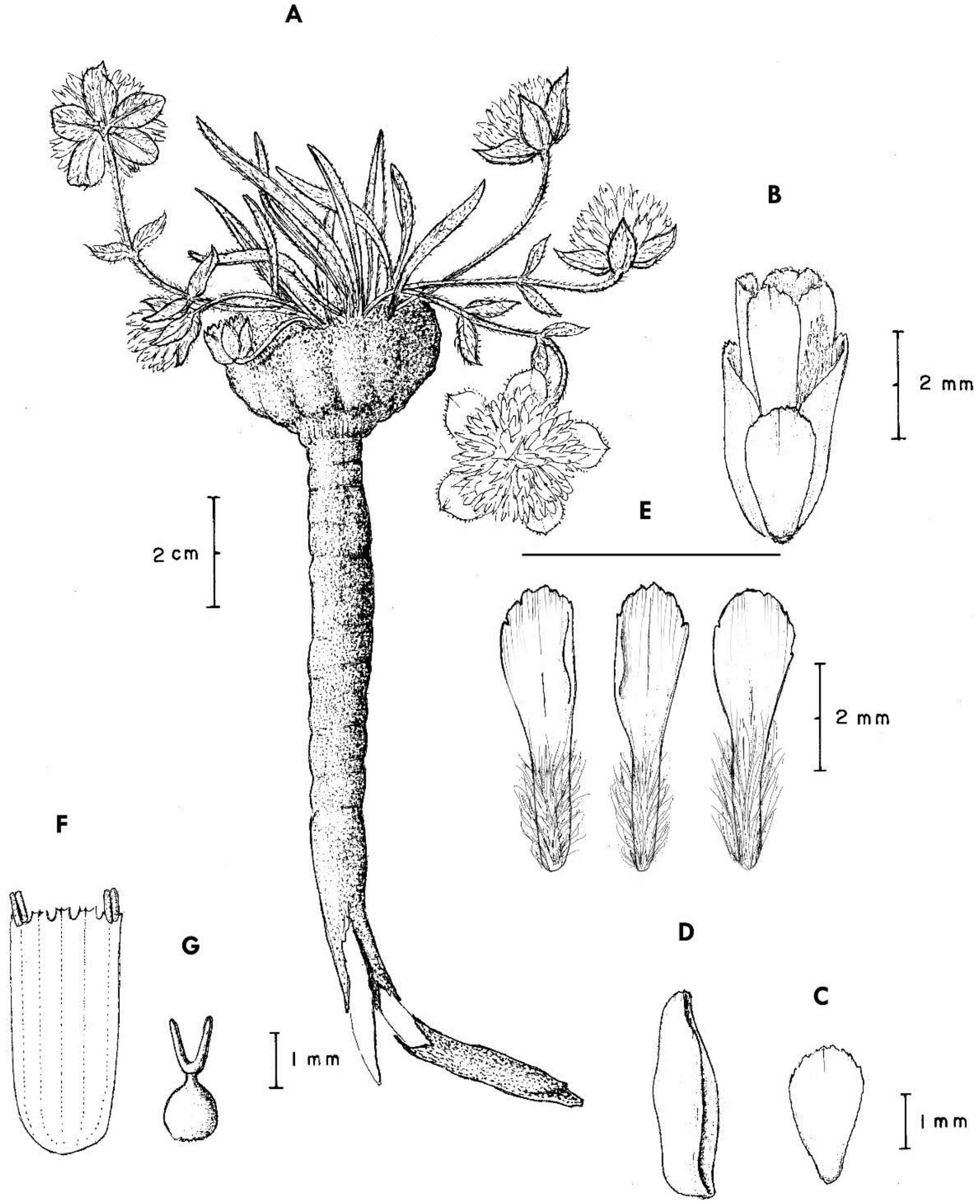


Fig. 4-74. *G. meyeniana* var. *flaccida*. A) Habit. B) Flowers. C) Bract. D) Bracteoles. E) Tepals all with trichomes on the dorsal side. F) Detail of the androecium. G) Gynoecium [voucher: Borsch & Ortuño 3663].

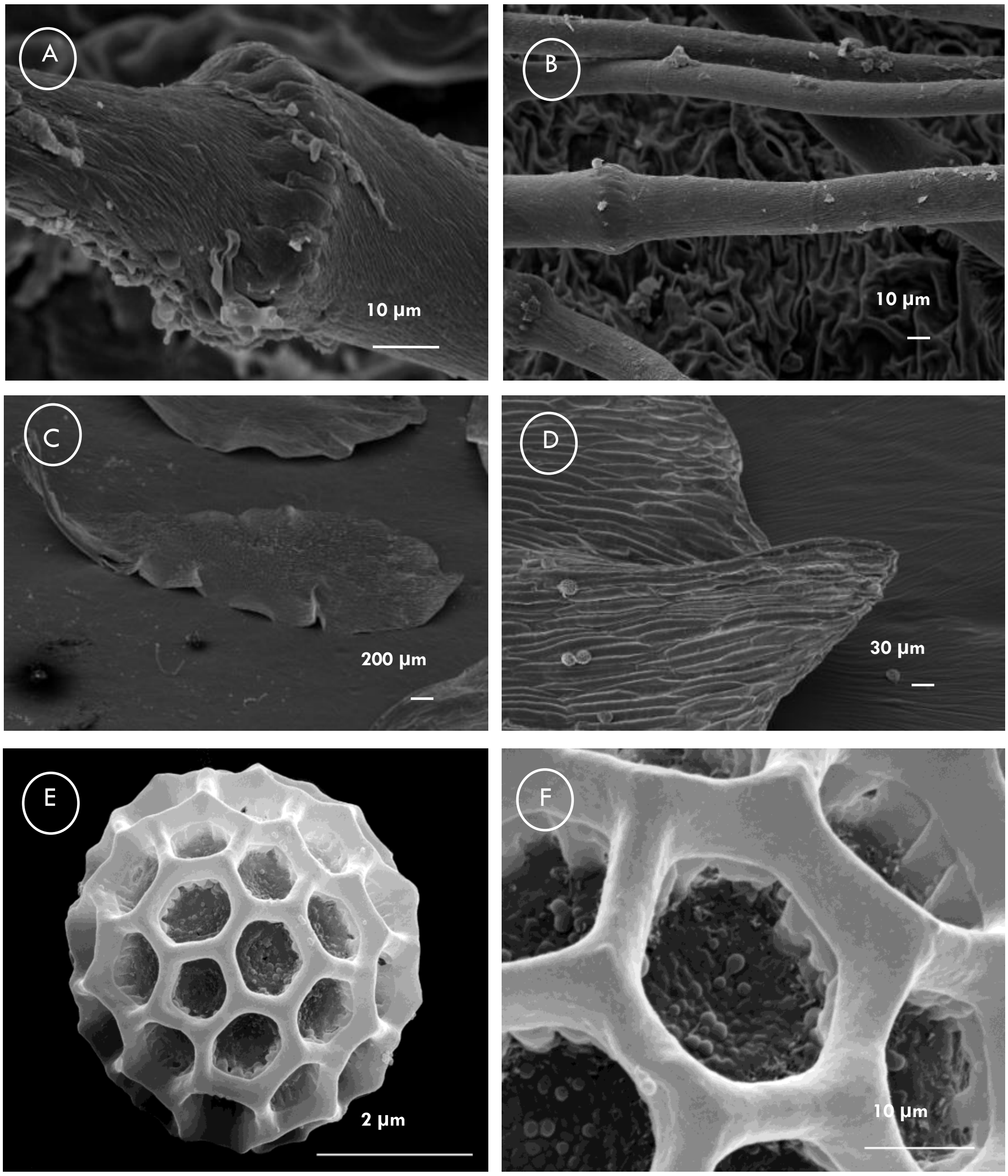


Fig. 4-75. *Gomphrena meyeniana* Walp. Trichomes of cauline leaves. A) Detail of the interlocking junctions with linear overlapping scar. B) Detail of upper cells, without ornamentation. C) Tepals without trichomes. D) Detail of acute apex of the tepal, with elongate, fibrous cells. [voucher: Borsch & Ortuño 3954]. *Gomphrena meyeniana* var. *flaccida*. E) Pollen overview. F) Detail of aperture. [voucher: Borsch, Ortuño & Lopéz 3726].

4.3.8.3. *Gomphrena meyeniana* fa. *levitepala* Pedersen

≡ *G. meyeniana* var. *flaccida* fa. *levipetala.,* Bull. Mus. Natl. Hist. Nat., B, Adansonia Sér. 4, 12(1): 83. 1990.

Type: A.L. Cabrera & Kiesling 25166, Argentina, Province Jujuy, Dept. Yavi, subida al pie del Abra de Lizoite, 4000 m. 19.1974. (HT: LP 010894).

Gomphrena meyeniana var. *levitepala* is close in morphology to *G. meyeniana* var. *flaccida*. The main characters are: ***Stems*** decumbent to erect. ***Cauline leaves*** ovate 1.5 (--1.8) x 0.9 (--1) cm. ***Bract*** ovolanceolate, 2x1.5 mm, membranous, light brown. Only the external tepals glabrous, inner tepals with trichomes. Filament 5.9 mm, tube fused, 5.70 mm long. The ***Filament appendices*** are shorter but conspicuous as teeth of 0.2 mm. [voucher: Borsch & Ortuño 3770].

Habitat and ecology. Grows on stony open places between scrubs as *Fabiana densa* Remy, *Baccharis boliviensis* (Wedd.) Cabrera, and grasses such as *Festuca orthophylla* Pilg., *Bouteloua simplex* (Lag.) Pedersen, is restricted to xeric areas. The specimens examined occured in Semi humid Puna, Dry Puna, where the plants were collected between 3200-4200 m.

Distribution. Argentina, province Jujuy. Bolivia Provinces of Ladislao Cabrera, Sajama (Dept. Oruro). Mizque (Dept. Cochabamba) (see Fig. 4-78).

Specimens examined for distribution assessment. ***Argentina, Jujuy,*** Yavi. Camino de Yavi a Santa Victoria, [-65,16929, -22,13156], 3934 m, 4, 4, 2004, *Borsch, T., 3726*, (LPB, B). ***Bolivia, Oruro, Ladislao Cabrera,*** A un kilómetro de la Localidad de Jirira, [-68,73257, -17,88], 3640 m, 11, 3, 2008, *Acho, J., 1*, (LPB). ***Sajama,*** [-69,916667, -18,1666], 4200 m, 13, 2, 1998, *Loza de la Cruz, F., 71*, (LPB). Cerca a las aguas termales, [-68,73257, -17,88], 3950 m, 0, 4, 2011, *Ortuño, T., 1372*, (LPB). Cerca a las aguas termales, [-68,73257, -17,885589], 3950 m, 4, 2011, *Ortuño, T., 1375*, (LPB). ***Cochabamba, Mizque,*** Camino de Mizque a Cochabamba, [-65,5176, -17,73566], 3689 m, 15, 4, 2004, *Borsch, T., 3770*, (LPB).

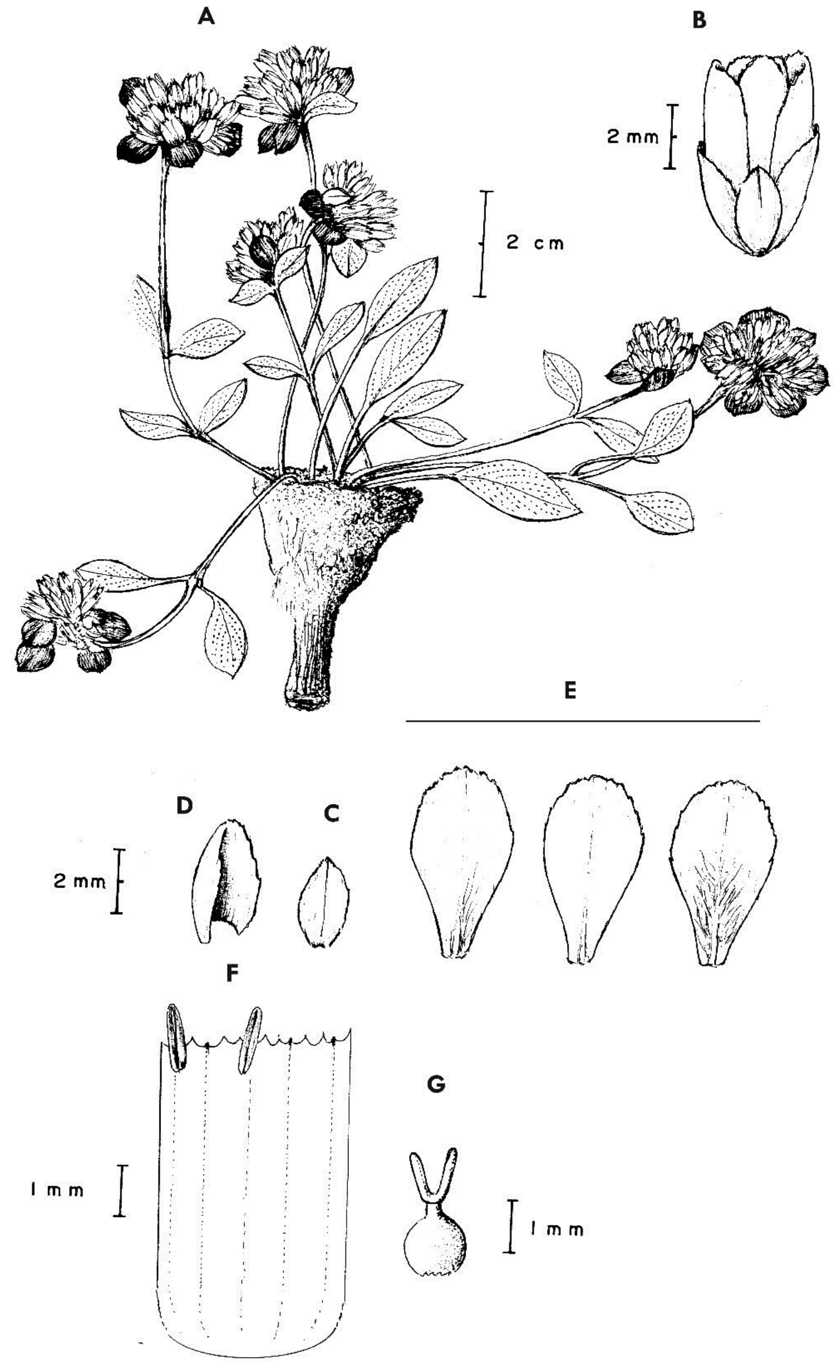


Fig. 4-76. *Gomphrena meyeniana* fo. *levitepala*. A) Habit. B) Flowers. C) Bract. D) Bracteoles. E) Tepals, all with trichomes on the dorsal side. F) Detail of the androecium. G) Gynoecium [voucher: Borsch & Ortuño 3770].

4.3.8.4. *Gomphrena meyeniana* var. *caulescens* Holzh., Mitt. Bot. Staatssamml. München 14-15: 229. 1956.

Type Argentinien, Province Jujuy, Dept. Volcán. Loc. Estación Volcán-Chilacayo, 2480 m, I. 1919. Castilon 6657. (HT: M 0241754).

Perennial herb, 5 cm tall. ***Root:*** A fleshy, woody taproot. ***Stems*** *acaule* 3 cm long, the acaule stems develop near the surface of the soil and are covered with many large uniseriate trichomes, protecting the buds, in the lateral part with adventitious roots that help to fix the plant to the soil. ***Stems*** erect, branched, 4-4.5 cm long, red to green, with dense appressed and lanate trichomes 1-3 mm long, white. ***Basal leaves*** lanceolate, in rosettes, 2.2 x 0.33 cm, acute at apex, 2.5-3.5 cm petiolate, decurrent, trichomes similar to the stems, colour white or light brown. ***Cauline leaves*** lanceolate, 1.6 x 0.3, acute at apex, alternated, densely appresed to lanate on adaxial side of leaf, sparsely in the abaxial side of leaf, white. ***Apical leaves subtending paracladia*** (inflorescences) 5-6, leaves arranged symmetrically, ovolanceolate, 1.5 x .4 cm, apiculate at apex, green olive, similar density trichomes in the adaxial and abaxial side leaf (similar to the stems). ***Inflorescences*** globose, terminal, 1.1 (--1.7) cm in diameter, consisting of 1-5 partial florescences. ***Flowers*** 4.8 mm long. ***Bracts*** ovolanceolate, 2 x 1.5 mm, membranous in texture, translucent white or light brown coloured, rounded at apex, dentate in the margin. ***Bracteoles*** ovolanceolate, 3.8 x 2.5 mm, membranous, light yellow, rounded to acute apex. Tepals bigger than the bracteoles. ***Tepals*** spatulate-lanceolate, membranous in texture, white or light yellow coloured, rounded at apex, few teeth in the apex and margin of all tepals. Size unequal. External tepals 4.8 x1.5 mm, intermediate tepals 4.6 x 1.5 mm, inner tepals. 4.5 x 2 mm. ***Filaments*** tube 5.1 mm long, fused for 4.6 mm, yellow. ***Filament appendages*** inconspicuous, 0.5 mm long, of a broadly rounded filament. ***Anthers*** oblong, 1 mm long. ***Gynoecium*** with two filiform stigma branches, of 0.8 mm length, style 0.4 mm, ovary 0.8 mm [voucher: Beck 33882 (LPB)].

Habitat and ecology. Occurs in flat open places between sparse scrubs and grassland. In the ecoregions Semi humid Puna, Prepuna, where the plants were collected between 3400-4000 m.

Distribution. Bolivia, province of Sud Chichas (Dept. Potosí) and Jose Maria Aviles (Dept. Tarija) (see Fig. 4-78).

Specimens examined for distribution assessment. ***Bolivia, Potosí, Sud Chichas***, Al oeste-nor-oeste en línea recta de la comunidad de Espicaya aprox. 8.87 km, [-65,876, -21,5786], 4000 m, 29, 2, 2012, *Beck, S.G., 33807*, (LPB). Mirador Boris, al oeste en línea recta de la ciudad de Tupiza aprox. 11.93 km, [-65,8297, -21,4513], 3950 m, 4, 3, 2012, *Beck, S.G., 33883*, (LPB). Al oeste-sur de la comunidad de Espicava aprox. 6.18km, [-65,848332, -21,5975], 3448 m, 29, 2, 2012, Zenteno-R, F., 11632, (LPB). Al oeste-sur-oeste de Kucho en línea recta hacia Mojinete aprox. 8.8 km, [-66,0905, -21,534167], 4168 m, 12, 3, 2012, Zenteno-R, F., 12094, (LPB).

Camino Mirador Boris al oeste en línea recta de la ciudad de Tupiza aprox. 11km, [-65,82194, -21,45055], 3885 m, 4, 3,

2012, Zenteno-R, F., 11791, (LPB). Queñua Pampa, al este-sur-este en línea recta de Supira aprox. 12.45 km, [-65,407, -21,62249], 3765 m, 5, 3, 2012, Zenteno-R, F., 11830, (LPB). Tarija, José María Aviléz, Tajzara, cerca Rosillas, [-65,046389, -21,71611], 3650 m, 10, 3, 1986, Bastian, E., 1028, (LPB).

