

A New Circumscription of the Genus *Stomatanthes* (Asteraceae, Eupatorieae)

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Abstract—A revision of the genus *Stomatanthes* (Asteraceae, Eupatorieae) is presented. A cladistic analysis of 43 qualitative and eight quantitative morphological characters resulted in one tree that suggests a narrower delimitation of the genus relative to previous circumscriptions. *Stomatanthes* thus comprises three species, one widespread in sub-Saharan Africa and the other two endemic to restricted areas in central Africa. A cluster analysis and a non-metric multidimensional scaling were also performed. Of the 25 quantitative traits originally measured for the analysis, eight (blade length and width, involucre length, corolla length, corolla limb width, corolla tube width, thecae length, anther apical appendage length) provided clustering information and indicated the same groupings as the cladistic analysis. This revision also includes full descriptions of species, photographs, illustrations, and distribution maps.

Keywords—Africa, Compositae, Eupatoriinae, phenetic analysis, phylogenetic analysis.

The Eupatorieae, with 182 genera and ca. 2,200 species (Hind and Robinson 2007), is unusual among Asteraceae tribes because the delimitation of subtribes and genera is especially difficult. The core of the tribe is represented by the genus *Eupatorium* L., from which many genera, such as *Stomatanthes* R. M. King & H. Rob., have been segregated on the basis of microcharacters. These taxonomic changes were summarized in the monographic treatment of King and Robinson (1987), which shows a subtribe Eupatoriinae that includes *Austroeupatorium* R. M. King & H. Rob. (13 species), *Eupatorium* (ca. 45 species), *Hatschbachiella* R. M. King & H. Rob. (two species), and *Stomatanthes*, the latter comprising 15–16 species with a disjunct distribution in eastern South America and sub-Saharan Africa (King and Robinson 1987; Hind and Robinson 2007). Initial morphological and molecular phylogenies (Bremer 1994; Schmidt and Schilling 2000) that included *Stomatanthes* were contradictory regarding generic and subtribal relationships, but only one species of *Stomatanthes* was sampled in these studies. More recent taxonomic treatments of Eupatorieae assign *Stomatanthes* to subtribe Eupatoriinae (Hind and Robinson 2007; Robinson et al. 2009).

Stomatanthes, as defined here, consists of three small herbaceous to sub-shrubby species endemic to Africa. As a member of Eupatorieae, *Stomatanthes* possesses the characteristic discoid heads with tubular, actinomorphic corollas. The long style branches are often the color of the corolla, with stigmatic lines in two rows restricted to the lower half, and with an apical appendage. It is distinguished from other tribal genera by its stomata on the corolla lobes, carpoidial cells of the cypsela oblong and sub-quadrate with the outermost layers with thickened walls, and ramose hairs in the cypselae.

Geographically, one species of *Stomatanthes* is widespread and extends through eastern, central, western and southern continental Africa [*S. africanus* (Oliv. & Hieron.) R.M. King & H. Rob.], whereas the other two species are endemic to narrow areas in southern Democratic Republic of Congo and northern Zambia, and in the Kaffa Province of Ethiopia.

King and Robinson (1970) originally described *Stomatanthes* to accommodate one African species of *Eupatorium* (*E. africanum* Oliv. & Hieron.). The stomata and hairs on the corolla lobes, thickened cells of the anther collar, and fruits with abundant twin hairs and distinctive carpoidium were cited as diagnostic for the genus. Additional distinguishing characters included the leaves mainly alternate, low number of florets (four to five) per capitula, and the pappus apical cells sub-acute. In the

same year, Robinson (1970) transferred 11 South American species of *Eupatorium* to *Stomatanthes* and described the new species *S. hirsutus* H. Rob. This not only broadened the generic concept of *Stomatanthes* with new morphological characters, but changed drastically the original African distribution, which became an African-South American disjunction. Later, new species were added, including the African *S. zambiensis* R. M. King & H. Rob., *S. meyeri* R. M. King & H. Rob. (King and Robinson 1975), and *S. helenae* (Buscal. & Muschl.) Lisowski (Lisowski 1991), and the South American *S. reticulatus* M. A. Grossi & J. N. Nakaj. (Grossi and Nakajima 2009), which raised to 17 the total number of species in the genus. *Stomatanthes zambiensis* R. M. King & H. Rob. was distinctive due to its verticillate leaves, leading to creation of subgenus *Verticifolium* R. M. King & H. Rob. (King and Robinson 1975).

These additional species obscured delimitation of the genus, and some features became exceptions to the original diagnostic characters of *Stomatanthes*. For example, the corolla stomata and the distinctive carpoidium may be present or absent in the South American species (Grossi 2011a). On the other hand, the New World species brought new characters to the genus definition, such as style branches with clavate tips, and short and stout stamen filaments. Therefore, it has become necessary to establish the true value of certain morphological characters for genus delimitation.

We apply here a new approach by combining phenetic and cladistic analyses. Phenetic analyses have been used successfully to delimit species boundaries and to resolve intra- and inter-specific relationships among difficult taxa (e.g. Kephart et al. 1999; Sweeney and Price 2001). We perform a cladistic analysis of morphological characters combining qualitative and selected quantitative data. Quantitative traits are rarely included in cladistic analyses of morphological data because it is difficult to objectively assign character states (Pimentel and Riggins 1987; Cranston and Humphries 1988), although many so-called qualitative characters in fact conceal quantitative characters since these are usually transformed into discrete characters (Stevens 1991; Goloboff et al. 2006). However, quantitative characters may provide relevant phylogenetic information and there is no reason to exclude them from the analysis (Rae 1998; Wiens 2001; Goloboff et al. 2006; Donato 2011). Coding quantitative variation as continuous quantitative characters may be preferable to qualitative coding because it can potentially solve common problems in morphological phylogenetics, such as

vague character definition and arbitrary character state delimitation (Wiens 2001).

The present study provides a taxonomic revision of the genus *Stomatanthes* with an analysis of some morphological features, species descriptions, an identification key, and illustrations. The generic delimitation is based on a phylogenetic analysis of morphological data with support from a phenetic approach.