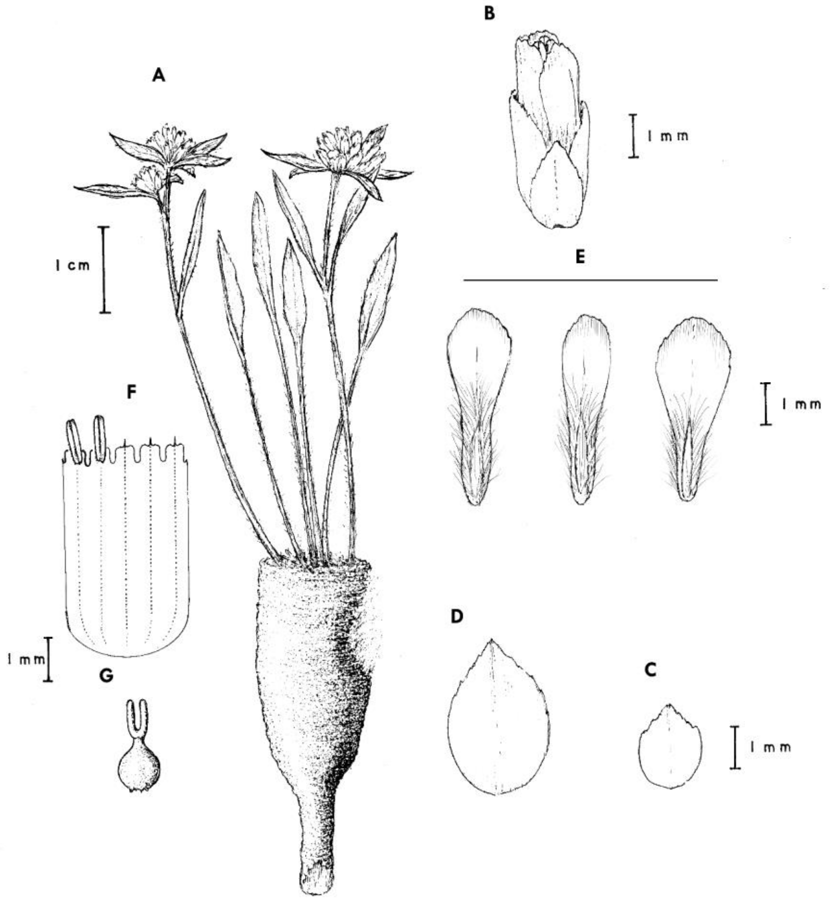


Fig. 4-77. *G. meyeniana* var. *caulescens* Holzh., alternate cauline leaves and all tepals with trichomes. A) Habit. B) Flowers. C) Bract. D) Bracteoles. E) Tepals. F) Detail of the androecium. G) Gynoecium [voucher: Beck 33883].

4.3.8.5. ***Gomphrena meyeniana*** var. ***conwayi*** Rusby. Suess., Repert. Spec. Nov. Regni Veg. 35: 314. 1934

Type: Peru, Puno, near Juliaca, 12.5.1902, Williams 2519. (NY00324498).

≡ *Gomphrena conwayi* Rusby, Bull. New York Bot. Gard. 8: 89. 1912.

Gomphrena meyeniana var. *conwayi* is morphologically close to *G. meyeniana:* But var. *conwayi* differs by two characters: One are the stems with only terminal inflorescences and without cauline leaves, and the other are that all tepals have a densely lanate indumentum in the dorsal part.

Taxonomic remark. Pedersen (1990) mentions that *G. conwayi* was described of a specimen from Sourthern of Perú, and reduced to varietal rank by Suessenguth. The concept of Suessenguth about this taxon and its limits seem not clear. The difficulty to define these taxa is because the molecular studies do not include all the varieties and data from specimens from diferent places are still lacking. For example *G. meyeniana* var. *conwayi* is not included in the present molecular study, but was determined using the key from Pedersen (1990) in some specimens in the herbarium LPB. This is the reason for including them in this treatment of the *G. meyeniana* clade.

Habitat and ecology. Occurs in open places in stony slopes close to forest of *Polylepis besseri* Hieron. Ecoregions are Inter-Andean dry forest, Semi humid Puna, where the plants were collecting between 3800-3900 m.

Distribution. Bolivia, provinces of Quillacollo, (Dept. Cochabamba), Bautista Saavedra (Dept. La Paz), and Eduardo Avaroa (Dept. Oruro) (Fig. 78).

Specimens examined for distribution assessment**.** ***Bolivia, Cochabamba*****,** ***Quillacollo*****,** camino Sipe-Sipe a Kami cuenca del valle de Cochabamba, [-66,457230, -17,65290], 3800 m, 23, 4, 1989, *Beck, S.G., 18053*, (LPB, SI). ***La Paz, Bautista Saavedra*****,** Amarete, [-68,989722, -15,234444], 3900 m, 4, 2, 1980, *Feuerer, T., 8411e*, (LPB). ***Oruro, Eduardo Avaroa*****,** Challapata, Suni, Cerro Toro,[-66.431291, -18.9225], 4800 m, *Zenteno, F. 16876* (LPB).

4.3.8.6. ***G. meyeniana* var. *genuina* Stuchl.**, Repert. Spec. Nov. Regni Veg. 12: 345. 1913.

= *Gomphrena acaulis* J. Rémy, Ann. Sci. Nat., Bot. sér. 3, 6: 350. 1846.
Type: Bolivia Coteaux des monts de las laguna de Potosí, Orbigny A.D. 1479. (LT: PP00623703, ITLT (P P00623704, (P) P00623705).
= *Gomphrena meyeniana var. albiflora* Stuchlík, Beih. Bot. Centralbl., Abt. 2. 30(2): 406. 1913 Fedde, Rep. Spec. Nov. 12: 521. 1913. Type: Bolivia, La Paz, 19.3.1907, 4100 m. Otto Buchtien s/n (HT: M, M0241755).
This variety morphologically are close to *G. meyeniana* Walp., they have main difference are: i) the stems with only terminal inflorescence, without cauline leaves, ii) the second all the external tepals are blabrous and the inner with trichomes in the dorsal part.

Taxonomic remark. Pedersen (1990) included and accepted the variety *Gomphrena meyeniana* var. *genuina* and chose the specimens of Orbigny 1459 as lectotype. He mentioned that the type of *G. meyeniana* var. *albiflora* is morphologically identical to the *Gomphrena meyeniana* var. *genuina*. The molecular analysis does not include any sample of this variety, but the specimens were reviewed in the Herbarium LPB for the description.

Habitat and ecology. Mostly cloud-covered mountain ranges with alternating passes and streams with thin heavily grazed stony grassland and occasional rock outcrops and cliffs. Rare on moist slopes on high altitude grassland. Ecoregions are Humid Puna, (Puna Northern), Altoandine, "Nival and Subnival", where the plants were collected in a range between 3400-4600 m.

Distribution. Bolivia, provinces of Jaime Zudañez (Dept. Chuquisaca), Cercado (Dept. Cochabamba), Charcas (Dept. Potosí), Franz Tamayo, Ingavi, Murillo (Dept. La Paz) (Fig. 4-78).

Specimens examined for distribution assessment. ***Bolivia, Chuquisaca, Jaime Zudañez,*** On S side of high pass in Cordillera de los Sombreros between Icla and Tarvita, [-64,66354, -19,548158], 3900 m, 3, 12, 1999, *Wood, J.R.I., 15274*, (LPB). ***Cochabamba, Cercado***, Pajcha, [-66,134444, -17,3188], 3470 m, 7, 3, 2004, *Gutiérrez, E., 660*, (LPB). ***La Paz, Franz Tamayo***, Justo al norte de la Estación, [-69,233, -15,050], 4500 m, 7, 8, 1982, *Dennis A., 857*, (LPB). **Sajama**, Al pie del cerro Sajama, cerca al pueblo, [-68,961755, -18,1352556], 4200 m, 11, 1, 1986, *Beck, S.G., 14168*, (LPB) ***Ingavi***, Granja de CORDEPAZ en Huacullani, [-68,7361, -16,4525], 3950 m, 7, 2, 1979, *Beck, S.G., 333*, (LPB). ***Murillo***, Milluni, 18 km al NE de La Paz, [-68,15, -16,3166], 4600 m, 9, 2, 1996, *Meneses, R., 585*, (LPB). Milluni, 18 km al NE de La Paz, [-68,15, -16,316], 4600 m, 9, 2, 1996, *Meneses, R., 533*, (LPB). ***Potosí, Charcas***, In the zone of Aradia on the highest part of the road from Torotoro to San Pedro, [-65,850278, -18,12], 3561 m, 9, 2, 2007, *Wood, J.R.I., 22663*, (LPB).

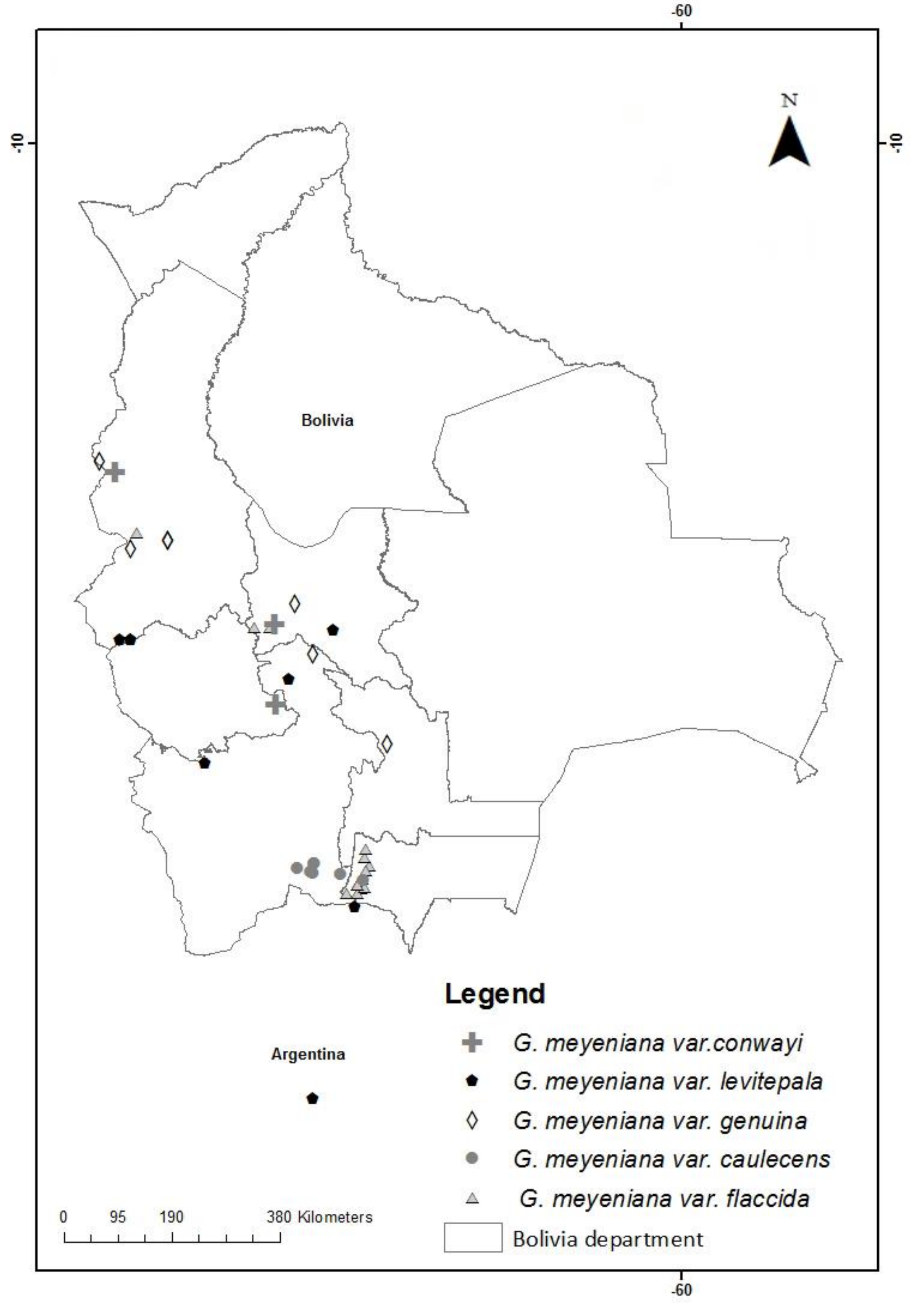


Fig. 4-78. Distribution of varieties of *G. meyeniana* based on collections from Bolivia, and Argentina (*G. meyeniana* var. *meyeniana*, *G. meyeniana var. caulecens*, *G. meyeniana var. conwayi*, *G. meyeniana var. flaccida*, *G. meyeniana var. levitepala y G. meyeniana var. genuine*).

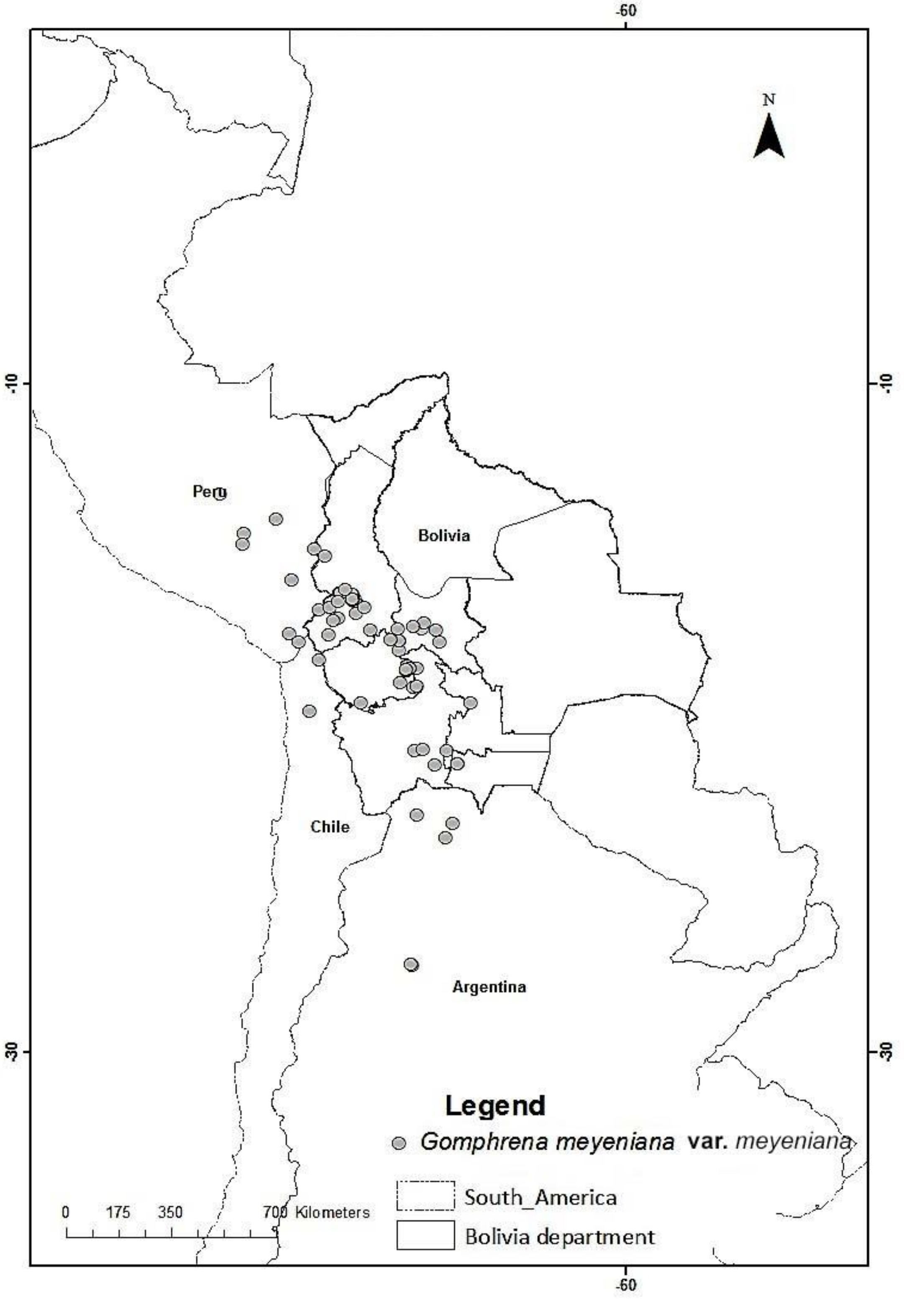


Fig. 4-79. Distribution of the typical variety *G. meyeniana* var. *meyeniana*.

4.3.9. Gomphrena tomentosa CLADE

The *Gomphrena tomentosa* clade emerged monophyletic with high support in the *matK-trnK* tree (1.00 PP, 100 BS, 100 JK), and it appears sister clade of *Gossypianthus brittonii* (0, 75 PP, 40 BS, 63 JK), and *G. meyeniana* clade (1, 00 PP, 100 BS, 100JK). The *Gomphrena tomentosa* clade has two subclades, the first includes the specimens of *G. tomentosa* (1.00 PP, 99 BS, 100JK) and the second includes specimens of *G. radiata* and *G. umbellata* (0, 75 PP, 40 BS, 63 JK).

The ITS tree shows similar relationships than the plastidial tree, with a *G. tomentosa* clade with high support (1,00 PP, 100 BS, 100JK). Philippi (1862) created the genus *Choanthus* to describe the new species *G. mendocina.* Philippi's work was not cited by the other studies, except by Fries, who reviewed this genus. However, Fries in 1920, transfered the genus *Choanthus* to *Gomphrena* at section level, and included the species *G. tomentosa*, *G. radiata*, and *G. umbellata.* Most of the specimens revised by Fries (1920) were collected from Southern Bolivia and the North and center of Argentina.

The features detected in the earliest studies (Philippi 1862, Fries 1920, Holzhammer 1956), distinguishes the species of "*Choanthus*" by having spathulate tepals, rounded apex and a narrow base, with woolly indumentum, and the androecium with the filaments fused into a long and narrow tube, with the free parts of the filaments being narrow and filiform, without any presence of lateral appendages. In addition, Hunziker (1977) reviewed the species of *Gomphrena tomentosa* and allies, and included the tissue of the tepals and the type of the indumentum in the different parts of the plants as characters.

Key to the species in the *Gomphrena tomentosa* CLADE

1. Perennial plants with taproot, fleshy. Plants with indeterminate type of growth

2. Flowers 4, 8-5 mm long. Bract rounded-ovate and bracteoles ovate- lanceolate, covered with tomentose trichomes at the apex dorsally.....................................*G. tomentosa* (Fig. 4-81)

2'. Flowers 1.4-2 (--2.4) mm long. Bract and bracteoles ovate, rounded to spatulate, without trichomes ....*G. radiata* (Fig. 4-87)

1'. Annual plants with fibrous root. Plants with determinate type of growth.

3. Flowers 1.4-2 (--2.4) mm long. Stems prostrate, always with tertiary and quaternary stems, terminating in a radial umbrella shape.......................................*G. umbellata* (Fig. 4-83)

4.3.9.1. *Gomphrena tomentosa* Griseb., R.E. Fr. Ark. Bot. 16: 34. 1920

Type: Argentina Northeast, Prov. Catamarca, Quebrada del Tala, 1872, Lorentz, P.G. 407 (HT: GOET006514).

≡ *Gossypianthus tomentosa* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 35. 1879.

≡ *Guilleminea tomentosa* (Griseb.) Hosseus, Bol. Acad. Ci. Córdoba XXVI (1921), p.58.

= *Gomphrena discolor* Ark. Bot. ser. 12, 16. 1920.

Type: Bolivia, Tarija, alt. 1900 m, 16.1.1901, R.E. Fr. 1101 (HT: S-R-2437, IT: CORD 00002557, G00236953, P 000623702, S 07-12319).

Perenial herb 17 (--25) cm long. ***Root*** a fleshy, woody taproot. ***Stems*** prostrate, with secondary and tertiary branches, arranged in radial form, striate, red, with dense tomentose indumentum, with trichomes 1 to 3 mm long, especially on the young stems, white to light yellow. ***Basal leaves*** ovate to lanceolate, 6-7 x 1.5-2 (--3) cm, acute at apex, coriaceous in texture, crenate at margin, middle and secondary nerve prominent, dense tomentose with trichomes similar than on stems. ***Cauline leaves*** ovate-lanceolate, 1-1.5 (--2.5) x 0.5-0.7 (--1.5) cm, acute at apex, entire or crenate at margin, green, white trichomes on all the leaves usually denser on the adaxial side of leaf, trichomes similar than on the stems. ***Apical leaves subtending paracladia*** 2-4 (--5), arranged symmetrically around the inflorescences, ovate-lanceolate, 0.5-0.8 (--1.5) x 0.3 - 0.5 (--0.7) cm, apiculated at apex, with dense tricomes, mostly on the abaxial side leaf. Not all the inflorescences have apical leaves subtending paracladia, because some inflorescences arise in the axillar node (Fig. 4-81A). ***Inflorescences*** terminal and axillar, 0.4-1.2 (--1.4) cm in diameter, consisting of 3partial florescences. ***Flowers*** 4.8-5 mm long. ***Bracts*** rounded-ovate, 2 x 1.5 mm, undulate to entire at margin, membranous in texture, white hyaline, trichomes on the external dorsal part near the apex or on all the dorsal part. ***Bracteoles*** ovate- lanceolate, 1.4 (--2.6) x 1 (--1.5) mm, rounded at apex, membranous, trichomes denser on the external dorsal part near the apex. Bracteoles smaller than the tepals. ***Tepals*** spathulate to lanceolate, acute at apex, scarious at the base at maturity, all tepals with trichomes in the lower dorsal half, woolly white to yellow or light brown, usually dentate in the margin; especially near the apex. Size unequal. External tepals 4,7x 0.9 -1 mm, intermedian tepal 4.6 x-0.9(--1) mm, inner tepals 2 x 0.4 mm. ***Filaments*** 1.4 (--3) mm long, fused in into a tube for about half, 0.8-2.2 mm, light yellow, the free part of the filament tapering into a linear filament that is 0.5-0.6 mm long. ***Filament appendages*** lacking (Fig. 4-81F). ***Anthers*** oblong, 0.4 (--1) mm long (Fig. 4-81G). ***Gynoecium*** with two filiform branches, stigma 0,6 mm long, style 0.2 mm, ovary subglobose 0.8 mm [voucher: Borsch & Ortuño 3649 =AC167 (LPB, B)].

Fig. 4-80. *Gomphrena radiata* Pedersen. A) Tupiza, province Sud Chichas (Dept. Potosí). B) *Gomphrena tomentosa*. C). *Gomphrena radiata*. D) San Antonio de los cobres, province Jujuy, Argentina. E) *Gomphrena umbellata*. F) Jirira, province Ladislao Cabrera (Dept. Oruro).

Micromorphology of trichomes: Multicellular, uniseriate. On ***stems and cauline leaves*** with a 1-2 basal cells. These cells collapsed, striated in sculpture and salicose ornamentations on the cuticle walls, 4-6 upper cells with collapsed to flexible walls, distinctly striate in sculpture of the cuticule. ***Interlocking junctions*** not conspicuous, only a node; on ***apical leaves subtending paracladia***,similar than on the stems; on ***tepals*** similar than on stem but thinner. ***Anatomy of tepals.*** Tissue composed by elongate straight cells, arranged in one row fitting parallel perfectly, the cuticle walls has an undulate appearance (Fig. 4-82D), [voucher: Ortuño 1235 = AC793 (LPB, B)].

Pollen. Size ~16.3 µm. Pore number: 50-5 6. Pores: 3.4 µm in diameter, pore membrane with ektexinous bodies. Mesosporia forming irregular hexagons or pentagons, apical surface undulate and dentate, corner with sharp and acute protusions (as microspine). *Tectum*: a distal band columnellae freely visible in the lower half of the mesoporium (Fig. 4-82 E and F), [voucher: Beck & Paniagua 26642 (LPB)].

Taxonomic remark. The specimen Borsch & Ortuño 3649 was described here because it is morphologically very simililar to the specimens described by Fries (1920), Holzammer (1956) and Hunziker (1977). The concept of *G. tomentosa* fits perfectly with this voucher because it has lanceolate to spathulate tepals, that are acute at the apex, presents dense tomentose trichomes in the dorsal part of the tepals and on the bracts and bracteoles; the epidermis cell walls of the tepal tissues are parallel and straight with undulate walls. This specimen is also included in the molecular analysis, and is very close to the vouchers Borsch & Ortuño 3722 & 3739 and Ortuño 1235. The specimen Beck 33662 is similar to the previous, but it differs in that the cauline leaves on the abaxial side do not have trichomes. According to descriptions of Fries 1920 and Holzammer (1956), this corresponds to *G. discolor* which actually is synonymous of *G. tomentosa*. Hunziker (1977) thought that the type of indumentum on the cauline leaves colud help to differentiate *G. tomentosa* of other close species, as is the case for *G. mendocina* that has a setose indumentum but this is evidently absent in the revised specimens from Bolivia or the North of Argentina. Besides the other characters mentioned above, there are other important characteristics for this species, one is the type of androecium or filament appendices without lateral appendages. The absence of lateral appendages is, according to Fries (1920), the principal character to distinguish the C*hnoanthus* group. He thought that *Gomphrena* includes a series of species with more and more reduced filament appendages. So, *G. tomentosa* was believed to represent final step of this evolution because has the most reduced filaments.

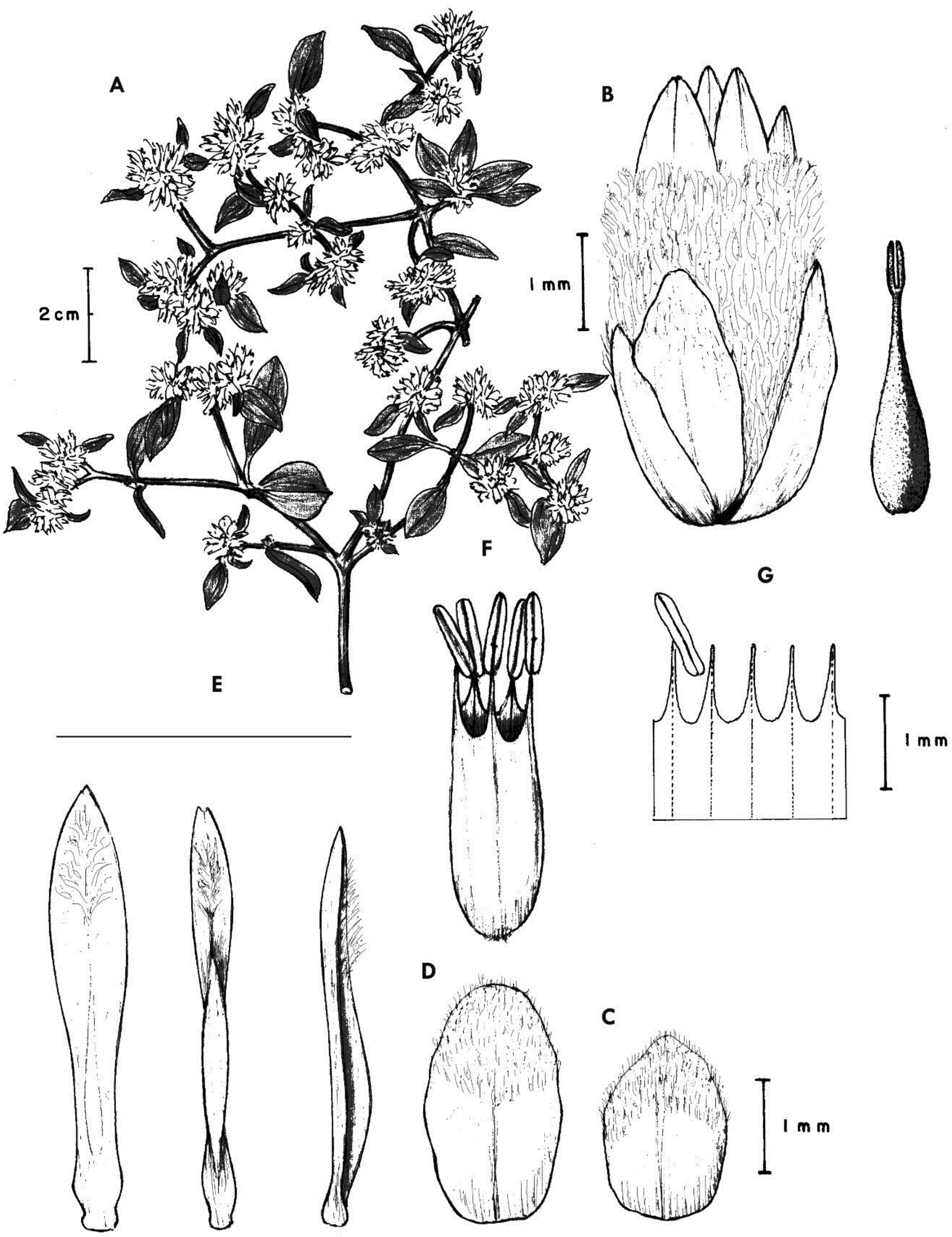


Fig. 4-81. *Gomphrena tomentosa* (Griseb.) R.E. Fr. A) Habit. B) Flower. C) Bract. D) Bracteoles. E) Tepals. F) Detail of the androecium with anther inserted on the tip of the filament. G) Gynoecium. [voucher: Borsch & Ortuño 3649=AC167].

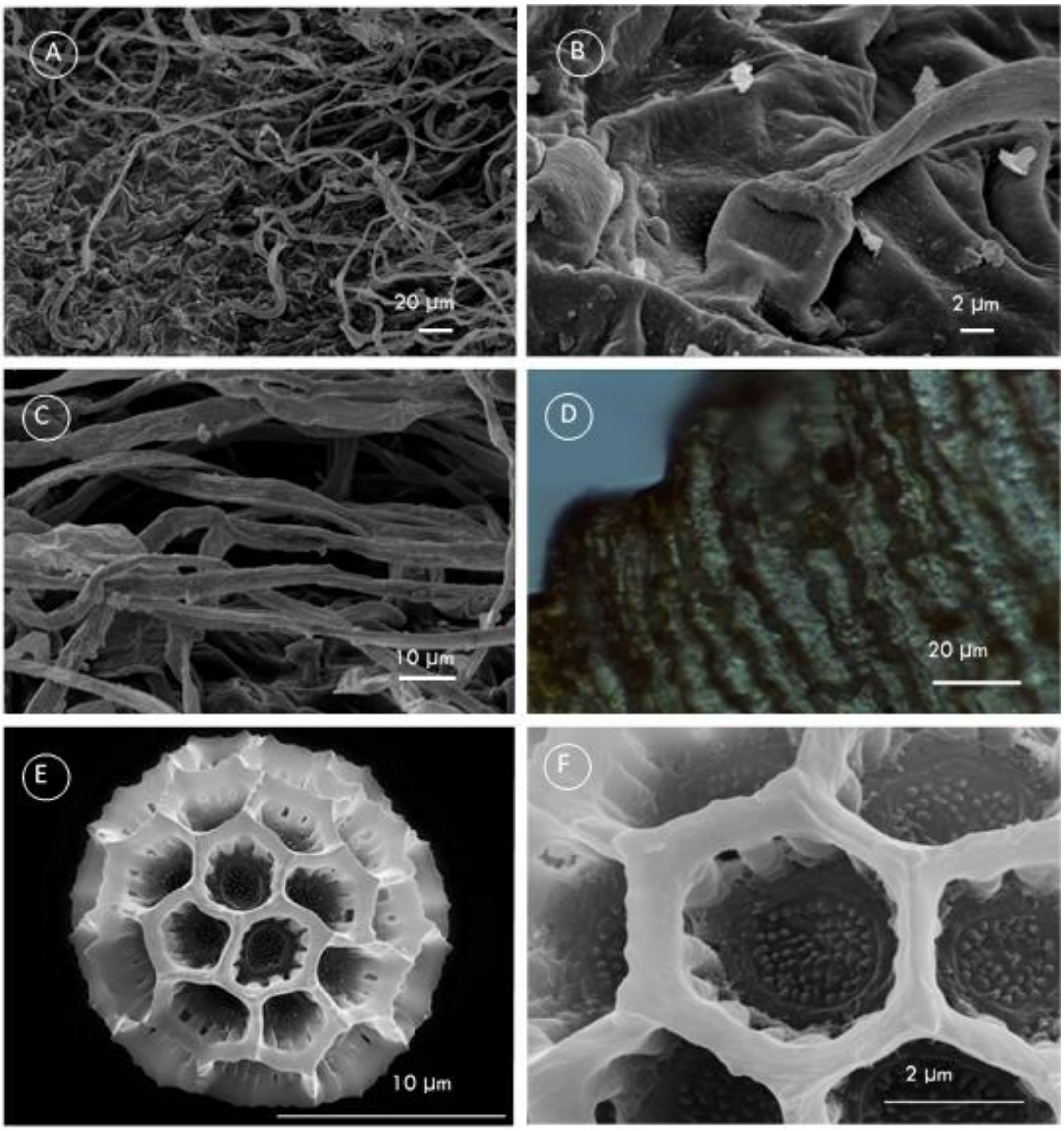


Fig. 4-82. *Gomphrena tomentosa* (Griseb.) R.E. Fr A) Dense trichomes of the adaxial side of the cauline leaf. B) Detail of the collapsed basal cells of trichomes of cauline leave and stems. C) Detail of simple not conspicuous interlocking junctions [voucher: Ortuño et al. 1235]. Tepal tissue. D) Detail of undulated, elongate and fibrous epidermis cells of the tissue [voucher: Tepals Borsch & Ortuño 3749]. E) Pollen overview. F) Detail of aperture [voucher: Beck & Paniagua 26642 (LPB)].

Habitat and ecology. Frequent on bare stony ground usually with sandy well drained soil, on broad valley bottoms with scattered or dominated by spinous shrubland with species such as *Prosopis ferox* Griseb., *Senegalia gilliesii* (Steud.) Seigler, *Senegalia emilioana* (Fortunato & Ciald.) Seigler, & Ebinger, columnar Cactaceae *Trichocereus herzogianus* Cárdenas, and trees like *Schinopsis cornuta* Loes. ex Herzog. In the ecoregion of Inter-Andean dry forest, Semi humid Puna, Prepuna, Gran Chaco, Tucuman-Bolivian forest, Chaco Serrano, where the plants were collected between (110) 250 - 3600 m.

Distribution. North-to center of Argentina, Provinces: Catamarca, Córdoba, Jujuy, La Rioja, Mendoza, Salta, San Juan del Estero, San Luis, Tucumán. Paraguay, Province of Boquerón. Southern Bolivia, Provinces of Sud Chichas, Nor Chichas (Dept. of Potosí), North Cinti, Belisario Boeto, (Dept. Chuquisaca). Cercado, José María Avilés, Aniceto Arce (Dept. Tarija). Manuel Maria Caballero (Dept. Santa Cruz). Cercado (Dept. Cochabamba) (see Fig. 4-88).

Specimens examined for distribution assessment. ***Argentina, San Juan,*** Valle Fértil, Ischigualasto, [-64,000065, -30,123511], 711 m, 6, 3, 1982, *Cortez, 122,* (SI). ***Tucumán,*** Tafí, Ruta 307. camino de El Infiernillo a Amaicha del Valle, [-65,8, -26,66666], 2840 m, 11, 2, 2002, *Cuidadela, A.M., 188,* (SI). ***Jujuy, Tilcara,*** arriba de Tilcara hacia la garganta del diablo, [-65,385633, -23,588462], 3000 m, 27, 1, 1999, *Beck, St.G., 26642*, (LPB). ***Bolivia, Tarija, José Maria Avilés,*** Serrania de Almendros. Hacienda comunal Pampa Grande, [-64,6, -21,766667], 1815 m, 10, 2, 1994, *Subieta, M., 42*, (LPB). Serranía San Nicolás norte, [-64,6, -21,766667], 1840 m, 30, 3, 1994, *Subieta, M., 136*, (LPB). ***Cercado,*** Camino a Bermejo saliendo de Tarija, [-64,6247, -21,646], 1774 m, 25, 4, 2009, *Fuentes Bazan, S., 166*, (LPB, B).Cerca a Angostura, [-64,59388889, -21,69305556],1750 m, 4, 3, 1988, *Bastian, E., 949*, (LPB). Bereich Gamoneda, [-64,654, -21,497222], 2050 m, 24, 1, 1982, *Gerold, 50,* (LPB, CTES). ***Méndez,*** cantón Paycho, [-64,959216, -21,14449], 2800 m, 26, 2, 1991, *García, E., 2308,* (LPB). ***Arce,*** 5 Km antes de llegar al abra de la Cruz, camino a Padcaya, [-64,65472222, -21,79916667], 1900 m, 30, 1, 1988, *Liberman, M., 1886*, (LPB). Padcaya, hacia Tarija, abajo del Abra de la Cruz, [-64,6727778, -21,85527778], 1991 m, 30, 1, 1988, *Beck, St.G., 16263*, (LPB). 2 km de Padcaya, [-64,6963333, -21,92083333], 1905 m, 10, 4, 2003, *Borsch, T.,* ***3649***, (LPB, B). ***Bolivia, Santa Cruz, Juan Manuel Caballero***, Saipina, ca. 3-4 Km W de Saipina, sobre el camino hacia Aiquile, [-64,591, -18,10066667], 1823 m, 20, 2, 2003, *Wood, J.R.I., 19141, USZ*, (LPB). ***Comarapa***, Jardin de cactaceae de Pulquina, [-64,4311, -18,0992], 1564 m, 28, 2, 2006, *Biggs, N, 86*, (LPB). ***Vallegrande,*** Suelo negruzco, algunos árboles aislados, [-64,292222,-18,525556], 1066 m, 4, 2, 2013, *Parada, G. A., 5427*, (MO, USZ). ***Chaco, Parque Nacional Kaa-Iya,*** puesto militar 27 de Noviembre, 11km al NO por la brecha al cerro Ustarez, [-61,861944, -19,945556], 318 m, 16, 7, 1998, *Fuentes, A.*, 2569, (LPB). ***Chuquisaca, Nor Cinti,*** Camargo 26 kms. hacia Villa Abecia, [-65.2255, --20.86166], 2410 m, 24, 3, 1979, *Beck, St.G., 704,* (MO, LPB, B, CTES, NY, SI). Saliendo de Camargo, [-65,229444, -20,7286111], 2426 m, 14, 4, 2010, *Ortuño, T.,* ***1235***, (LPB). Camino Camargo-Villa Abecia. Suelo rojizo pedregoso. Cabras, [-65,255, -21,0186111], 2394 m, 15, 4, 2010, *Ortuño, T., 1237,* (LPB). Las Carreras, [-65,21666, -21,25], 2744 m, 22, 2, 2008, *Ortuño, T., 1358,* (LPB). ***Belisario Boeto***, Bajando Nuevo mundo hacia Santa Rosa en dirección hacia el río grande, [-64,294444, -18,91], 1200 m, 2, 3, 2006, *Wood, J.R.I., 22334*, (HSB). ***Bolivia, Potosí, Nor Chichas***, Parinolqui, [-65,56068, -20,72222], 3106 m, 18, 4, 2010, *Ortuño, T., 1248*, (LPB). [-65,56068, -20,72222], 3106 m, 18, 4, 2010, *Ortuño, T., 1251*, (LPB). Cascabel, [-65,63095, -20,75086667], 3140 m, 22, 2, 2008, *Ortuño, T., 1284*, (LPB). Planicie surcada por cárcavas y pequeñas quebradas, [-65,5, -

20,25], 2960 m, 2, 4, 1999, *Lopez. R., 549*, (LPB). Parinolqui, [-65,5691, -20,72724167], 3100 m, 22, 2, 2008, *Ortuño, T., 1303,* (LPB). Parinolqui, [-65,488833, -20,69688333], 3000 m, 22, 2, 2008, *Ortuño, T., 1331*, (LPB), Ca. 7 km al Norte de Cotagaita, [-65,518, -20,0825], 3030 m, 2, 4, 2004, *Borsch, Th., 3722*, (LPB, B).Tupiza, Al borde de la ciudad subiendo en la quebrada de Palala. Quebrada ancha con abanicos laterales de sedimentos y roca semidesierto de cactaceas columnares, [-65,76916667, -21,4219444], 3050 m, 1, 1, 2012, *Beck, St.G., 33662*, (LPB, B). Quebrada de Palala between Tupiza and El Sillar, [-65,74305556, -21,42277], 3100 m, 29, 3, 1997, *Wood, J.R.I., 11939*, (LPB).