MATERIALS AND METHODS

This study was conducted using herbarium collections, digital images, and photographs of herbarium specimens from: B, BM, BR, BRLU, C, CORD, G, GH, HUFU, ICN, K, LE, LP, M, NY, P, POZG, S, SI, SPF, UEC, and US (acronyms as in Holmgren et al. 1990). For microscopic examination, vegetative and reproductive parts were rehydrated, treated with a clearing process using sodium hypochlorite 5%, stained with 2% safranin for 3–5 minutes depending on the structures, washed in water for 10 minutes, and mounted on microscope slides with gelatin-glycerin. Leaves and stems were isolated and free hand cut transversely. Observations and drawings of morphological and anatomical features were performed using a Nikon Eclipse E200 light microscope equipped with a camera lucida. Light microscope photographs were taken with a Nikon Coolpix S10. For scanning electron microscopic (SEM) studies, rehydrated material was critical point dried with Baltec equipment, model CPD-30, or dry material was placed directly on the stubs and coated with gold. The samples were scanned and photographed in a Jeol JSM-T 100 SEM. In general, the terminology for morphological and anatomical structures follows Ramayya (1962), Font Quer (2000), Hickey (1973), King and Robinson (1987), Bremer (1994), and Harris and Woolf Harris (1994).

For the parsimony analysis (Fitch 1971), a total of 26 species were sampled, including all 17 putative species of *Stomatanthes*, both species of *Hatschbachiella*, two species of *Austroeupatorium*, and three species of *Eupatorium*, all taxa belonging to Eupatoriinae, as well as two outgroups of the subtribe Gyptidinae: *Campuloclinium macrocephalum* (Less.) DC. and *Gyptis commersonii* Cass. (Appendix 2).

Our previous attempts to run the analysis with the exclusive use of qualitative data yielded poorly resolved trees. Therefore, quantitative characters were included after selection based on phenetic methods (neighbour joining–NJ–and cluster analysis) (Sosa and De Luna 1998), using the program PAST ver. 2.08b (Hammer et al. 2001). We measured 260 plants (10 specimens per species) with three measurements by organ trait in order to analyze the morphometric variation in 25 vegetative and reproductive characters. The goals of this analysis were to verify if interspecific variation of quantitative characters was greater than intraspecific variation, and to detect which of the quantitative traits contribute to grouping information. Of the 25 quantitative traits originally measured, only eight (blade length and width, involucre length, corolla length, corolla limb width, corolla tube width, thecae length, anther apical appendage length) provided clustering information and therefore were included in the cladistic analysis (see Supplemental Appendix 1 online). The quantitative characters were treated as standardized ranges given that character standardization ensures equal character contribution and to prevent characters with extremely large numbers from exerting more influence than those with smaller values (Sokal 1961; Donato 2011).

After examining the morphological traits of all 26 species, some polymorphic characters were discovered (e.g. characters 2, 5, 7). There is a tradition in systematics of excluding polymorphic characters under the presumption that they are less reliable in phylogenetic inference (Wiens, 1995). However, ignoring these characters may result in data matrices that contain insufficient information to reconstruct the phylogeny (Kornet and Turner 1999), therefore we decided to include them in the analysis. There are several methods for coding polymorphic characters (Crisci and López Armengol 1983; Wiens 1995; Kornet and Turner 1999), but two are extensively used: a species with two traits is coded as polymorphic (i.e. if the species has the character states 0 and 1, it is coded as 0, 1), or the polymorphism is coded as a separate character state in an unordered transformation series (i.e. if the species has the character states 0 and 1, it is coded as 2). We prefer the latter method because no special connection is implied between polymorphic and fixed conditions, so it is as parsimonious to evolve a derived state independently in a fixed and polymorphic species as to have the state change from polymorphism to fixation (Campbell and Frost 1993). In addition, it seemed more logical to code the polymorphism as a separate character state than to allow the software

program to choose the variable state that minimizes the tree length, which represents a non-real biological situation. Nevertheless, we secondarily coded the polymorphisms as 0, 1 in a separate analysis to compare the delimitation of *Stomatanthes* in both outputs.

Thus, parsimony analysis was performed by combining 43 qualitative (polymorphic and non-polymorphic) and eight quantitative traits (Appendix 1; Supplemental Appendix 1; Supplemental Table 1 online) using TNT (Goloboff et al. 2000). All characters were treated as unordered and of the same weight. A tree bisection-reconnection (TBR) algorithm with 1,000 replicates and saving 100 trees per cycle was used to find the most parsimonious trees. Internal support was estimated by Jackknife (Farris et al. 1996), with 1,000 replicates. The characters were explored with WinClada (Nixon 2002).

A non-metric, multidimensional scaling and a cluster analysis were also performed using the Jaccard index and the UPGMA (unweighted pair group method using the arithmetic averaging) clustering method (Sneath and Sokal 1973) in the program PAST ver. 2.08b (Hammer et al. 2001).

RESULTS AND DISCUSSION

Phylogenetic and Phenetic Analyses and Generic Delimitation—The phylogenetic reconstruction of *Stomatanthes* and closely related genera yielded one tree (Fig. 1) with length = 189 steps, consistency index (CI) = 0.34, and retention index (RI) = 0.50. The low (or lack of) support for some branches (less than 50%), together with the low consistency index, reflect the high levels of homoplasy in the group under study. Molecular phylogenetic analyses of Eupatoriaceae also showed moderate to low branch support, which was explained by a rapid radiation of lineages within the tribe (Ito et al. 2000; Schmidt and Schilling 2000; Schilling 2011). Rapid evolutionary radiations have been proposed to explain poorly resolved phylogenies in many groups of organisms, including higher plants (Whitfield and Lockhart 2007). Reconstruction of recent radiations is hampered by insufficiently rapid sequence evolution and problems with incomplete lineage sorting and reticulate evolution (Fishbein and Soltis 2004). Regarding Asteraceae, it has been hypothesized that the relatively young age (17 Myr) of subfamily Asteroideae was the result of a family-wide, rapid Oligocene–Early Miocene diversification (Funk et al. 2009). According to Panero and Funk (2008), the extraordinary cladogenesis of some of its more derived lineages, such as Eupatoriaceae, suggests that the family may contain groups with some of the fastest diversification rates among flowering plants. Therefore, it is not surprising that current molecular-based phylogenetic analyses are inconclusive in providing resolution to problems of taxa delimitation within subtribes. They do not allow classification based on molecular phylogenetic results, but continue to require interpretation to portray a somewhat messy phylogeny (Schilling 2011).