4.3.9.2. *Gomphrena umbellata* Remy, Ann. Sci. Nat., Bot. ser. 3, 6: 349. 1846.

Type: Orbigny, A. d' 1523, Bolivia, Prov. Carangas, cerca de Cotora, (HT: P 00623731, IT: P 00623733, P00623732).

≡ *Xeraea umbellata* (Remy) Kuntze., Revisio Generum Plantarum 2: 545. 1891. (5 Nov 1891).

= *Gomphrena pearcei* Oliv. Hooker's, Icon. Pl. 11: t. 1073. 1870 Type: Ruiz & Pavon, 30/26; 1778-88; Perú (F).

Annual plants, 3-4.5 (--6) cm. ***Root*** simple-fibrous. ***Stems*** prostrate, always with tertiary and quaternary stems, terminating in a radial umbrella shape, red to green or pink, thin, smooth, with few tomentose trichomes 1 (--3) mm, white in the nodes the rest glabrous. ***Basal leaves*** linear-spathulate, 1-1.3 (--1.5) x 0.1-0.2 (--0.3) mm, rounded at apex, at base decurrent, fleshy in consistence, marmolate green, few lanate trichomes generally in the basal node, white. ***Cauline leaves*** ovolanceolate to spatulate, 0.3-0.6 (--1) x 0.1-0.2 (0.3) mm, acute to rounded, fleshy consistence. ***Apical leaves subtending paracladia*** (inflorescences) 3-5, leaves arranged symmetrically, ovolanceolate to spathulate, 0.4 (--0.5) x 0.1 (--0.3) cm, rounded at apex, connate at the base, green marmolate, glabrous or scarse trichomes in the margin, white. ***Inflorescences*** (paracladia), globose, subglobose, terminal, 0.4-0.5 (--0.7) cm in diameter, consisting of 1-3 partial florescens. **Flowers** 2.2-2.8 (--3.2) mm long. ***Bract*** oval-rounded, 1 (--2) x 0.8 (--1.5) mm, involve the flowers undulate margin, middle nerve promined and thick membranous, white translucent. ***Bracteoles*** oval-rounded, 1.8-2.2 (--3) x 1.3 (--2) mm, membranous in texture, white, the lower part is thin, the upper part is rounded and undulate. Bracteoles bigger than the tepals. ***Tepals*** spatulate-rounded, fine membranous texture, ligth yellow, dentate apex obsolete, very fine tepals, difficult to see, because the tissue are fine membranous and thin, and stickiness in the androceum tube, few trichomes in the margin. Sizes unequal. External tepals 1 (--1.3) x 0.4 (--0.6) mm, intermediate tepal 0.9 (--1.2) x 0.2 (--0.4) mm and inner 0.9 (--1) x 0.2 (--0.3) mm (Fig. 4-83F). ***Filaments*** 1.4 (--1.8) mm, fused part 1.2 (--1.6) mm long, yellow, light brown. ***Filament appendages*** conspicuous, 0.2 mm long, undulate, rounded. ***Anthers*** oblong in shape, 0.4(--0.5) mm long, inserted is in the apex of the only one filament appendices. ***Gynoecium*** with two filiform stigma branches, of 0.4 (--0.6) mm, style 0.2 mm, ovary 1.6 mm. [voucher: Acho, 2= AC102 (LPB)].].

Micromorphology of trichomes. Multicellular, uniseriate. On ***stems and cauline leaves*** with 1-2 firm rounded basal cells, 4-5 upper cells with striate and foveolate texture, scarce spinous ornamentations on the cuticule walls. ***Interlocking junctions*** conspicuous, linear, scars or projections of the extreme border cells overlapping zero angle degrees. Trichomes on ***apical leaves subtending paracladia*** similar than the cauline leaves or glabrous. Trichomes on ***tepals*** very thin, trichomes with collapsed cells. ***Anatomy of tepals.*** Tissue composed by elongated strait, cylindrical cells, arranged in one row, the extremes fitting perfectly [voucher: Acho, 2 = AC102 (LPB)].

P***ollen.*** Size ~16.4 µm. Pore number: 50-56. Pores: 3.8 µm in a diameter, pore membrane with ektexinous bodies, widely arranged circularly in a mosaic like a pattern. Mesosporia forming irregular hexagons or pentagons, apical surface undulates as dentate shape, at corners with sharp and acute protusions (as microspine). *Tectum* as a vertical ligament at distal side, with columellae in the lower two thirds of the vertical sides freely visible. C*olumellae* 15-20, these are arranged in a row around the pore, they are nearly equal in size and ~0.9 µm high, but the distance between them differs [voucher: Borsch & Ortuño 3727= AC437].

Taxonomic remark. The species identified currently as *G. umbellata* are peculiar plants growing in a specific xerophytic habitat usually in soil with high proportions of sand. The morphological characteristic of this species is the annual habit, and the branches that are divided many times forming an umbrella shape. These are two important characteristics to easily recognize this species.

The voucher choosen for the description is Acho, 2. This specimen is similar to the one described by De Saint Remy (1846), and Holzhammer (1956). His morphological characteristics are bract and bracteoles ovate to rounded, undulate at apex, and the tepals that have a fine membranous texture. The majority of specimens reviewed in the Herbarium LPB are similar to this type. But some specimens vary in the shape and size of the bract; this is the case in the vouchers: Wood, J.R.I 10741, and Beck, St. 23706, where the bracts show greenish marmolate colour, similar to the apical leaves subtending the inflorescence; they also show trichomes on the margin, and also in the dorsal part. These types of bracts were observed in the specimens reviewed in the flora of Perú (Mac. Bride 1937) according to the descriptions. Mc. Bride includes these specimens as *G. umbellata* into the concept proposed by De Saint Remy (1846). This work follows this idea.

Habitat and ecology. The species occurs in the South East of Bolivia, usually in open areas with sandy soil, between open shrubland with species as *Fabiana densa* Remy, *Parastrephia quadrangularis* (Meyen) Cabrera, *Parastrephia* ssp., grasses as *Festuca orthophylla* Pilg.; also it is found in areas surrounding quinoa crops and in areas “pampa Tajzara” with shrublands near dry forest. *Gomphrena umbellata* Remy always are usually covered with sand. Common in wet season, in the ecoregions of Semi humid Puna, Dry Puna, Desertic Puna, where the plants have been collected between 2800 - 4000 (4400) m.

Distribution. The species is distributed in the north of Argentina, provinces of Catamarca, Jujuy, Salta. Paraguay, and in the Southern East of Bolivia, provinces of Sajama, Ladislao Cabrera, Carangas (Dept. Oruro), provinces, Daniel Campo, Uyuni, Tomas Frias (Dept. of Potosí), provinces, Aroma (Dept. La Paz), province Jose Maria Avilez (Dept. Tarija) (see Fig. 4-88).

Specimens examined for distribution assessment. ***Argentina, Jujuy,*** Camino de Yavi a Santa Victoria, [-65,28216667, -22,2193333], 4438 m, 4, 4, 2004, *Borsch, Th.*, *3727*, (LPB, B). ***Salta,*** La Poma, Ruta 40, 57 km de San Antonio de Los Cobres, 3 km antes de límite con Jujuy, frente a Salinas Grandes, [-66,033333, -23,783333], 3424 m, 19, 2, 2002, *Cialdella*, *Ana M.*, *Deginani*, *Norma B.* & Giussani, *Liliana M.*, 461, (SI). *San Antonio de los Cobres*, Dept. Busario & Perua. Camino a San Antonio. Ladera del cerro, [-66,319167, -24,225556], 3763 m, 26, 12, 1929, *Venturi*, *Santiago, 10010*, (LPB). ***Bolivia, Oruro, Sajama,*** 20 Km al S del poblado de Turco (Estación Experimental de CORDEOR), [-67,9769444, -17,49555], 3820 m, 5, 5, 1981, *Liberman*, *M.*, *3009*, (LPB). ***Ladislao Cabrera,*** A un Km de la localidad de Jirira, [-67,5683333, -19,84333], 3813 m, *Acho, J., 2*, (LPB, B). **Carangas** near Cotora, [-68,6333, -17,9, 4139], 0, 0, 1826, *d'Orbigny*, *A.C.V.*, 1523, (F, P). ***Potosí, Daniel Campos***, a 3 km de la localidad Chacoma, [-68,505556, -19,714167], 3794 m, 15, 3, 2008, *Acho, J.*, 105, (LPB). **Antonio Quijarro**, Uyuni, Delta del Río Grande de Lípez, en el borde sur del salar de Uyuni, [-67,026328, -20,704236], 3705 m, 28, 2, 2006, *Milliken, W, 4073*, (LPB). ***Tomás Frias,*** On the hill west of Cayara leading to the reservoir, [-65,91416667, -18,3625], 2865 m, 20, 2, 1996, *Wood, J.R.I, 10741*, (LPB). ***La Paz, Aroma,*** "Ayhuir Phiti" 28 Km al Sur de Patacamaya, ribera Norte del rio Desaguadero, [-67,696392, -17,365181], 3832 m, 28, 4, 1991, *Liberman, M., 3009,* (LPB).*Pacajes,* Ulloma, [-68,5, -17,5], 3750 m, 16, 2, 1927, *Troll, C., 3124*, (JE). ***Tarija, José María Avilés,*** cerca Copacabana, [-64,080555, -21,82416667], 3519 m, 30, 1, 1986, *Bastian, E., 658*, (LPB). Tajzara, cerca Arenales, [-65,04972222, -21,81138889], 3700 m, 10, 3, 1986, *Bastian, E., 1037*, (LPB). Pampa de Tajzara, Arenales, [-65,04388889, -21,8158333], 3790 m, 18, 4, 2000, *Beck, St.G., 27052*, (LPB). Quiliaras Ulloma, 3800 m, 29, 12, 1926, *Troll, C., 3018,* (LPB). Arenales cerca a Copacabana, [-65,083333, -21,85], 3750 m, 6, 3, 1998, *Beck, St.G., 23706*, (LPB).

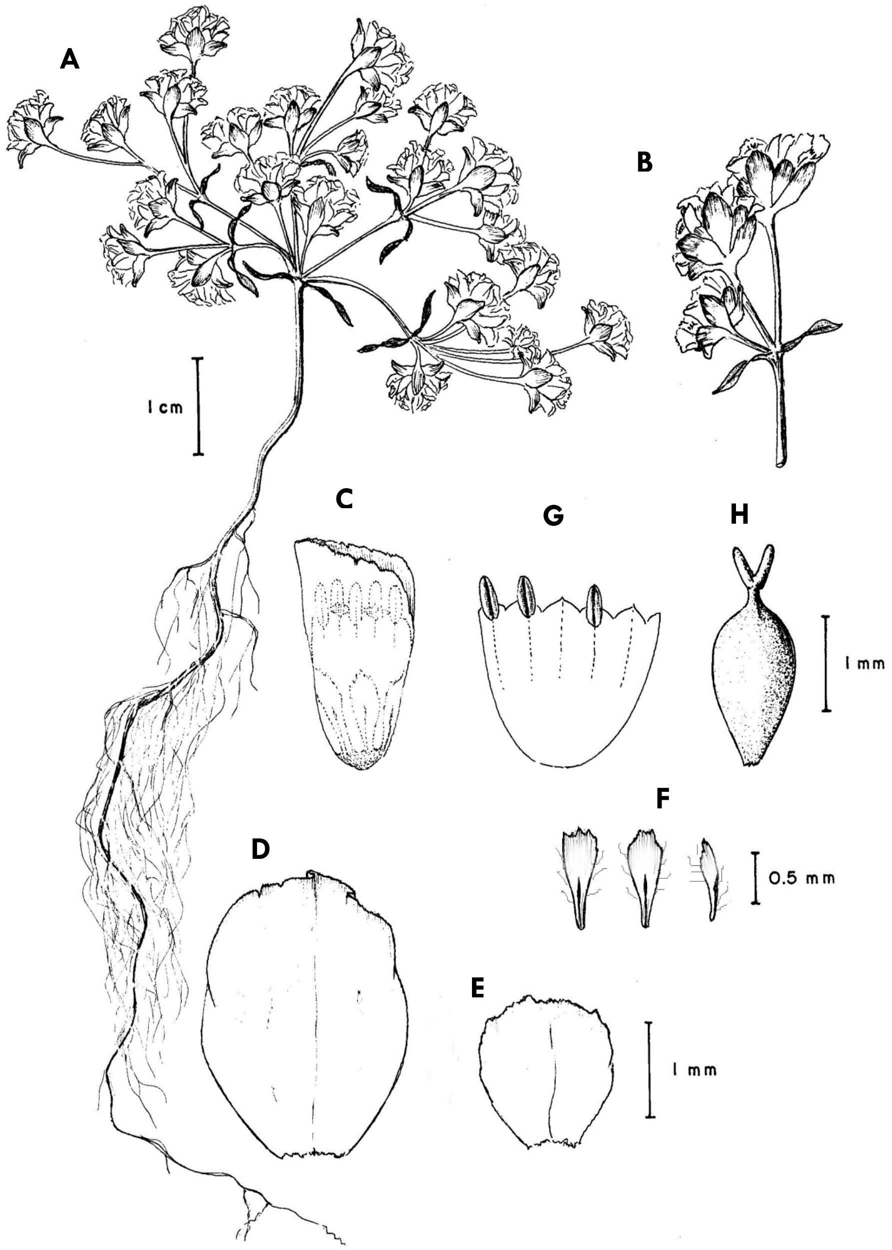


Fig. 4-83. *Gomphrena umbellata* Remy. A) Habit. B) Paracladia. C and D) Bracteole. E) Bract. F) Tepals. G) Detail of the androecium. H) Gynoecium [voucher: Acho 2 = AC1025].

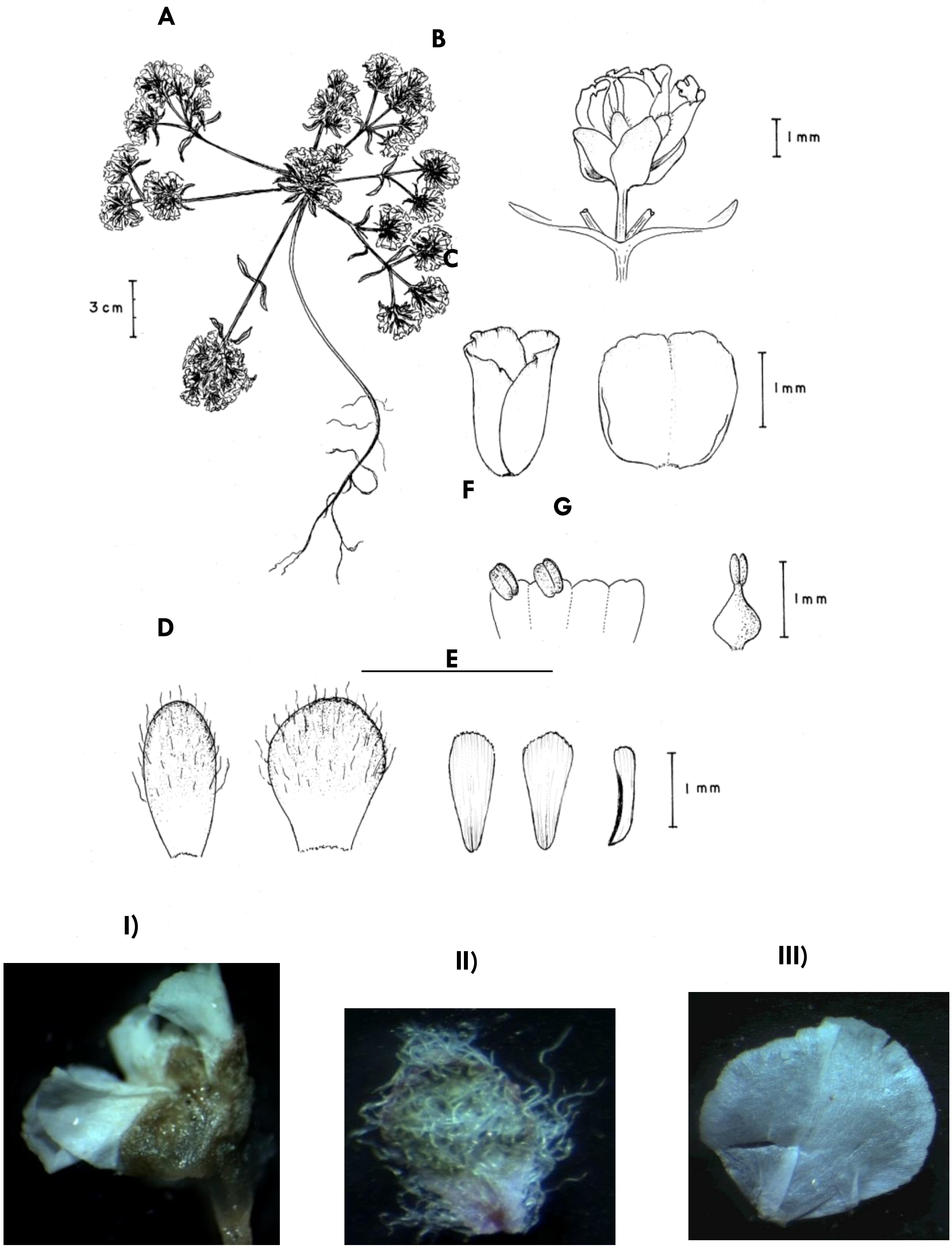


Fig. 4-84. *Gomphrena umbellata* Remy. A) Habit. B) Paracladia. C) Bracteole. D) Bract. E) Tepals. F) Detail of the androecium. G) Gynoecium. I. Paracladia, II. Bract. III. Bracteole [voucher: Wood 10741= AC171].