The most noteworthy result of the phylogenetic analysis is that the genus *Stomatanthes*, as traditionally considered with 17 species, is non-monophyletic. Three African species, *S. africanus* (the type species of *Stomatanthes*), *S. helenae*, and *S. meyeri* form a group supported by stomata in the corolla lobes, carpopodial cells oblong and sub-quadrate, with the outermost layers thickened, and twin, ramose, and glandular hairs in the cypselae (Fig. 1). This group is sister to the remaining taxa except the outgroups *Campuloclinium* and *Gyptis*. *Stomatanthes zambiensis*, the other African species, appears as independent from the previous clade, and sister to *Austroeupatorium* and *Eupatorium*, a relationship supported by verticillate phyllotaxis and leaf shape ovate or obovate. As previously mentioned, King and Robinson (1975) already noted this group as a distinctive taxon, which they included in subgenus *Verticifolium*.

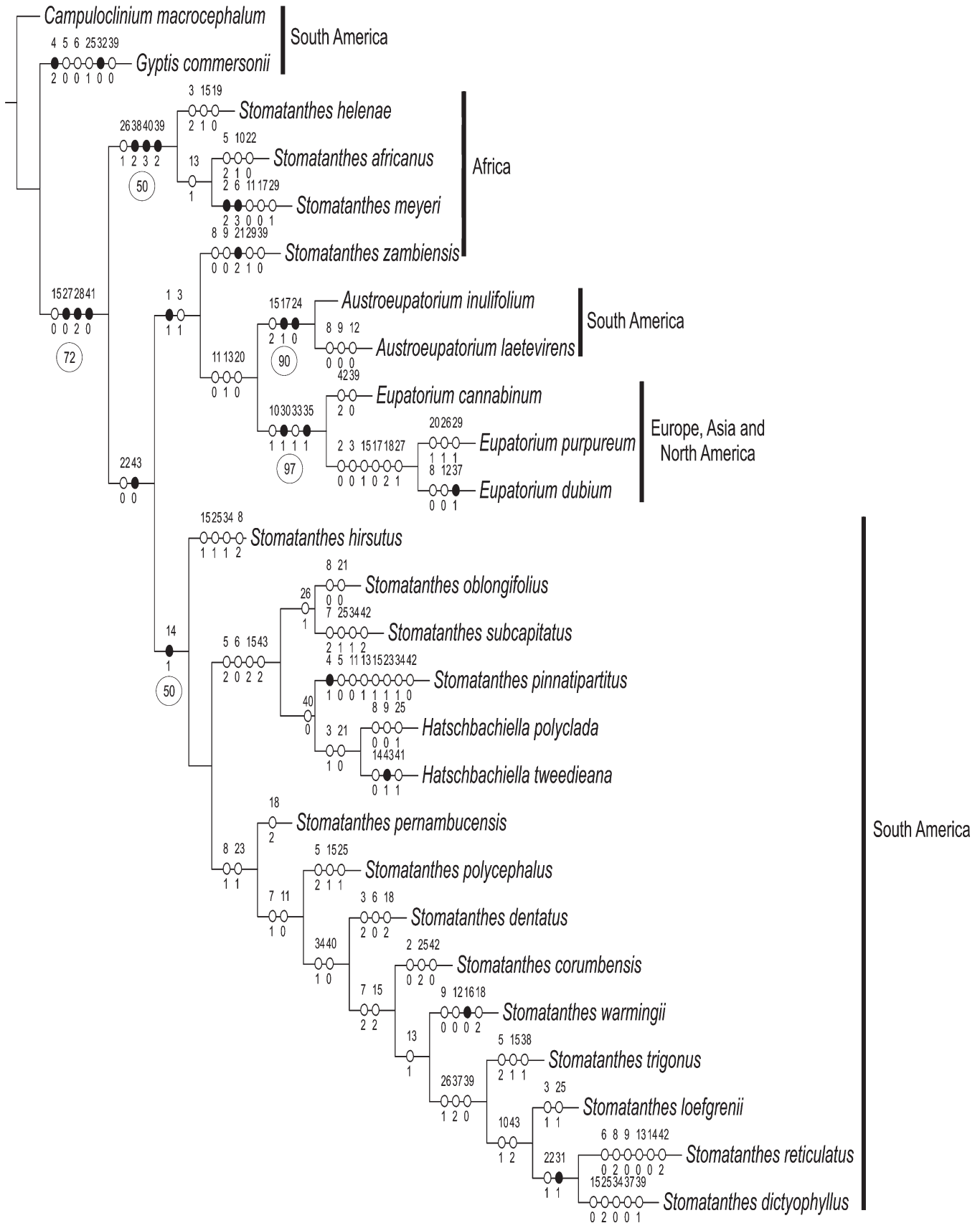


FIG. 1. Tree from the maximum parsimony analysis of 43 qualitative and eight quantitative characters of *Stomatanthes* and related genera. Black circles represent synapomorphies and white circles represent homoplasies (parallelisms and reversals). Numbers within circles below branches are Jackknife support values; only values equal to or above 50 are indicated.

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The remaining nominal species of *Stomatanthes*, all South American, form a group supported by paniculiform inflorescences and are divided into three clades, one containing *S. hirsutus*, one with three species of *Stomatanthes* sister to *Hatschbachiella*, and the third with nine species of *Stomatanthes* (Fig. 1).

With the polymorphic characters coded as polymorphisms, one tree (not shown) was obtained with CI = 0.37, RI = 0.50, and length of 192 steps. In this analysis, *Stomatanthes* was similarly circumscribed (*S. africanus*, *S. helenae*, and *S. meyeri*), and sister to the remaining taxa except the outgroups. Support for the *Stomatanthes* lineage was slightly lower (47%) compared to the first analysis (50%). Also, *Stomatanthes zambiensis*, *Austroeupatorium*, and *Eupatorium* formed a monophyletic group, although in this case the group was nested among the South American taxa. This tree showed some polytomies in the South American taxa, whereas the tree displayed in Fig. 1 was completely resolved. In addition, the implied weighting of TNT was employed in both analyses applying different alternative concavity constants ($k = 5-16$) to examine the sensitivity of the nodes; a more concave decreasing function (> 3) is more reliable as it would resolve relationships in favour of those with less homoplasy (Goloboff 1993). The tree of Fig. 1 maintained the same topology in all cases, whereas the tree with polymorphisms coded as 0, 1 changed its topology. From a biogeographic perspective the tree of Fig. 1 is also more consistent with current hypotheses of Eupatoriaceae, with the North American taxa sister to (instead of nested within) the South American species. A North American origin of Eupatoriaceae and Heliantheae sensu lato was postulated (Schmidt and Schilling 2000; Funk et al. 2005) and supported by dispersal-vicariance analysis (Baldwin et al. 2002). From this area, dispersal events occurred to the north (Europe) and the south (South America), with some taxa reaching Africa (Baldwin et al. 2002). For these reasons we consider that polymorphic characters should be treated as separate character states. Consequently, we believe the tree shown in Fig. 1 is preferable.

Overall, the results of the cluster analysis (Fig. 2) and the non-metric, multidimensional scaling (Fig. 3) show species groups congruent with the topology of the phylogenetic tree (Fig. 1). The African species, with the exception of *S. zambiensis*, form a cluster, and *S. zambiensis* groups in the dendrogram with *Eupatorium* and *Austroeupatorium* as it did in the phylogenetic analysis. The remaining South American species of *Stomatanthes* cluster with *Hatschbachiella*, but show some different relationships among them in comparison to the phylogenetic analysis. There is no doubt, however, that *Stomatanthes* constitutes a paraphyletic assemblage with species assigned to this genus falling into three groups: (a) the African species *S. africanus*, *S. helenae*, and *S. meyeri*; (b) *S. zambiensis*, the other African species; and (c) the South American species plus *Hatschbachiella*, independent from the African groups.

This is the first study that combines phylogenetic and phenetic approaches to this group, with a broad sampling that includes all 17 species of *Stomatanthes* according to the traditional concept of the genus and other members of subtribe Eupatoriinae. Also, this is the first time that qualitative and quantitative characters are combined into a single matrix for a phylogenetic analysis of Asteraceae. The addition of quantitative characters to the analysis was fundamental to resolve several polytomies that exist with the exclusive use of quali-

tative characters. Both phylogenetic and phenetic approaches support a new circumscription of the genus *Stomatanthes* because the results indicate that *Stomatanthes* as traditionally recognized (e.g. King and Robinson 1987; Hind and Robinson 2007; Robinson et al. 2009) is not monophyletic. Therefore, a new delimitation of the genus *Stomatanthes* is proposed, which consists of just the three African species: *S. africanus* (type species), *S. helenae*, and *S. meyeri*.

Stomatanthes is distinguished from other genera of Eupatoriinae by its alternate to opposite leaves (verticillate in *S. zambiensis*), corymbiform inflorescences (paniculiform in *S. zambiensis*, *Hatschbachiella*, and the nominal species of *Stomatanthes* from South America), and the fruit with ramose hairs (absent in the remaining Eupatoriinae taxa).

Morphology—GROWTH FORMS—The three species of *Stomatanthes* are sub-shrubs and herbaceous perennial geophytes, but *S. africanus* and *S. helenae* may be one or the other depending on the environment and stage of plant development. These two species also have a globose, lignified xylopodium, a tuberous underground organ for water storage in response to severe environmental conditions. Since it arises from the hypocotyl and part of the primary root, the xylopodium has mixed features of stem and root (Figueiredo-Ribeiro 1972). This structure is a mechanism of water-use efficiency typical of savanna-like vegetation (Peter and Katinas 2003) that is dormant during drought and sprouts at the beginning of the rainy season. Drought survival of the herbaceous plants is dependent on carbohydrates stored in these reserve organs (Braga et al. 2006). When the aerial parts of the plants are damaged by fire or die in the dry season, the underground shoot buds of the xylopodium, which are well protected against overheating by the soil layer, repeatedly sprout (Jeník 1994).

STEM—The stems may be glabrous or pubescent, covered principally with simple, filiform, non-glandular hairs, although glandular biseriate hairs may appear on occasion. Anatomically, the stem transection displays a vascular cylinder with primary growth (sometimes with intermediate features of a stem with secondary growth), and a parenchymatous pith with thickened cell walls. Each vascular bundle is surrounded by a sclerenchyma sheath, sometimes forming conspicuous ribs, which constitute a continuous cylinder adjacent to the phloem. The epidermis is uniseriate with a thick cuticle, and there are several layers of collenchyma below the epidermis followed by parenchyma tissue (Fig. 4A).

LEAVES—*Stomatanthes* has simple, sessile or shortly petiole leaves, with trinerved, actinodromous venation in *S. meyeri*, or trinerved acrodromous (Hickey 1973) venation in *S. africanus* and *S. helenae*. The variation between an acrodromous and actinodromous venation pattern could be a consequence of blade width, with actinodromous in wide blades and acrodromous in narrower blades. Within the genus, variation occurs in shape and size of the leaves, as well as degree of pubescence. Leaf size of *S. africanus*, for example, varies from 0.8–6.20 cm long. Contrary to the commonly opposite phyllotaxis in Eupatoriaceae, alternate and sub-opposite leaves occur in *Stomatanthes*.