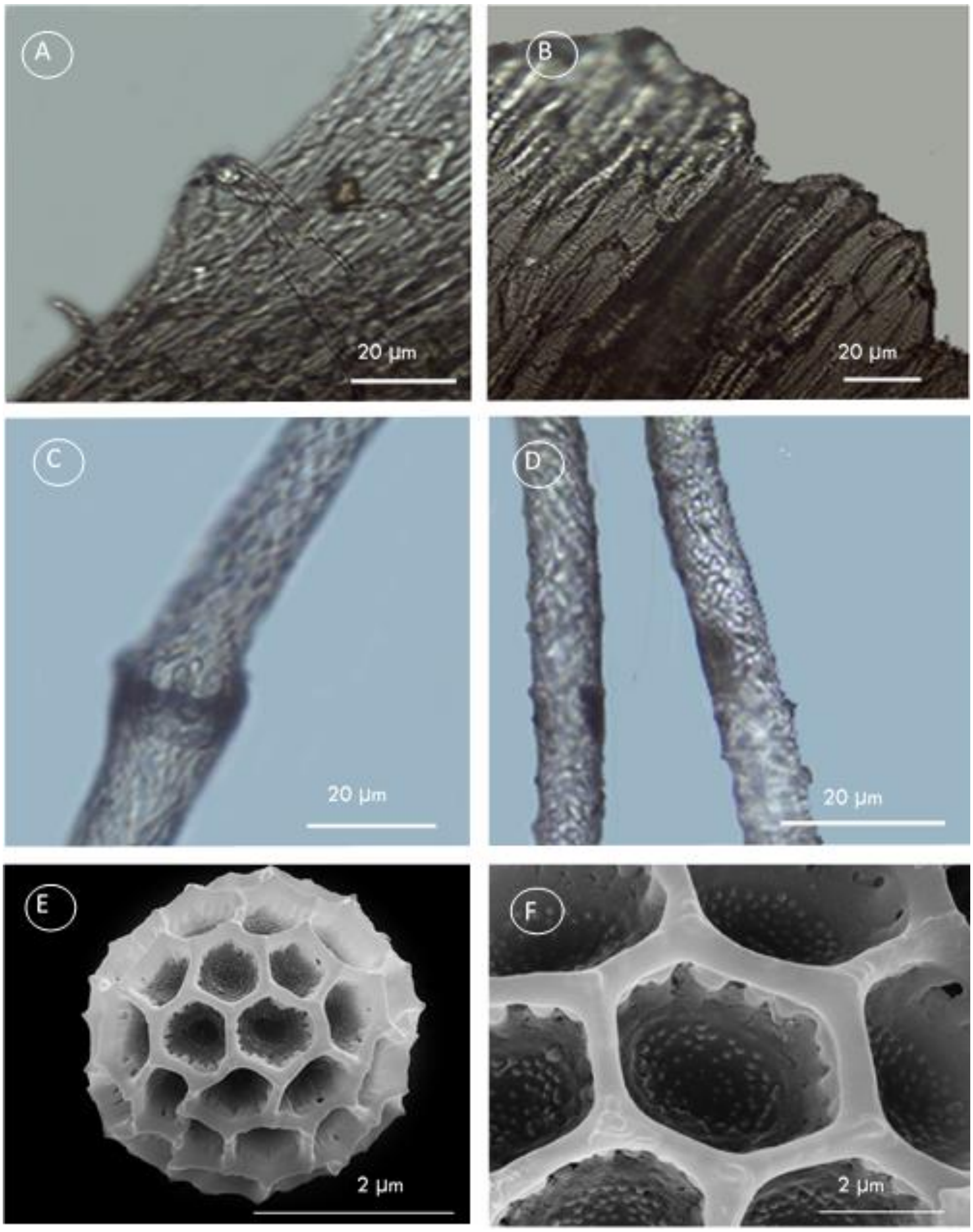


Fig. 4-85. *Gomphrena umbellata* Remy. A) Detail of trichomes that are lanate on the margin and tissue of the tepals B) Detail of the rounded apex. C) Detail of simple interlocking junctions, D) striate to feovelate, and spinous ornamentation of cuticle walls [voucher: Acho, 2.]. E) Pollen general overview. F) Detail of pore, mesosporium, with hexagons or pentagons, corners with sharp and acute protusion [voucher: Beck & Paniagua 26642 (LPB)].

4.3.9.3. *Gomphrena radiata* Pedersen, Darwiniana ser. 20, (1-2): 294. 1976.

Type: Argentina Distrito Federal, San Antonio de los Cobres, ad Tipan in loco Campo de la Paciencia dicto die 13, 1945, Cabrera, 8705 (LP LP010865).

Annual herb, 4-9 (--17.7) cm. ***Root*** fibrous, simple. ***Stems*** prostrate, always with secondary branches arranged in radial form, striate, red, glabrous or with few trichomes of 1 to 3 mm long (other samples can be present major density tomentose trichomes). ***Basal leaves*** lanceolate-ovate 0.4-1.3 (--1.5) x 0.2-0.4 cm, acute at apex, decurrent at base, indumentum tomentose. ***Apical leaves subtendig paracladia*** (inflorescences*)* 4-6, leaves arranged symmetrically, lanceolate-ovate, 0.7 (--1.5) x 0.3 (--0.7) cm, apiculate at apex, green olive, indumentum tomentose, thin trichomes denser than on the basal leaves, near the node, white. Some inflorescence axillar, apical leaves subtending the paracladia not present. ***Inflorescences*** globose, terminal and axillary, 0.5-0.8 (--1) cm in diameter, consisting of 3-4 partial florescences, yellow. ***Flowers*** 1.4-2 (--2.4) mm long. ***Bracts*** ovate to spatulate, 1-2 x 1-2 mm, membranous in texture, white, cuspitate at apex, entire or undulate at margin. ***Bracteoles*** roundish to spathulate, 1.4-1.5 (--2.2) x 1.5 (--2) mm, membranous in texture, light yellow, rounted at apex, undulate margin. ***Tepals*** spathulate, membranous texture, ligth yellow, rounded apex. With trichomes denser lanate indumentum in the dorsal half part. Size unequal. External tepals 2-2.2 x 0.7 mm, intermedian tepal 2-2.2 x 0.4-0.7 mm, inner tepals 0.8-1 (--2) x 0.4-05 mm. ***Filaments*** 2 mm long, fused into a tube, the fused part is 1.8 mm long, the free part is 0.2 mm long. ***Filament appendages*** 0.2 mm long, with convex projections, rounded at apex, yellow or light brown. ***Anthers*** oblong, 0.4 mm long, inserted in each of five ondulate lobules apex. ***Gynoecium*** with two filiform stigma branches, 0.4 mm long, style 0.4 mm, ovary 0.8 mm. [voucher: Borsch, Ortuño, & López 3740 = AC443 (LPB, B)].

Micromorphology of trichomes. Multicellular uniseriate. On ***stems and cauline leaves* with**1-2 basal cells, the first firm and rounded, the second can be collapsed; flat in sclupture, without ornamentation, striated. The upper cells collapsed to flexible cells, prominently striated in sculpture, of cuticule walls. ***Interlocking junctions*** not conspicuous, only a node. Trichomes on ***apical leaves subtending paracladia*** similar than on the stems. Trichomes ***on tepals*** similar than on stem but thinner. ***Anatomy of tepals.*** Tissue with longer parallel cells, some broad with straight or undulated walls, tubular [voucher: Borsch & Ortuño 3749= AC445 (LPB, B)].

Pollen. Size ~15.7 µm. Pore number: 40-46 Pores: 3.2 µm in a diameter, pore membrane with ektexinous bodies, dispersal, margins appear confluent. Mesosporia forming irregular hexagons or pentagons. *Tectum* only distal, undulate in the distal margin, and with pronounced corner as spines. Columellae,visble, only connected with the tectum below the end of the corners [voucher: Borsch, Ortuño, & López 3740] (Fig. 4-87 e and F).

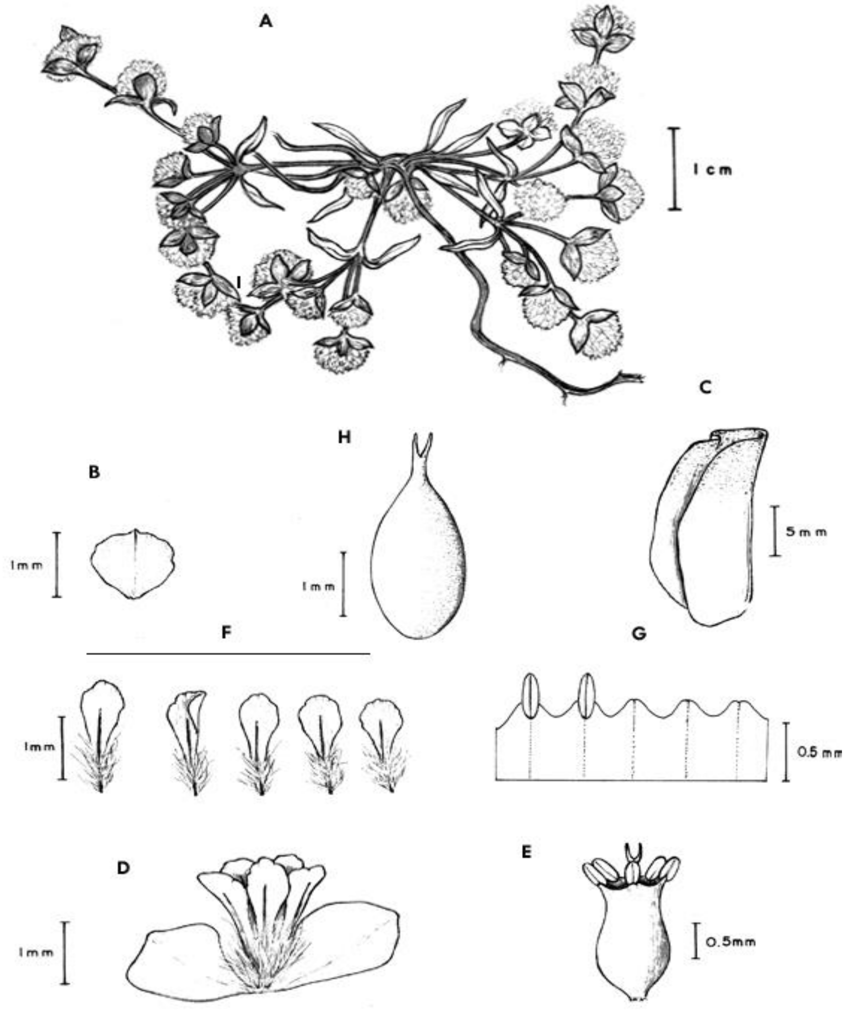


Fig. 4-86. *Gomphrena radiata* Pedersen. A) Habit. B) Rounded apex of bract. C) Ovate, undulate margin of bracteoles. D) Flowers. E) Tube of androecium. F) Tepals with trichomes in the basal dorsal part. G) Detail of the androecium. H) Gynoecium [voucher: Borsch & Ortuño 3749].

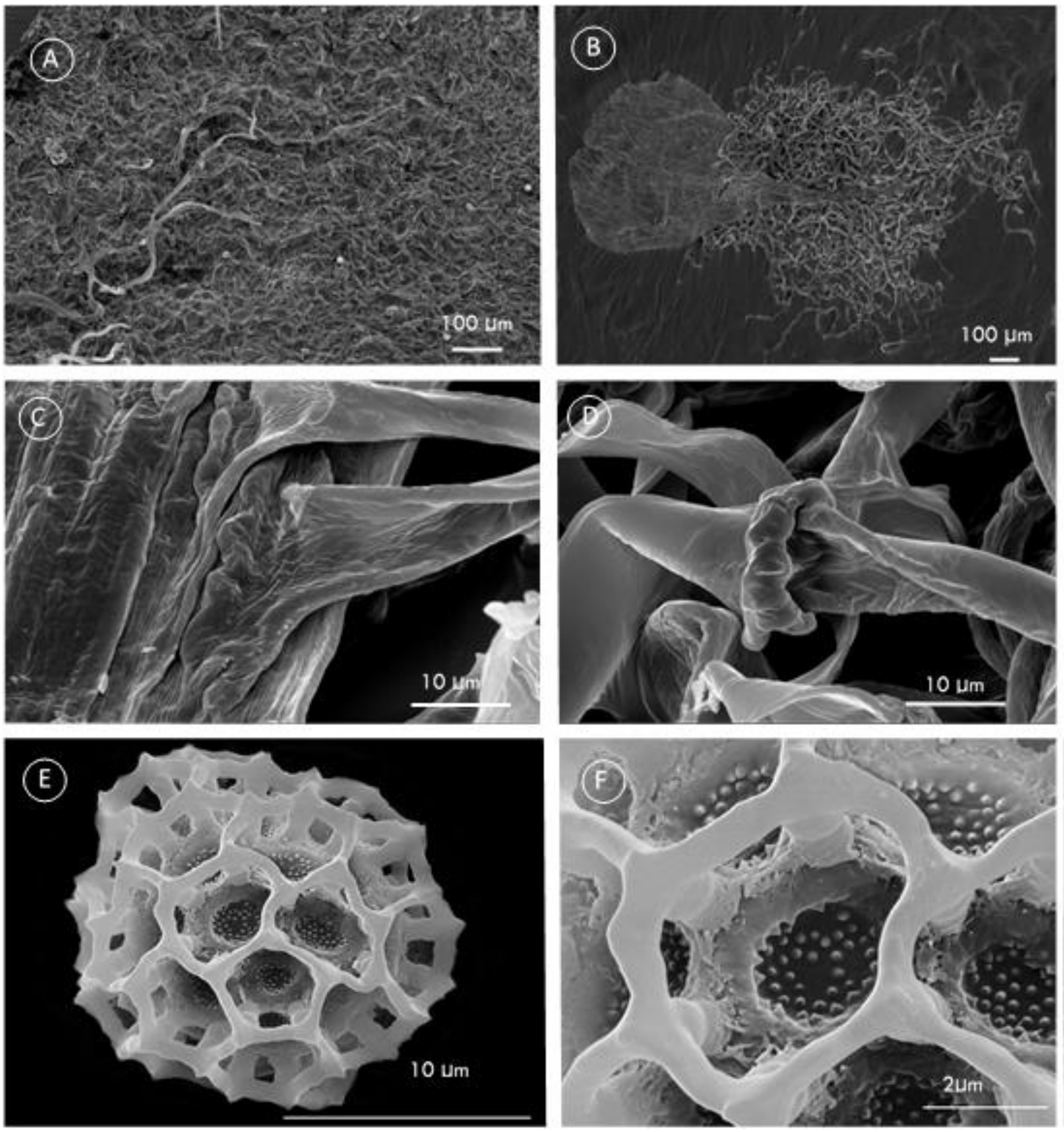


Fig. 4-87. *Gomphrena radiata* Pedersen. A) Trichome scares with collapsed cells of the abaxial side of cauline leaf. B) Detail of the spathulate tepals with dense trichomes in the dorsal side. C) Detail of basal cells of the trichomes. D) Detail of simple interlocking junctions. E) Pollen with distal tectum band, and with pronounced corner as microspines. F) Detail of the aperture. [voucher: Borsch & Ortuño 3749=AC445].

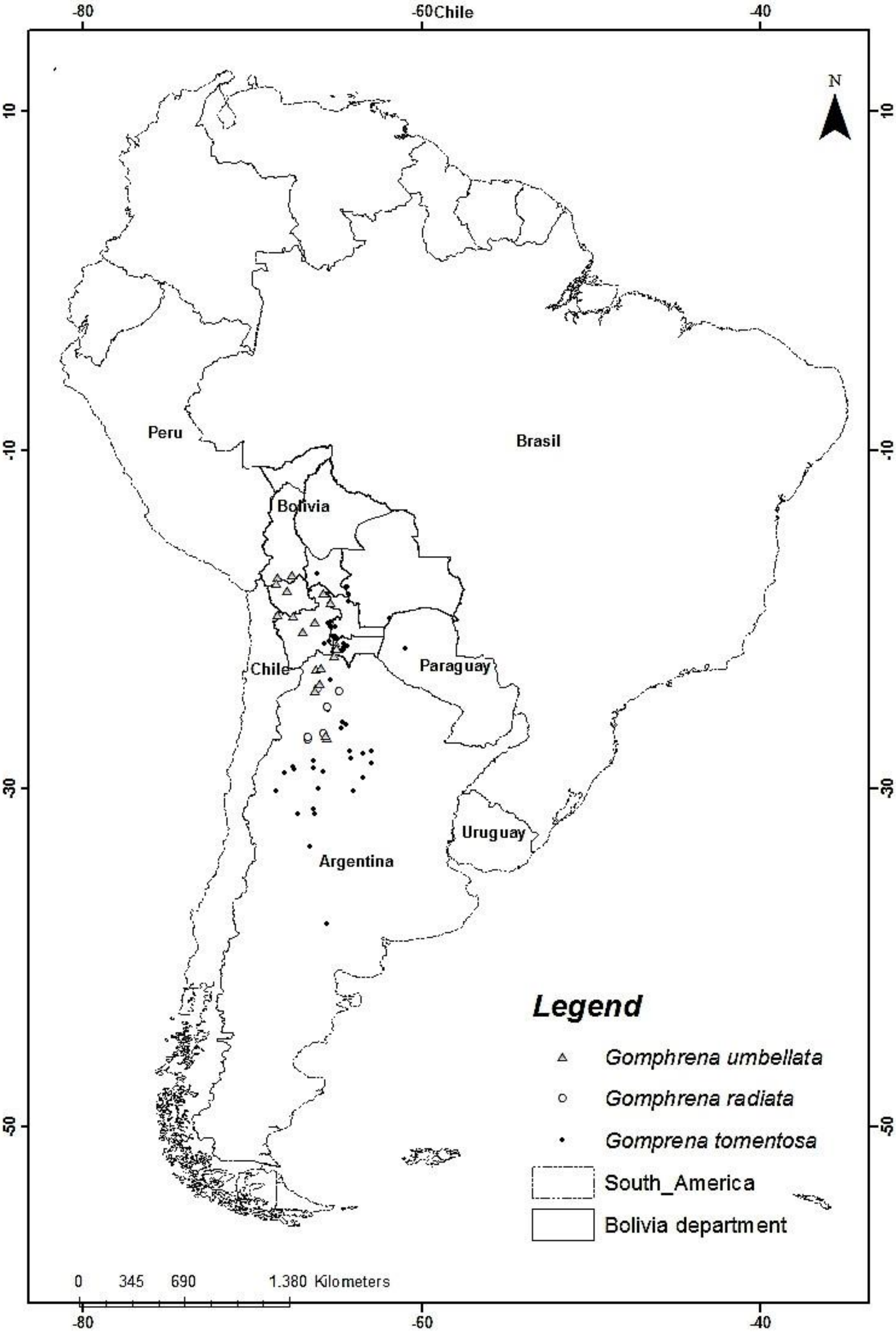


Fig. 4-88. Map of distribution of *Gomphrena umbellata*, *G. radiata*, and *G. tomentosa*.