Anatomically, all species of *Stomatanthes* have one layer of epidermal cells, which in transverse section are either isodiametric or rectangular. The lower epidermal cells are normally smaller than the upper ones. The outer periclinal epidermal cell walls are cutinized. The main vascular collateral bundles are usually surrounded by a sheath of sclerenchyma

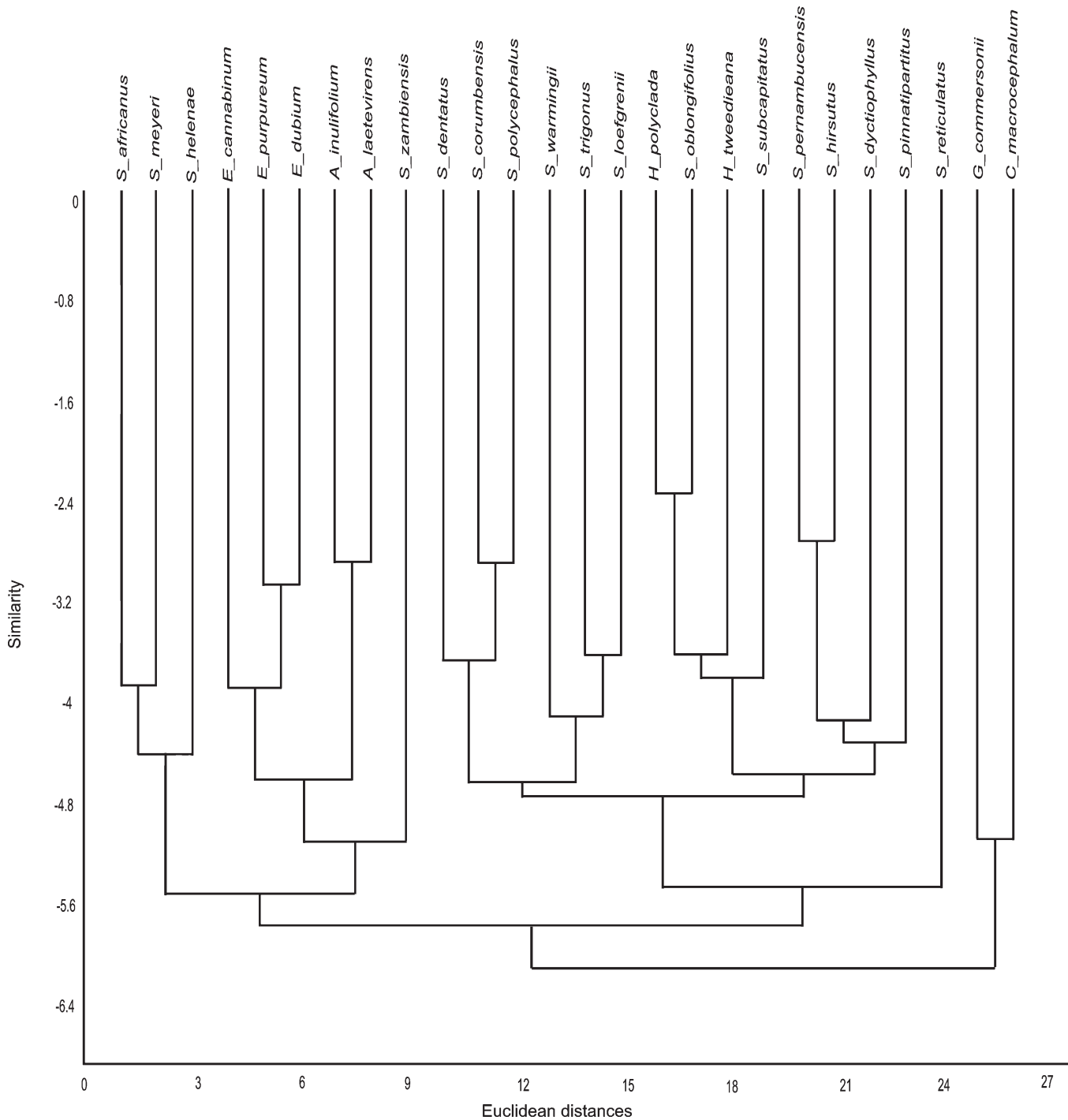


FIG. 2. UPGMA dendrogram for species of *Stomatanthes* and related genera. Euclidean distances were used as global distances.

fibers; lateral vascular bundles are arranged in one row, approximately equidistant from the abaxial and adaxial epidermal layers. Secretory canals are found close to the phloem. Leaves are amphistomatic and stomata are of the anomocytic type. *Stomatanthes africanus*: In outline the midribs are protruding both adaxially and abaxially, and the lateral veins are non-protruding. Leaf symmetry is isobilateral 2–3-layered, with adaxial palisade chlorenchyma, occasional colourless parenchyma, and abaxial palisade chlorenchyma. Distinctive anatomical features include adaxial epidermal cells with thick cuticle, sunken stomata with small stomatal chambers, and sunken and abundant glandular hairs. Collenchyma tissue

usually surrounds the midvein (Fig. 4B). *Stomatanthes helena*: In outline the veins are non-protruding or slightly protruding adaxially and abaxially. Leaf symmetry is isobilateral 2–3-layered, with adaxial palisade chlorenchyma, areas of lignified parenchyma that connect the sclerenchymatous bundle sheaths, and abaxial palisade chlorenchyma. Distinctive anatomical features include adaxial and abaxial epidermal cells with thickened walls and a thick cuticle layer, and superficial stomata with large stomatal chambers, either glabrescent or with very scarce, sunken glandular hairs (Fig. 4C). *Stomatanthes meyeri*: In outline the midrib is protruding both adaxially and abaxially, whereas most lateral

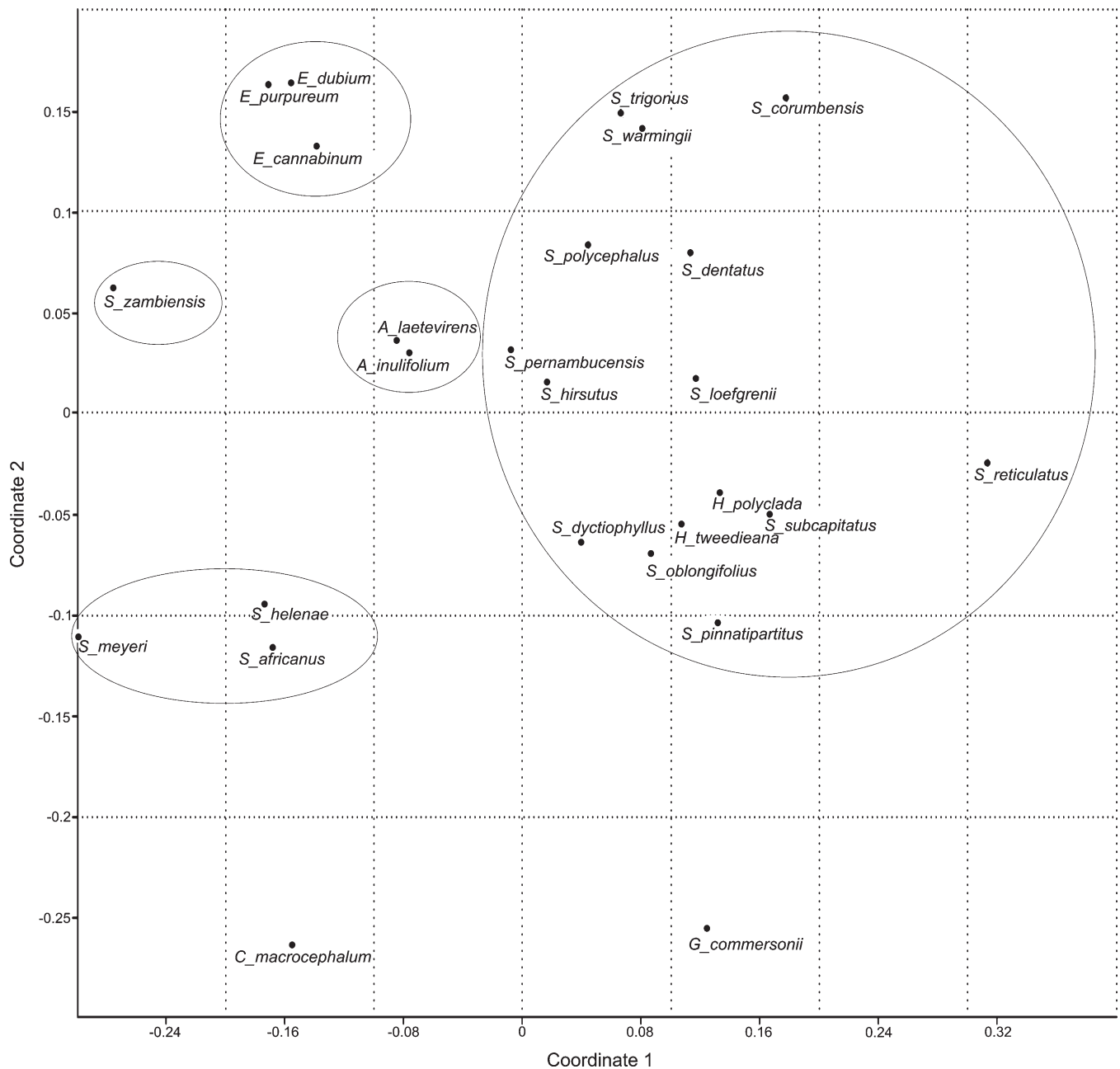


FIG. 3. Non-metric multidimensional scaling for species of *Stomatanthes* and related genera. Black circles represent the main groups defined by minimal spanning tree.

veins are non-protruding or protruding only abaxially. Leaf symmetry is bifacial, with adaxial palisade chlorenchyma and abaxial spongy chlorenchyma. Distinctive anatomical features include adaxial and abaxial epidermal cells with a thick cuticle layer, elevated stomata with large stomatal chambers, abundant non-glandular hairs, scarce sunken glandular hairs on the adaxial side, and non-sunken on the abaxial side (Fig. 4D).

HAIRS—There are two main types of hair: glandular and non-glandular. Glandular hairs are: (a) Capitate, with a foot one to many-celled, body uniseriate, one to four-celled, and a one-celled, spherical head with thickened walls. This type is present on the leaves, generally sunken in the epidermis, of *S. africanus* and *S. helenae* (Fig. 5A). (b) Biseriate (simple biseriate glandular, subtype β ; Ramayya 1962), different from

the former by its biseriate, two- to 10-celled body and a cuticular vesicle at the apex sometimes collapsed. This type is commonly found on the leaves of *S. meyeri* and *S. africanus* sunken in the epidermis, in the latter species mixed with capitate hairs; it is also present on the corollas and cypselae, and occasionally on the stems of the three species (Fig. 5B).

Non-glandular hairs are: (a) Simple filiform, with a foot one to many-celled, body uniseriate, five to more-celled, the basalmost cell sometimes wider than the rest, and a long, tapering apical cell, with a transparent or opaque content. This type is found on the leaves of *S. meyeri*, and on the stem, peduncles, phyllaries of the involucre, and sometimes on the corollas of the three species of *Stomatanthes* (Fig. 5C, 6A). (b) Twin hairs (*Zwillingshaare*; Hess 1938) are formed by two triangular or rectangular short basal cells (one sometimes