Habitat and ecology. Frequent in open areas with sandy soil, between shrubland of *Parastrephia quadrangularis* (Meyen) Cabrera, *Fabiana densa* Remy, few herbs and grasses such as *Bouteloua simplex* Lag. Endemic of Northern of Argentina in Xeric Puna, where the plants are collected between 2850-3660 m.

Specimens examined for distribution assessment. Northern Argentina. Province of Catamarca, Jujuy, Salta, Tucumán. ***Argentina, Catamarca,*** Belén, 46 km on Ruta 53 (given as Ruta 43 on some maps) from turnoff from Ruta 40 towards Antofagasta de la Sierra, 2 km below turnoff of access road to Los Nacimentos de San Antonio, [-66,752447, -27,087243], 2850 m 20, 2, 1994, *Leuenberg, B, 4288*, (Conicet). ***Salta,*** 10 km pasando San Antonio de los Cobres, [-66,302333, -24,1555], 3660 m, 8, 4, 2004, *Borsch, T., 3749*, (LPB, B). 10 km pasando San Antonio de los Cobres, [-65,952666, -25,231666], 3064 m, 8, 4, 2004, *Borsch, T., 3740*, (LPB, B). ***Jujuy,*** San Antonio, ad Tipán in loco Campo de la Paciencia, [-68,3, -24,216667], 3090 m, 13, 2, 1945, *Cabrera, A. L., 8705*, (MO). ***Tucumán***, Tafí, Infiernillo, [-65,784517, -26,73519], 3000 m, 26, 3, 1989, *Pedersen, T.M., 15345*, (CTES, SI).

4.3.10. Gomphrena martiana CLADE

The phylogenetic results showed with high resolution that the *G. martiana* and *G. boliviana* are belonging to a monophyletic group. The nuclear nrITS tree presents high support (1PP, 100 JK) similar to the chloroplast tree (*matK-trnK*), (1.00 PP, 100 BS, 100JK). However, the first showed one subclade, including two specimens determined as *G. martiana*, and the specimen of *G. boliviana* that emerge alone as a sister of a *G. martiana* subclade (see Chapter 3).

The species *Gomphrena martiana* and *G. boliviana* are morphologically similar and it is very difficult to find differences between them. Therefore, it is morphologically useful and important to consider as a diagnostic character the size of the bract in relation to the bracteoles (Pedersen 1990, 1997).

Key to the species of *Gomphrena martiana* and *G. boliviana* clade

1. Plants with stems decumbent to prostrate, < 20 cm usually 7 to 15 cm….G. spissa (Fig. 4-92)

1’.Plants with stems decumbent to erect, ramose, > 40 cm to 150 cm. (2)

2. Plants with basal leaves, Apical leaves subtending the paracladia short than the inflorescence, with the bract is shortly then the middle half of the bracteoles …….…… *G. martiana* (Fig.4- 89)

2’. Plants without basal leaves Apical leaves subtending the paracladia bigger than the inflorescence. With bract bigger than the half part of the bracteoles
……………………………………………………………………… *G. boliviana* (Fig.4-91) (3)

3. Flowers with the outer tepals without indumentum the inner tepals with dense trichomes.

………………………………………………………………………… *G. boliviana* fa. *robusta*

4.3.10.1. *Gomphrena martiana* Gillies ex Moq., Prodr. A. DC., ser.13, (2): 400.1849.

Type: Argentina, San Luis, El Morro, Gillies s/n (LT: K 000634970, ISLT: P P00622698, designed by Bena 2017)

= *Gomphrena argentina* Seub. Flora Brasiliensis 5(1): 208. 1875.

Type: Lorentz n. 386 Cordoba, Argentina, Brasiliae contermina, crecit ad fluviorom ripas pr. (HT: F F0BN003240, M M0241752)

≡ *Gossypianthus martiana* Hook.f. Bentham, G. & J. D. Hooker.Genera Plantarum I (3):40.1880

= *Gomphrena glutinosa* R.E. Fr. Arkiv för Botanik utgivet av K. Svenska Vetenskapsakademien 16(12): 28. 1920.

Type. Fries 1669, Bolivia, Gran Chaco, 21-4-1902, in ripa argillacea fluminis (HT: S-R-2440S).

= *Gomphrena martiana* var. *glutinosa* (R.E. Fr.) Pedersen Adansonia, série 3, 19: 230. 1997.

Type. Fries 1669, Bolivia, Gran Chaco, 21-4-1902, in ripa argillacea fluminis, (S).

Annual or biannual herb, 30-140 cm. ***Root*** fibrous,simple. ***Stems*** decumbent, prostrate to erect, divided in secondary and terciary branches, striate, light brown, few denser appressed, trichomes white. ***Basal leaves*** ovate-lanceolate, 3-4.5 (--5.5) x 1.5 (--2.5) cm, acute apex, middlenerve and secondary nerves prominent, mucronate 0.4 mm, few denser trichomes in the both faces of leaves, trichomes white ***Cauline leaves*** ovolanceolate-decurrent, 4.5-5.3 (--5,5) cm, acute apex, margin entire, coriaceae texture, green, trichomes type equal than the stem. ***Apical leaves subtending paracladia*** (inflorescences) 5, leaves arranged symmetrically, ovolanceolate 1-1.5 (--1.8) x 0.4-0.5 cm, acute apex, green, with few dense trichomes in the margin and on the nerve, white. ***Inflorescences*** globose to subglobose, terminal, 0.5-1.2 (--1.5) cm in diameter, consisting 2-6 partial florescens, yellow-white. ***Flower*** 3.6-4 (--4.5) mm long. ***Bract*** ovolanceolate, 2 (--2.4) x 1 (--1.2) mm, membranous texture, white translucent colour, acuminate apex, entire margin, white (Fig.4-89B). ***Bracteoles*** ovolanceolate, 4 x 1.5 mm, membranous in texture, white, middle nerve dorsal prominent. ***Tepals*** oblong to lanceolate, membranous in texture, white, abruptly acute at apex, with middle nerve, connate at the base, lanate trichomes in the dorsal part, few teeth in the margin and the apex. Size unequal. External tepals 3.6 (--3.8) x 0.8-1 mm, intermediate tepal 3.6 (--3.8) x 0.8 mm, inner tepal 3.5 (--3.6) x 0.6 mm. ***Filaments*** fused into a tube, 3-3.5 (3.6) mm long, fused part 1.8 (--2.0) long, free part 1 (--1.2) long, narrowly linear. ***Filament appendages*** lacking. ***Anthers*** oblong, 1.2 mm of long, united in the apex of the each single lobes of filament appendices (Fig. 89F). ***Gynoecium*** with two filiform stigma branches 0.6-1 mm of long, style 0.2-0.4 mm, ovary 1 mm long [voucher: Borsch, 3535= AC495].

Micromorphology of trichomes. multicellular uniseriate: ***Stems and caulinar leaves*** with a 1-2 cells, the first rounded shaped, flat texture, narrowly in the apex, with granulate ornamentation in the around the apical part of the cells. The upper next, 4-6 cells, granulose to salicose ornamentations, firm to flexible consistence, striated texture in the walls cuticule. *Interlocking junctions*, conspicuous linear, scars arranged in angle zero angle degrees. ***Trichomes on apical***

leaves subtending paracladia, similar than the stems. ***Trichomes on tepals,*** in dorsal 2(--3) mm. firm rounded shaped in the basal 1-2 cells, the upper cells with collapsed cells, flexible, without ornamentation, flat texture, and simple node Interlocking junctions (Fig. 4-90F), ***Anatomy of tepals.*** Tissue are compose by elongate strait, cylindrical dermal cells, arranged in one row, the extremes fitting perfectly. [voucher: Borsch 3535].

Pollen. Size 17.3 µm. Pore number 44-50. Pore ~3 µm in a diameter, pore membrane with ektexinous bodies, outstanding as a granule (subglobose), arranged circularly in a mosaic like a pattern. Mesosporia building hexagons and pentagons, acute (sharp) at corners. *Tectum*: ligament is complete, with a broadly columellae in the lower half of the vertical parts. C*olumellae*: situated just under the conjunction points broadly, forming big open areas free (Fig.4- 90 G and H).

Habitat and ecology. Abundant and sometimes dominant as weed to the exclusion of other plants, in secondary vegetation, disturbed places such as urban areas or pasture, crop fields in rocky steep slopes, border on roadsides. Huge alluvial plain between mountains. In ecoregions of Inter-Andean dry forest, Prepuna, Gran Chaco, Chiquitano dry forest, Tucuman-Bolivian forest, Chaco Serrano, where the plants are collected between 300-2800 m.

Distribution. ***Argentina***, Province of Catamarca, Córdoba and Jujuy, La Pampa, La Rioja, Salta, San Luis, Tucuman, ***Paraguay***, province of Boqueron, Chaco and Nueva Asunción. ***Bolivia***, Prov. Luis Calvo (Dept. Chuquisaca), province of Cercado and Mizque, Quillacollo (Dept. Cochabamba). Nor Chichas (Dept. Potosí), province of Andres Ibañez, Cordillera, Florida, Manuel Maria Caballero, Ñuflo de Chavez and Valle Grande (Dept. Santa Cruz). Province of Cercado and Gran Chaco, (Dept. Tarija).

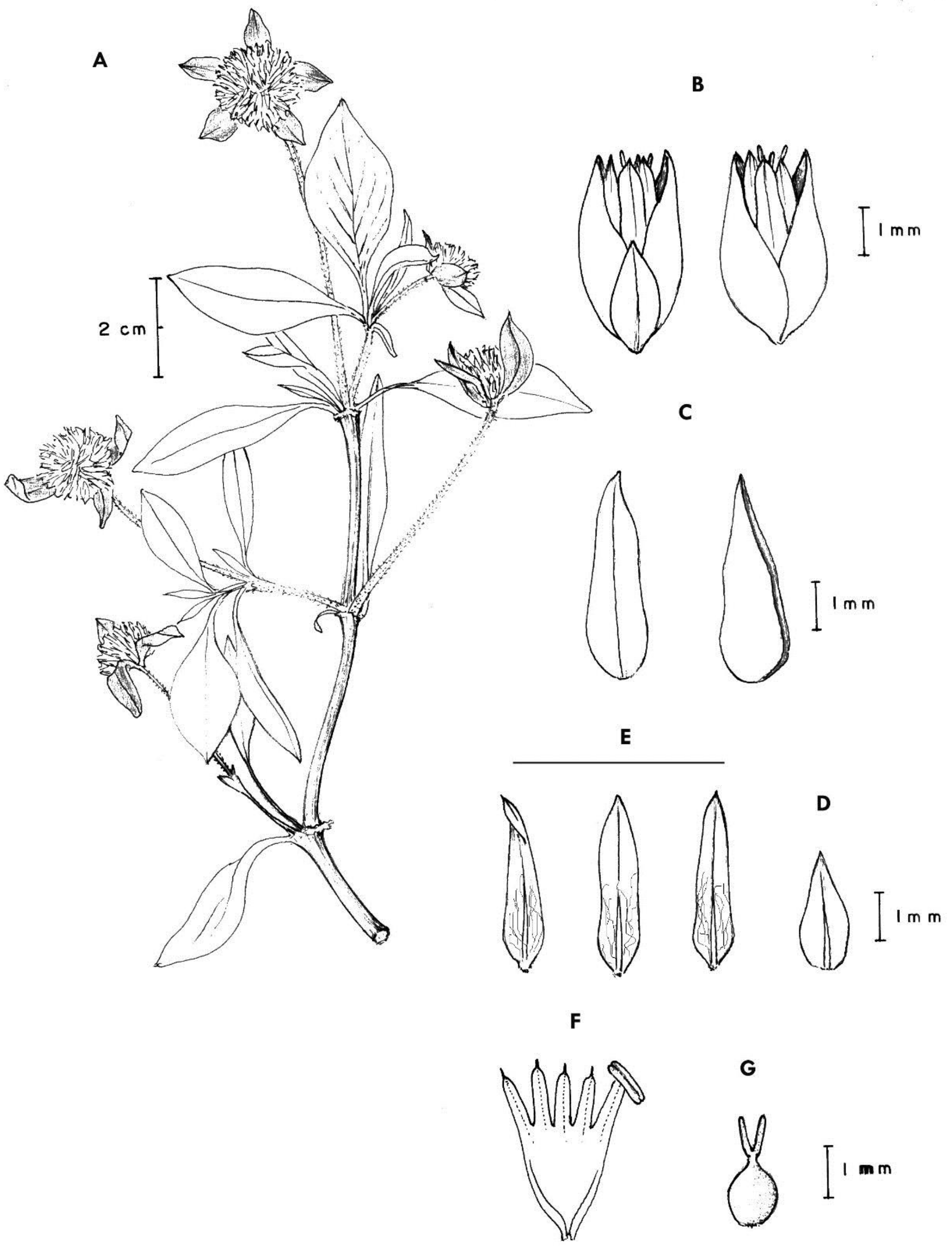


Fig. 4-89. *Gomphena martiana* Gillies ex Moq. A) Habit. B) Flower. C) Bract. D) Bracteoles. E) Tepals. F & G) Detail of the androecium [voucher: Borsch 3535].

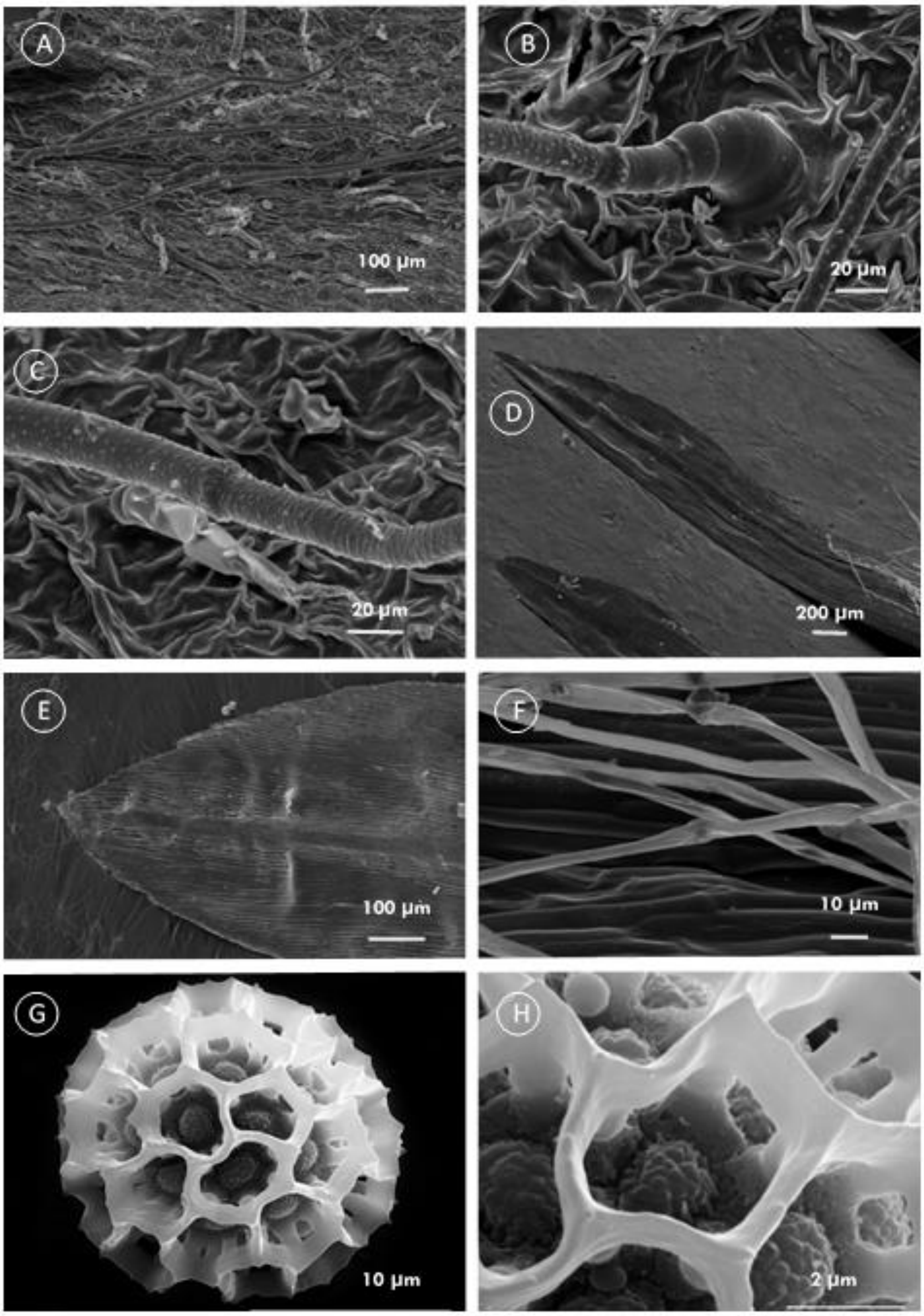


Fig. 4-90. *Gomphrena martiana* Gillies ex Moq. Trichomes A) Cauline leaves with appressed trichomes. B) Detail of the rounded, broad basal cells. C) Detail of the interlocking junctions with linear overlapping scar. Tepals. D) All the tepals with trichomes in the dorsal part. E). Detail of acute apex. F) Detail of the simple node and collapsed cells of lanate trichomes [voucher: Borsch 3737]. G) Pollen overview. H) Detail of pore [voucher: Borsch 3535].