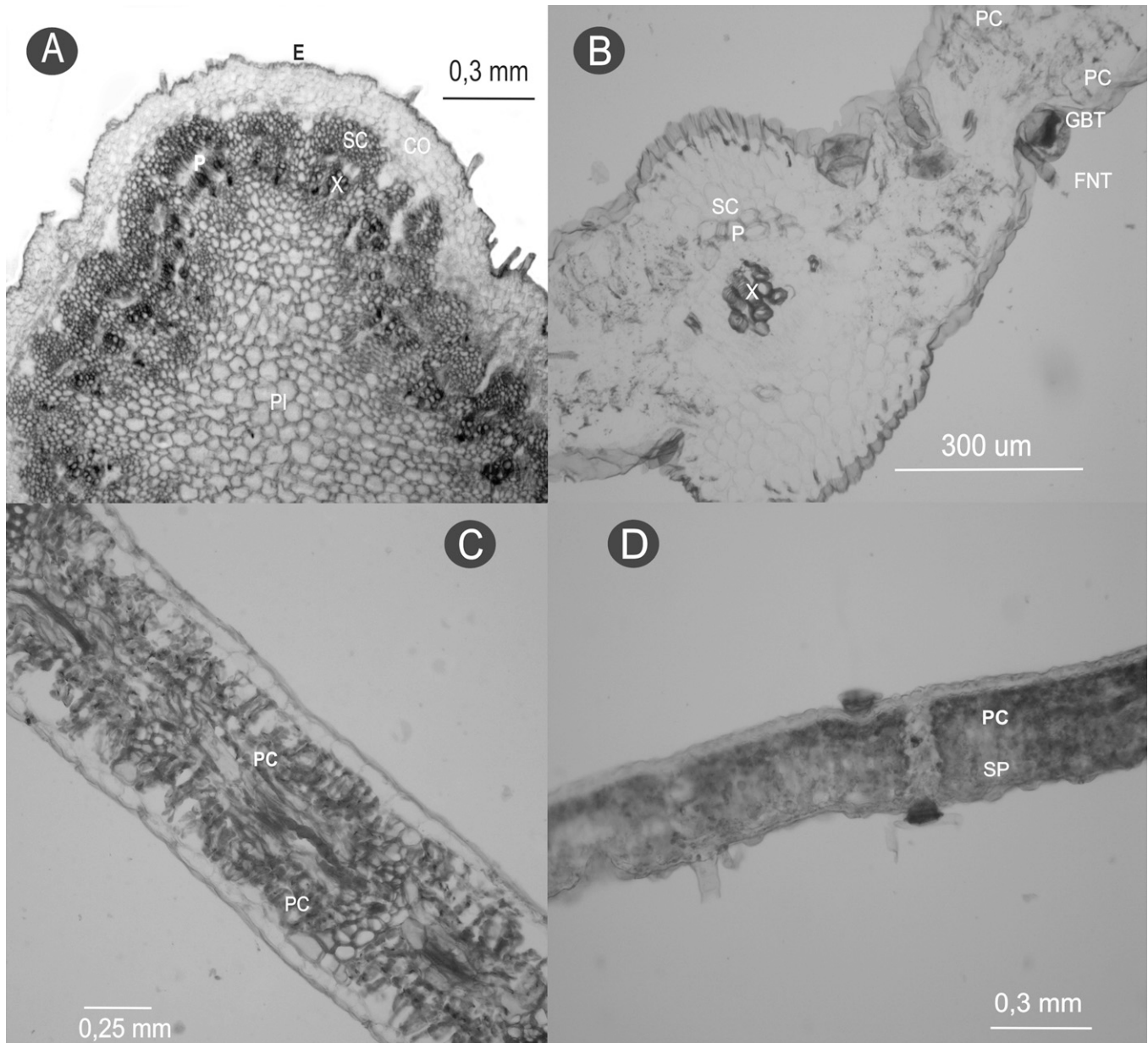


FIG. 4. Anatomy of vegetative organs of *Stomatanthus*. A. Stem transection of *S. helenae* (Duvoigneaud 4503, BRLU). B. Leaf transection of *S. africanus* (Biholong 441, P). C. Leaf transection of *S. helenae* (Duvoigneaud 4503, BRLU). D. Leaf transection of *S. meyeri* (Meyer 7966, US). E = epidermis, CO = collenchyma, FNT = filiform non-glandular hair, GBT = glandular biseriate hair, P = phloem, PC = palisade chlorenchyma, PI = pith, SC = sclerenchyma, SP = spongy chlorenchyma AA -, X = xylem.

reduced), and two elongated cylindrical hair cells, with thick walls, completely united with each other on their longitudinal walls or diverging, equal in length or one shorter, sometimes septate. They are found on the cypselaes of the three species, usually at the base above the carpodium or partially covering it (Fig. 5D, 6B). (c) Ramose (Ramayya 1962), with a foot one-celled, body uniseriate, four to more-celled, and a head few to many-celled, appearing unichasially branched. This type of hair is exclusive on the cypselaes of the three species of *Stomatanthus*, and allows differentiation from closely related taxa (Fig. 5E, 6C).

CAPITULA—The capitula are homogamous and grouped in corymbiform cymes forming corymbiform or paniculiform inflorescences of second order. The involucre is cylindrical or campanulate, consisting of a low (five to 15) number of

phyllaries disposed in one to four series; when more than one series, the phyllaries are sub-imbricate, i.e. they are progressively longer in overlapping series, but at least the outer bracts spread at maturity and do not fall (King and Robinson 1987). The receptacle is naked and glabrous, planate or slightly convex.

FLORETS—The number of flowers per capitulum is low, four or five in *Stomatanthus africanus* and *S. meyeri*, and six to eight in *S. helenae*. They are bisexual and fertile, with actinomorphic, funnellform or sub-funnelform, five-lobed corollas. The corolla lobes are often thickened at the margins and always bear stomata (Fig. 6D). Even though this is a distinctive feature of *Stomatanthus*, some South American Eupatoriinae may also have stomata in their corolla lobes. Anthers are ecalcarate, with the base rounded or obtuse; the apical appendages are