Specimens examined for distribution assessment. ***Argentina, Córdoba, Tulumba.*** Salinas Grandes al norte de Lucio Mansilla por el camino del gasoducto, [-64,756827, -29,7515], 195 m, 26, 4, 1964, *Hunziker, A.T., 17324*, (SI, LPB). ***Salta***, Camino de Salta al Parque Nacional los Cardones. Cerca al río, [-65,740556, -25,15], 1836 m, 7, 4, 2004, *Borsch, T.,* ***3737***, (LPB, B). ***Bolivia, Chuquisaca, Luis Calvo,*** Centro El Salvador-CIMBOC, [-63,16, -20,61], 800 m, 14, 4, 1993, *Saravia Toledo, C., 11813*, (CTES, LPB). ***Nor Cinti,*** Saliendo de Camargo a ca. 5 km hacia Villa Abecia, [-65,225278, -20,6991], 2446 m, 20, 6, 2006, *H. Huaylla & R. Lozano, 2107*, (B, HSB, MO). ***Cochabamba***, Local. Anzaldo, [-65,93027778, -17,778333], 2800 m, 5, 1987, *Aleman, F., 125*, (LPB). ***Cercado***, Falderio Tunari, [-66,1497222, -17,39166667], 2575 m, 10, 4, 1966, *Steinbach, R., 49*, (LPB). ***Mizque***, on N side of town, in weedy areas, [-65,33, -17,949], 2020 m, 4, 5, 2005, *Nee, M., 52943*, (LPB, NY). ***Quillacollo***, [-65,217222 -17,39166667], 2600 m, 9, 3, 2006, *Wood, J.R.I., 22412*, (LPB, MO). ***Potosí, Nor chichas***, [-66,176389, -20,9575], 3792 m, 10, 4, 2009, *Fuentes Bazan, S., 120*, (LPB, B). ***Santa Cruz, Andrés Ibáñez,*** carretera antigua a Cochabamba, el Torno, [-63,2267, -17,6164], 400 m, 22, 9, 2002, *Borsch, T.,* ***3535***, (LPB, B). 5.5 km S. of Basilio on road from Santa Cruz to Camiri, [-63,191667, -18,0625], 500 m, 21, 1, 1994, *Nee, M., 44570*, (NY, LPB). 3.5 Km W of the Santa Cruz, Abapó highway and San Joaquín, along gravel road to the turnoff 5.5 Km S of Basilio, [-63,2166, -18,1833], 570 m, 24, 5, 2005, *Nee, M., 53128*, (LPB, NY). On "Brecha 5, Km 38", [-63,1,-18,0666], 460 m, 28, 12, 1997, *Nee, M., 47582*, (LPB, NY). Area central de Santa Cruz, [-63,17361, -17,7933], 2005, *Unterladstatter, R., 1*, (LPB). ***Cordillera***, 200 km hacia el Sud, proyecto Abapó Izozog, cerca al Río Grande, [-63,0338889, -18,924161], 300 m, 12, 3, 1981, *Beck, S.G., 6421*, (LPB, CTES,NY, B). Charagua, [-63,110427, -20,005628], 590 m, 5, 4, 2011, *F. Estrada, 333*, (HSB). [-62,55611,-19,54916], 300 m, 20, 5, 1999, *Michel, R.* de, *2565*, (USZ, LPB, NY). Comunidad de Aguarati, [-62,4715, -19,258933], 300 m, 25, 5, 1999, *Michel, R. de, 2766*, (USZ, LPB). Along highway from Abapó to Camiri, 17.7 km, NE of turnoff to Lagunillas at Ipatí and 33 km, SW of Ipitá, [-63,549, -19,61666], 960 m, 1, 6, 2005, *Nee, M., 53289*, (NY, LPB). [-63,56638, -19,64277], 985 m, *Nee, M., 53021*, (MO, LPB). Along highway from Camiri to Abapó, 4.4 km N of school in Tatarenda Viejo, 8.2 km S of center of Tatarenda Nuevo, [-63,49638, -19,176389], 790 m, 18, 4, 2007, *Nee, M., 55112*, (NY, LPB). Just S of Loma Blanca on highway from Santa Cruz to Abapó, [-63,200, -18,3833], 525 m, 27, 2, 1998, *Nee, M., 48490*, (LPB, NY). Mennonite colony, 6.2 Km E of Santa Cruz-Abapó highway, entering on Brecha 7, [-63,10, -18,1361], 430 m, 13, 5, 2007, *Nee, M., 55419*, (LPB, NY). Camino a Camiri, desde Santa Cruz, antes de llegar a Rio Seco, desvio que va a los rieles del tren. Cerca Rio Grande-Rio Seco, [-63,24472, -18,660556], 475 m, 25, 4, 2007, *Ortuño, T., 734*, (LPB). Camino a Totai. Saliendo de Santa Cruz hacia Camiri, desvío a Totai [-63,387138, -18,944827], 490 m, 28, 4, 2007, *Ortuño, T., 812*, (LPB). ***Florida***, Mairana, Centro Regional de Investigación (CRI) mejoramiento de variedades de maiz, [-63,95, -18,1], 1400 m, 22, 5, 1991, *Israel G. Vargas* C. *& Anna Lawrence, 994*, (MO, NY, USZ). 1 Km. NW of Pampa Grande on dirt road to the main highway from Samaipata to Comapara, [-64,120, -18,08], 1300 m, 28, 1, 1994, *Nee, M., 44723*, (LPB, NY). Samaipata, [-63,866667, -

18,1499], 1300 m, 14, 3, 1920, *José Steinbach, 3734*, (GH) ***Manuel María Caballero***, Comapara. Road Pulquina-San Jose, near bridge over River Pulquina, [-64,43519, -18,10164], 1520 m, 2, 3, 2006, *Biggs, N., 112*, (LPB, K, USZ). Comarapa, on NW side of town along río Comarapa, [-64,516, -17,916667], 1810 m, 11, 12, 1992, *Nee, M., 43072*, (LPB, NY).***Vallegrande***, El Estanque, 40 Km al S de la ciudad de Vallegrande, [-64,15, -18,933], 1400 m, 12, 1990, *Vargas, I., 864*, (LPB, USZ). ***Tarija***, ***Cercado***, Tarija, [-64,74195, -21,539289], 27, 4, 1983, *Krapovickas, A., 38659*, (LPB, CTES). ***Gran Chaco***, 0.4 Km E of Chuvere. [-63,8025, -21,53689], 860 m, 23, 3, 2007, *Nee, M., 54873*, (LPB, NY). ***Paraguay***, ***Boquerón***, Nueva Asuncion, Gral. E.A Garay, 13 km hacia Mariso. Estigarriba, [-56,1833, -25,91669], 410 m, 5, 10, 1983, *Beck, S.G., 9440*, (LPB).

4.3.10.2. *Gomphrena boliviana* Moq., Prodr. ser. 2, 13. 1849.

Type: Bolivia, Culta in hort. Luxemb. 4. VIII. 1836 e seminib. bolivianis, Gay, C. s/n (HT: FI 011264!).

= *Alternanthera boliviana* Rusby Memoirs of the Torrey Botanical Club 4: 249–250. 1895.
Type: Bolivian plateau, Vic. Cochabamba, 1891, *Miguel Bang 954*. (HT: BM BM000993111, IT: (F), F0047574F, US US00102754, GH GH0003695).
= *Gomphrena acrotepala* Suess. Repertorium Specierum Novarum Regni Vegetabilis 35: 308.
Type: Rioja, Nord Argentinien. 21. III. 1906. *Urriche-Haunthal s/n,* (LT: B100242299!) (lectotype designated by Holzhammer 1956: 233).
= *Alternanthera boliviana* (Moq.) Usteri, Fl. umgeb. S. Paulo. (1911: 178) [non. Alternanthera boliviana Rusby, Mem. Torrey Bot. Club (1895: 249)].
= *Alternanthera boliviana* ssp. *Amentaceae* Suess. Repert. Spec. Nov. Regni Veg. 42: 51.
Type: Argentinien, Buenos Aires, *Parodi 7219* (HT: B B10 0242324).
= *Gomphrena tarijensis* R. E. Fries Arkiv för Botanik 16(12): 27. 1920.
= *Gomphrena boliviana* var. *tarijensis* (R.E. Fr.) Pedersen. Adansonia, série 3, 19(2): 227. 1997.
Lectotype: Bolivia, Tarija, *Fries 1088* (LT: S07-12683, ITLC S S-R-2457) (lectotype designated by Bena 2017: 144)
= *Gomphrena globosa* var. *albiflora* Moq. Prodromus Systematis Naturalis Regni Vegetabilis 13(2): 409–410. 1849.
Lectotype: México, Oaxaca de l'ocean pacifique, Galeotti s. 429 – 443, (LT: P P00622632, ITLC: P P00622631, P00622633, BR 21450990, 021451003) (designated by Bena 2017: 134):
= *Gomphrena boliviana* fo. *leiantha* Pedersen. Bulletin du Muséum National d'Histoire Naturelle, Section B, Adansonia. sér. 4, Botanique Phytochimie 12(1): 76. 1990.
Type: Argentina, Prov. Salta, Dept., Cafayate: Tolómbon, between limited of Tucuman y Cafayate, 1500m. *Hunziker & Di Flucio 21047* (HT: CORD).

Annual biannual herb, 40-120 cm. ***Root*** fibrous, simple. ***Stems*** ramose decumbent to erect, striate, with secondary and terciary stem, few dense appressed, white trichomes. ***Cauline leaves*** ovate-lanceolate, 2.4-3.5 (--4.0) x 1.5-2.4 (--3.0) cm, acute apex, middlenerve and secondary nerves prominent, margin entire, green, with few dense trichomes in the abaxial side of leaf and the adaxial side of leaf densely covered, trichomes type equal to the stem, denser in the node and in the nerves. ***Apical leaves susbtending paracladia*** (inflorescences) with a 4-6 leaves arranged symmetrically, ovolanceolate, 1.3-1.5 (--2.5) x 0.5-0.8 (1.2) cm, abruptly acute apex, green, with few dense trichomes in the margin and on the nerve, white. ***Inflorescences*** globose to subglobose, terminal, 1-1.3 (--2.1) cm in diameter, consisting of 2-5 partial florescens, white. ***Flower*** 4.5.4.8 (--5) mm long. ***Bract*** ovolanceolate, 3-3.2 x 1.2 mm, membranous texture, white translucent colour, acuminate apex, and entire margin, white. ***Bracteoles*** ovolanceolate, 4-4.8 (5.6) x 1.5 mm, membranous-translucent texture, white colour, middlenerve prominent. ***Tepals*** oblong to lanceolate, membranous texture, white colour, acute apex, middle nerve, connate in the base, lanate trichomes in the base of the dorsal part in *dorsal* 2(--3) mm, few teeth in the margin and in the apex. Size unequal. External tepals 3.8-5.2 (--5.9) x 0.8 mm. Intermediate tepal 3.8-5 (--5.8) x 0.8 mm. Inner tepal 3.6-4.6 (--4.8) x 0.6 mm. ***Filaments*** 3.5-4.2 (--4.9) mm long, the fused part is 2.5-2.6 (--3.3) mm long, free part 1.6 mm long. ***Filament appendages*** small protrusions, rounded at to of free part. ***Anthers*** oblong, 1.4 mm long, united in the apex of each single lobe of the filament appendices. ***Gynoecium*** with two filiform stigma branches 0.8-1 (--1.6) mm long, style 0.2-0.4 mm, ovary subglobose 1 mm long [voucher: Borsch & Ortuño *3577* = AC140 (LPB, B)].

Micromorphology of trichomes. Multicellular uniseriate: ***Stems and cauline leaves*** with a 1-2 cells, the first cells with rounded shaped, flat texture narrowly in the apex. The upper next, 4-6 cells, salicose ornamentations, firm to flexible consistence, striated texture in the cuticle wall. ***Interlocking junctions***, conspicuous linear scars arranged in an angle of zero degrees. ***Trichomes on apical leaves subtending paracladia,*** similar than on the stems. ***Trichomes on tepals*** with1-2 basal cells, firm rounded, collapsed upper cells, flexible, without ornamentation, flat sculpture, and simple interlocking junctions.

Taxonomic remark. *G. martiana* and *G. boliviana* are closely related and form a natural group. The morphological differences between them are the basal leaves only present, and the absence of the filament appendages in apical part of the filaments in *G. martiana*, contrary to *G. boliviana* that has two small rounded lateral appendages. Another difference is the size of apical leaves subtending the inflorecence that is bigger in *G. boliviana* than in *G. martiana*. And the relation of the sizes the bract respect to the bracteoles in *G. martiana* with the bract is shorter than the middle half of the bracteole, contrary to *G. boliviana* where the bract is bigger than the half part of the bracteoles.

Another morphological difference is possible to see in the presence of the indumentum in the inner tepals. These specimens were designated as a new variety for Pedersen (1990, 1997). However, currently molecular data are missing for these samples to know more exactly the positions of these samples and their relation with *G. boliviana* and *G. martiana*.

Habitat and ecology. Frequently in big populations in dry gravelly or sandy soils, disturbed areas with disturbed soil such as on agricultural fields, in open places with full sun, near roadsides. The vegetation in the area of dry valleys, including *Schinopsis marginata* Engl, *Aspidosperma quebracho-blanco* Schltdl., *Acacia feddeana* Harms, *Solanum argentinum* Bitter & Lillo*, S. hieronymi* kuntze, *Zea may* fields of cultivations, in xeric forest species as *Bromelia serra* Griseb. Considered to be a weed, common in secondary vegetation. In ecoregions Inter-Andean dry forest, Gran Chaco, Chiquitano dry forest, Tucuman-Bolivian forest, Chaco Serrano, Pre-andean Amazonian forest, where the plants were collected between 200-2800 m.

Distribution. Occurs in ***Argentina***, Prov. Catamarca, La Rioja, Mendoza, Salta, San Juan. ***Paraguay***, Prov. Nueva Asunción. ***Bolivia**,* Prov. Luis Calvo, Oropeza, Tomina, Cercado, Narciso Campero, Quillacollo, Tapacarí, (Department Chuquisaca). Prov. Cordillera, Florida, Manuel María Caballero (Deparment Santa Cruz,). Prov. Burnet O'Connor, Cercado, Gran Chaco, José María Avilés(Department Tarija).

Specimens examined for distribution assessment. ***Argentina, Catamarca***, Andalgalá, [-66,31666, -27,6], 1019 m, *Pedro Jörgensen, 1688*, (LIL, SI). Capital, [-65,778872, -28,46894], 528 m, *Pedro Jörgensen, 1102*, (SI). ***Bolivia, Chuquisaca***, ***Luis Calvo***, Azero. Estacion experimental zootécnica "El Salvador", 27 km NW de Carandayti, 800 m, NE de la entrada a la estación experimental, [-63,2166667, -20,75], 500 m, 13, 4, 1977, *Krapovickas, A, 31261*, (CTES,LPB). ***Oropeza***, Teja Huasi, 12 m del puente, [-65,0, -18,9166], 2400 m, 27, 2, 1992, *Durán, M., 1*, (CHB, LPB). ***Cochabamba***, ***Cercado***, Zona Quintanilla, entre el Río Rocha y el Castillo, [-66,1162049, -17,396194], 2780 m, 2, 2, 1997, *De la Barra, N., 699*, (MO, LPB). Universidad, [-66,1461, -17,393281], 2587 m, 25, 1, 1985, *Pedrotti, F., s.n.*, (LPB, NY). [-66,180042, -17,402626], 2560 m, 29, 2, 1983, *Bohs, L., 2064*, (LPB). ***Narciso Campero Leyes***, Aiquile, [-65,178925, -18,196546], 2250 m, 17, 1, 1987, *Sigle, M., 311*, (LPB). ***Quillacollo***, common in low wet depressions at roadsides and edges of fields in Sipe Sipe. [-66,3616, -17,45], 2646 m, 7, 12, 1999, *Ross A. McCauley, 117*, (BHO, LPB, MO).

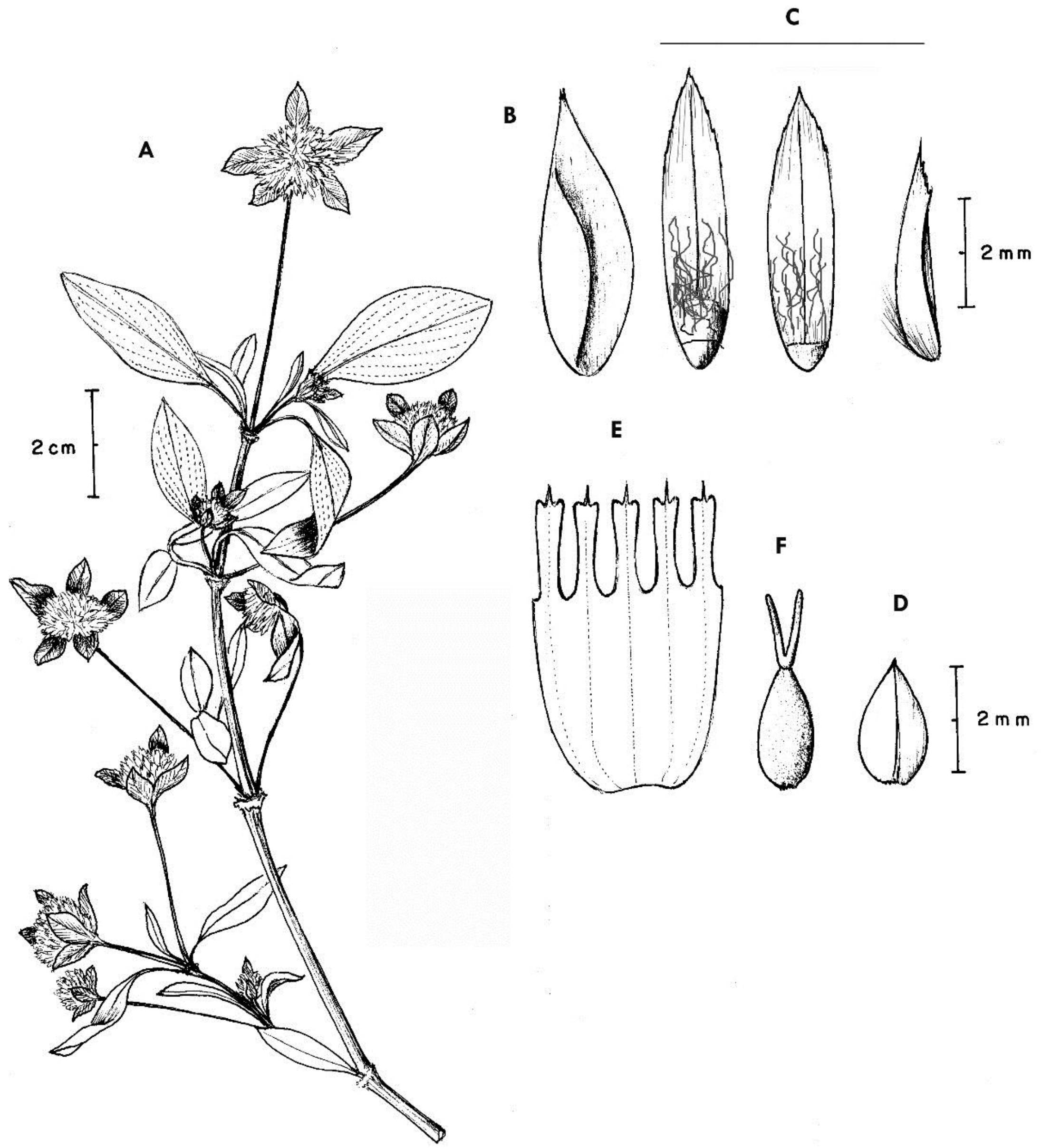


Fig. 4-91. *Gomphena boliviana* Moq. A) Habit. B) Bracteoles. C) Tepals. D) Bract. E) Detail of the androceum, F) Gynoecium. [voucher: voucher: Borsch & Ortuño 3577 = AC140].

Specimens examined ***Tapacarí***, Camino La Paz a Cochabamba, a cerca a Cochabamba en el puente Tapacarí, [-66,348333, -17,574333], 2500 m, 1, 4, 2003, *Borsch, T., 3577*, (LPB, B). Camino a Cochabamba, 26, 4, 1957, *Cañigueral, J., 531*, (LPB). ***Santa Cruz***, ***Andrés Ibañez***, 5 Km SSW of bridge over Río Piraí of the highway from Santa Cruz to Samaipata. Along Río Piraí, [-63,475, -18,149], 600 m, 30, 1, 1998, *Nee, M., 48174*, (LPB, NY). ***Cordillera***, Aguarati Izozog. Comunidad de Aguarati, [-62,47472222, -19,2514889], 300 m, 25, 5, 1999, *Michel, R. de, 2766*, (LPB, USZ).. Alto Parapeti "Hacienda Yabuimbia". Malezas dentro de cultivos, [-63,6386111, -20,0636111], 800 m, 15, 5, 1987, *Michel, R. de, 628*, (LPB). Alto Parapetí "Hacienda Yapuimbia", [-63,638611, -20,063611], 800 m, 1, 9, 1985, *Michel, R. de, 456*, (LPB). Alto Parapetí "Hacienda Yapuimbia", [-63,638611, -20,063611], 800 m, 27, 9, 1985, *Michel, R. de, 315*, (LPB, MO). Alto Parapetí, Hacienda Yapumbia, [-63,63694444, -20,065], 800 m, 8, 2, 1986, *Michel, R. de, 494*, (LPB). Alto Parapetí, Hacienda Yapumbia, [-63,638611, -20,063611], 800 m, 8, 2, 1986, *Michel, R. de, 499*, (LPB). Alto Parapetí, [-63,638611, -20,063611], 850 m, 8, 1, 1982, *Michel, R. de, 171*, (LPB, MO, CTES, NY). Along highway from Yacuiba to Camiri, 2.2 Km. by road SE of Salinas and turnoff to Charagua, [-63,455278, -20,239722], 915 m, 13, 2, 2006, *Nee, M., 54152*, (LPB, NY). Along new highway from Santa Cruz to Ibapó, 7.5 km S of Basilio. Former chaco forest, now completely cleared for cotton and other crops, this the only "hill" along the highway, a small rise with sandy, blowing soil, [-63,183, -18,18], 525 m, 21, 3, 1998, *Nee, M., 48753*, (NY,LPB). Ibasiriri Izozog. Cerca de la comunidad Ibasiriri, a 3 km de la Brecha, [-63,556111, -19,53916667], 300 m, 20, 5, 1999, *Michel, R. de, 2565*, (LPB, USZ, NY). ***Florida***, 9.5 Km (by road) NNE from turnoff to pampa Grande, 8 Km (by air) N of pampa Grande, along río Los Negros in canyon with highway from Mairana to Comarapa, [-64,09, -18,0166670], 1250 m, 2, 1, 1998, *Nee, M., 47743*, (LPB, NY). ***Manuel María Caballero***, San Juan del Potrero, [-64,29, -17,9166], 2021 m, 2, 11, 1992, *Coimbra, G., 2629*, (USZ, LPB). 2.5 kmal N de Tambo, Río San Isidro, [-64,448143, -18,016407], 1600 m, 23, 2, 1984, *Schmitt, G., 46*, (LPB, MO). ***Tarija***, ***Burnet O´Connor***, Puerto Margarita, Río Pilcomayo, [-63,78416667 -21,20027778], 3, 5, 1983, *Krapovickas, A., 39151*, (CTES, LPB). ***Cercado***, 2000 m, 2, 4, 1988, *Ehrich, R., 541*, (LPB). ***José María Avilés***, Concepción, rivera S de la quebrada de Rujero, [-64,5, -21,7666], 1705 m, 5, 4, 1994, *Subieta, M., 246*, (LPB). "Cerca Chocloca propiedad Kohlberg", [-64,76521, -21,746], 1801 m, 26, 12, 1985, *Bastian, E., 306*, (LPB). ***Paraguay, Nueva Asuncion***, Ruta Trans-Chaco, [-61,41666, -21,26], 224 m, *Schinini, A., 16442*, (CTES).

4.3.10.3. *Gomphrena boliviana* fa. *robusta*. (Hicken) Pedersen, Bull. Mus. Natl. Hist. Nat., B, Adansonia ser. 4, 12(1): 77. 1990.

Lectotype: Argentina, province Mendoza, Santa Rosa, 1905. Jensen Haarup s/n (LT: C C10005394 LTIT:S S-R-2444). (Lectotype designed by Pedersen 1990).

≡ *Gomphrena lanceolata* R.E. Fr. Arkiv för Botanik utgivet av K. Svenska Vetenskapsakademien 16(12): 26. 1920.

= *Philoxerus heliotropifolius* Griseb. Abh. Königl. Ges. Wiss. Göttimgen 19:82-83.1874.

Type: Argentina, Provincia Córdoba, Am Flussufer bei Córdoba, 1871 Sommer, Lorentz 386 (HT: GOET GOET 006519)

The main differences between *Gomphrena boliviana* and *G. boliviana* fa. *robusta* are that the external tepals are glabrous and the inner tepals are with dense trichomes in the dorsal part.

Habitat and ecology: Frequent in sandy soils, disturbed areas with removed soil as agricultural crops, in open places with full sun, near roadside. In ecoregions, Semi humid Puna, Prepuna, Gran Chaco, Tucuman-Bolivian forest. Were the plants are collected between 2000-2100 m.

Distributions. Bolivia, province of Tomina (Dept. Chuquisaca), provinces of Cordillera, Sara (Dept. Santa Cruz), Province of Gran Chaco (Dept. Tarija).

Specimens examined for distribution assessment. ***Bolivia, Chuquisaca, Tomina,*** On the west side of Tominga, [-64,4622, -19,18418333], 2073 m, 8, 5, 1993, *Spooner, M., 6697*, (LPB). Corso, 0.8 km de Tomina, [-64,49222, -19,14805556], 2000 m, 27, 3, 1995, *Teran, J., 199*, (LPB). Corso, 0.8 km de Tomina, [-64,49416667, -19,4638889], 2000 m, 10, 12, 1993, *Teran, J., 112*, (LPB). ***Santa Cruz, Cordillera,*** Alto Parapeti "Hacienda Yabuimbia", [-63,6386111, -20,0636111], 800 m, 18, 5, 1987, *Michel, R. de, 726*, (LPB, MO) 15 Km N of Río Seco and 10 Km S of La Mora, along new paved highway from Santa Cruz to Abapó, [-63,216667, -18,55], 550 m, 19, 4, 1998, *Nee, M., 49093*, (LPB, NY). ***Sara,*** W side of Rio Pirai, 0.5 km downstream and N of the Eisenhower bridge of the highway from Montero to Portachuelo, 7 km (by road) ENE of Portachuelo and 8 km (by air) W of Montero. Brushy disturbed areas on coarse dry sandy soil, [-63,3333,-17,31666], 275 m, 7, 11, 1990, *Nee, M., 39726*, (MO, LPB, NY). ***Tarija, Gran Chaco,*** Alrededores de Yacuiba, [-63,66667, -22,00], 0, 0, 1977, *Lara, R., 1*, (LPB).

4.3.10.4. *Gomphrena spissa* Pedersen, Adansonia sér. 3, 19(2): 232. 1997

Type: Bolivia, Aguas del Castillas, 12000 ft. 01.03 1949. Jocelyn Brooke 5248 (HT: BM BM000834418).

Annual annual herb, 8-14 cm. ***Root*** fibrous, simple. ***Stems*** decumbent to prostrate, deeper striate, with secondary and terciary stem, scarce appressed, white trichomes. ***Cauline leaves*** oblong -lanceolate, 2-2.5 (--3.5) x 1 (--1.5) cm, acute apex, middlenerve prominent, margin entire, green, with scarce trichomes to glabrous in both surfaces of leaf, densely covered, trichomes at margin, type equal to the stem, denser in the nodes. ***Apical leaves susbtending paracladia*** (inflorescences) 2-5, leaves arranged symmetrically, oblong lanceolate, 1-1.2 (--1.5) x 0.5-0.7 (0.8) cm, acute at apex, green, with few dense trichomes in the margin, scares on the leaf surfaces, white. ***Inflorescences*** globose to subglobose, terminal, 0.7-1(--1.5) cm in diameter, consisting of 2-5 partial florescens, white. ***Flowers*** 3.7 -4.6 (--5) mm long. ***Bract*** ovolanceolate, 3 x 1.5 mm, membranous texture, white translucent colour, acuminate apex and entire margin, white. ***Bracteoles*** ovolanceolate, 4-4.6 (5) x 1.5 mm, membranous-translucent texture, white colour, middlenerve prominent. ***Tepals*** oblong to lanceolate, membranous texture, white colour, obtuse apex, middle nerve, connate in the base, lanate trichomes in the base of the dorsal part in *dorsal* 2(--3) mm, few teeth in the margin and in the apex. Size unequal. External tepals 3.7) x 0.8 mm. Intermediate tepal 3.6 x 0.8 mm. Inner tepal 3.4 x 0.6 mm. ***Filaments*** 2 mm long, the fused part is 1.2 mm. ***Filament appendages*** 0.6 mm long, rounded at apex (Fig. 92D). ***Anthers*** oblong, 1 mm long, united in the apex of each single lobe of the filament appendices. ***Gynoecium*** with two filiform stigma branches 0.5 mm long, style 0.2 mm, ovary subglobose 1 mm long [voucher: Beck 29991].

Taxonomic remark. *G. spissa* is probably close related to *G. martiana* and *boliviana* based on the morphological data. Currently there is no molecular sequence data available of this species. The problem to collect new specimens was that the known localities are actually urbanized because the Oruro city is growing a lot. But examination of the herbaria of Cochabamba (BOLV) and La Paz (LPB), it was possible to find two collections. These specimens correspond exactly to *G. spissa* as described by Pedersen (1997) and collected by Broke in 1949.

Habitat and ecology. Occurs in rock soil and in the border of small streams. In ecoregion of Dry Puna, were the plants are collected between 3700- 3770 m. Distributions. Endemic of Bolivia, province of Poopó and Sebastian pagador (Dept. Oruro) (Fig. 93).Specimens examined. Bolivia Oruro, Poopó, Pazña, a 1 km al este del balneario de Urmiri, pasando la ex central eléctrica. [-66.866333, - 18.57265] 3750 m. 13.3.2006. *Torrico, L. LT745*, (BOLV). Sebastian Pagador, [-66.7686333, -19,01426667], 27.1.2008.2770 m, Beck, S.G. 29991 (LPB).

Distributions. Endemic of Bolivia, province of Poopó and Sebastian pagador (Dept. Oruro) (Fig. 93).

Specimens examined. Bolivia Oruro, Poopó, Pazña, a 1 km al este del balneario de Urmiri, pasando la ex central eléctrica. [-66.866333, - 18.57265] 3750 m. 13.3.2006. *Torrico, L. LT745*, (BOLV). Sebastian Pagador, [-66.7686333, -19,01426667], 27.1.2008.2770 m, Beck, S.G. 29991 (LPB).

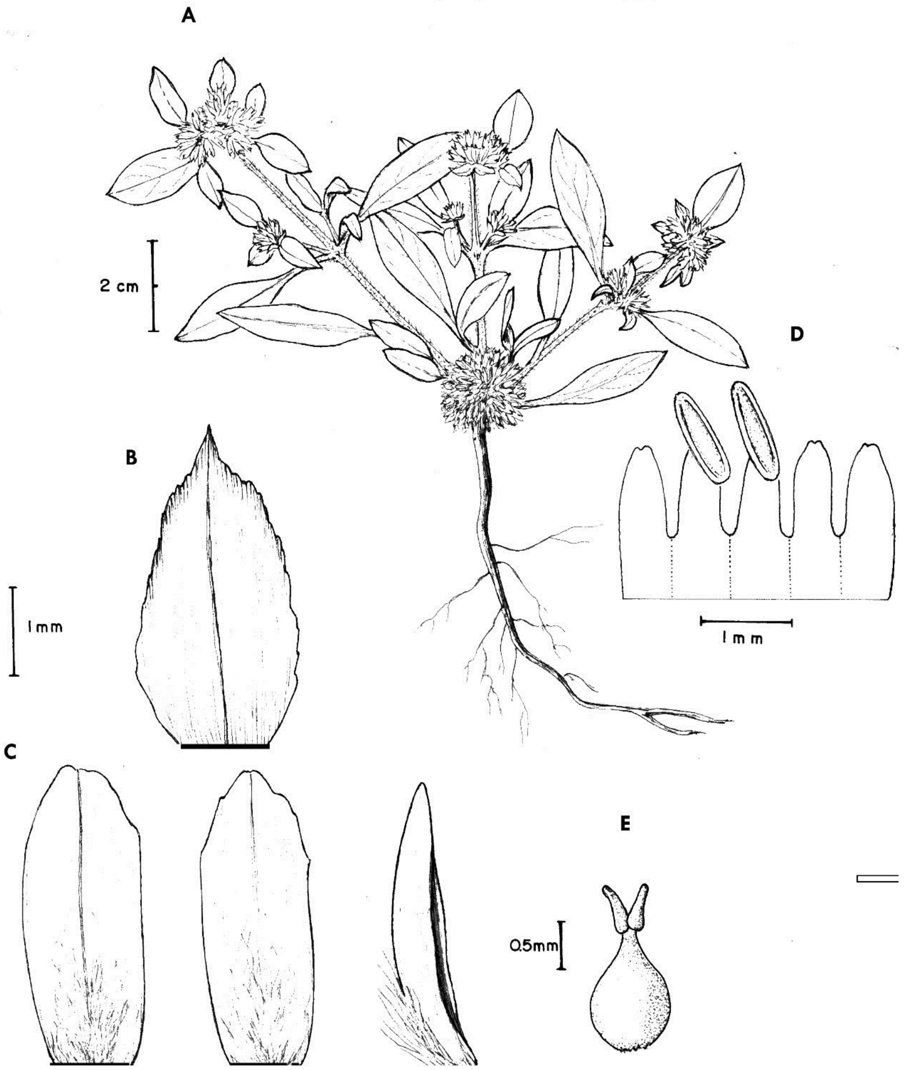


Fig. 4-92. *Gomphena spissa* Pedersen. A) Habit. B) Bracteoles. C) Tepals. D) Detail of the androecium, E) Gynoecium. [voucher: Beck, S.G. 29991].

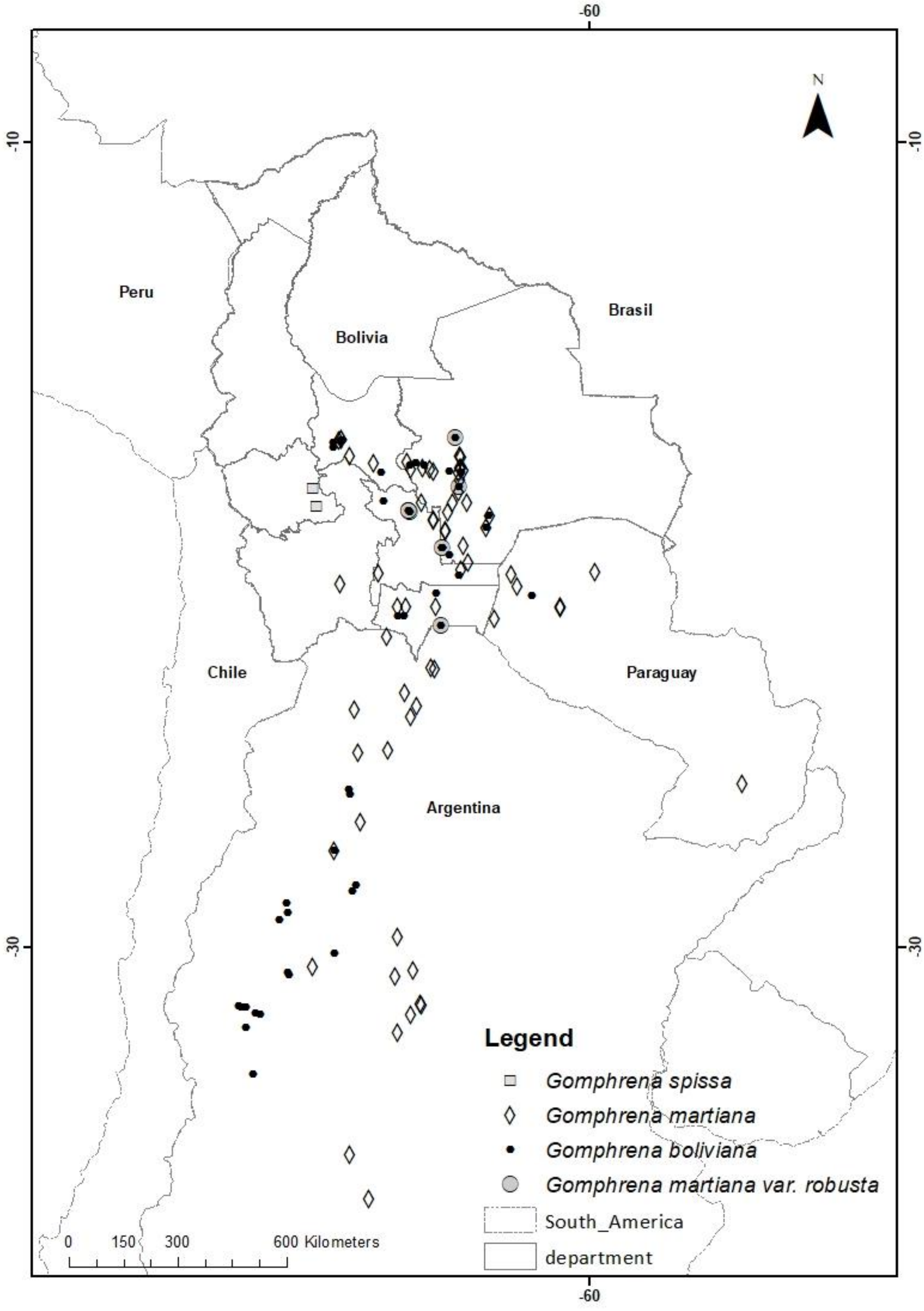


Fig. 4-93. Map of group the species *Gomphrena martiana* and *G. boliviana*, including *G. spissa*

Chapter 5

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6. **Erklärungen**

Eigenständigkeiserklärung

Hiermit versichere ich, dass ich meine Dissertation mit dem Titel "Systematic and Evolution of *Gomphrena* (Amaranthaceae) with an emphasis on the species in Bolivia selbständig, ohne unerlaubte Hilfe angefertigt habe und die benutztein Hilfsmittel vollständig angegeben worden sind; dass ich meine Dissertation ganz oder teiweise im Einvernehmen mit meinem Betreuer Herrn Prof. Dr. Thomas Borsch zur Veröffentlichung vorbereitet habe bzw. Vorbereiten werde; dass die Arbeit nicht schon einmal in einem früheren Promotionsverfahren angenommen, als ungenügend beurteilt oder abgelehnt worden ist; und dass ich meine Dissetation im Falle einer Ablehnung nur unter Hinweis auf diese Ablehnung für ein anderes Examen verwenden werde.

List of publication and own contributions

Chapter 3 "*Gomphrena* (Amaranthaceae, Gomphrenoideae) diversified as a C_4 lineage in the Neotropics with specializations in floral and inflorescence morphology, and an escape to Australlia".

This chapter has largely been prepared for publication to be submitted to a journal soon.

Own contribution: Performes field work (in part together with T. Borsch), laboratory work, data analysis and writing of manuscript.

Provision of commads and calibration points for molecular clock analysis with BEAST through T. Borsch. Corrections through T. Borsch .

5 Juli 2019