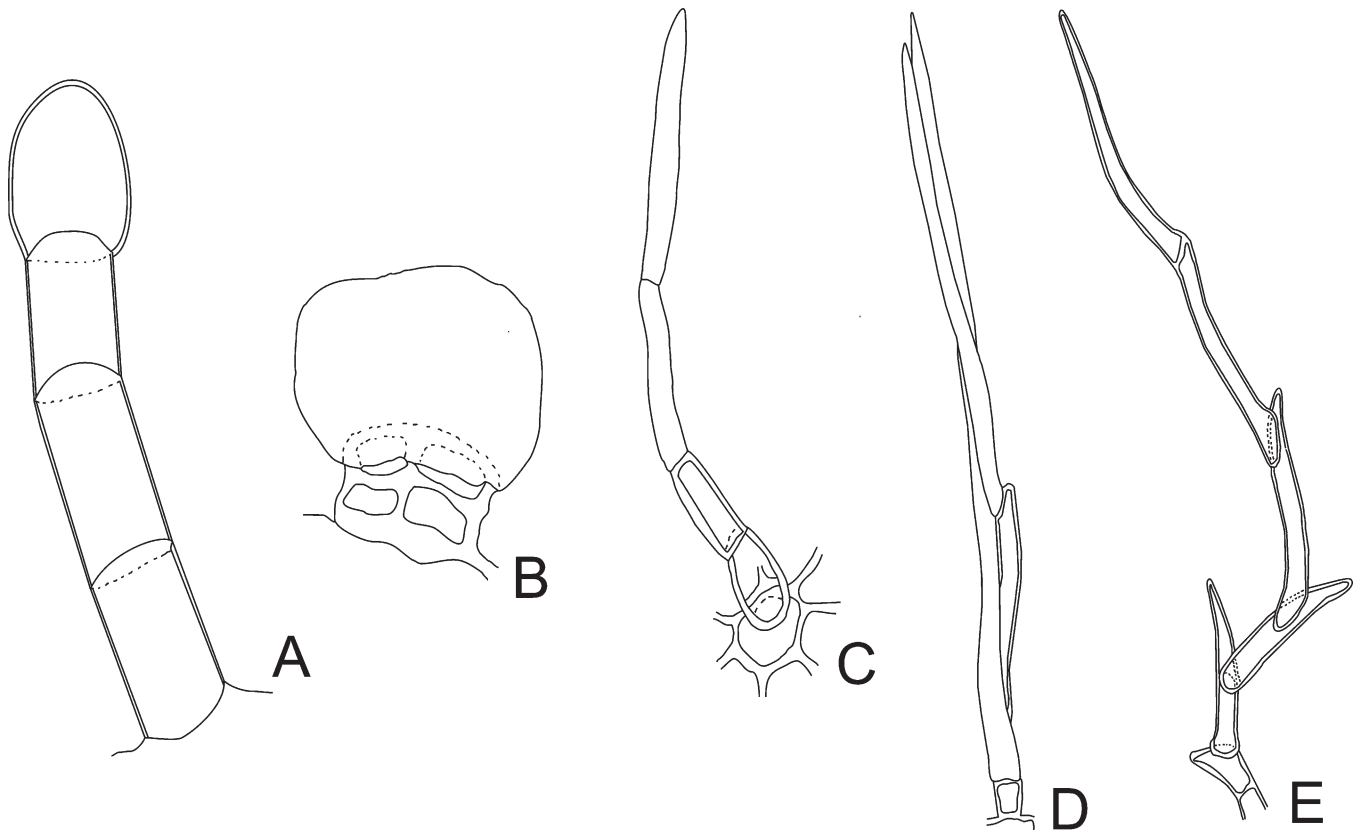


FIG. 5. Vegetative and reproductive hairs in *Stomatanthes*. A. Capitulate glandular, found in leaves, usually sunken in the epidermis (*S. africanus*, Biholong 441, P). B. Biseriate glandular, found sunken in the epidermis of leaves, on corollas and fruits, and occasionally on stems (corolla of *S. africanus*, Van der Ben 1642, US). C. Simple filiform, found on leaves, stems, peduncles, phyllaries, and sometimes on corollas (phyllary of *S. africanus*, Audru 5012, P). D. Twin hair, found on fruits (*S. africanus*, Fotius 2599, P). E. Ramose, found on fruits and a distinctive feature of the genus (*S. helenae*, Thienpont 35, BR).

conspicuous or reduced, rounded, or truncate and emarginate at the apex. The anther collar is conspicuous, well developed, with the tangential cell walls transversely banded, and the outer layers of cells have thicker walls than the inner layers. The style, as in most Eupatorieae, is very conspicuous and much-exserted, with two branches divided into an apical half corresponding to a sterile area called the branch appendage, and a basal half or fertile area. Externally the sterile area is covered by long papillae or sweeping hairs, whereas the fertile area is covered by shorter papillae. Internally the sterile area is also covered by long papillae and the fertile portion has two marginal bands of short, receptive papillae (stigmatic bands) separated by a glabrous area. The three species have long, multicellular, one-celled papillae at the base of the style.

CYPSELA—Cypselae are prismatic in shape, five- or six-ribbed, and have a conspicuous basal carpodium in the area of detachment from the receptacle (Fig. 6B). The carpodium cells are sub-quadrate or oblong. All species of *Stomatanthes* have pubescent cypselae, with the hairs usually gathered around the apical part of the carpodium (see Hairs).

PAPPUS—The pappus bristles are disposed in one series, and are capillary and scabrid, usually unequal in length, white or pale yellow. The apical cells may be acute or rounded.

POLLEN—Pollen of *Stomatanthes* (Fig. 7) is small ($16\text{--}20 \times 14\text{--}22 \mu\text{m}$) when compared with pollen from genera of other tribes of Asteraceae (King and Robinson 1987). It is prolate-spheroidal or spheroidal, tricolporate, echinate, with the tectum microperforate. The spines are evenly distributed, pointed, and the bases have perforations. Pollen grains have

a helianthoid pattern (caveate exines with internal foramina; Skvarla et al. 1977), with thickened margins and a microgranulate membrane. Overall, pollen of the three species of *Stomatanthes* is similar, except that in *S. meyeri* the spines are more densely distributed (Fig. 7D).

TAXONOMIC TREATMENT

STOMATANTHES R. M. King & H. Rob., *Phytologia* 19: 429. 1970.—TYPE: *Eupatorium africanum* Oliv. & Hiern.

Perennial herbs or sub-shrubs, with or without xylopodium. Stems erect, moderately branched, terete, striate, strigose-tomentulose. Leaves alternate, opposite, or sub-opposite, sessile or short-petiolate, blade membranaceous to sub-coriaceous, ovate, oblong-lanceolate, sub-triangular, or elliptic-lanceolate, rarely linear, base cuneate, cordate, or rounded, apex acute, acuminate or obtuse, margins entire, strongly serrate or irregularly lobulate, pubescent with glandular and non-glandular hairs, or glabrous; venation trinerved, acrodromous or actinodromous, strongly reticulate, prominent on both faces. Heads homogamous, grouped into lax or dense corymbiform cymes forming lax or dense corymbiform or paniculiform inflorescences, peduncles pubescent. Involucre cylindrical or campanulate, one to four-seriate; phyllaries five to 15, sub-imbriate, lanceolate, oblong to oblong-ovate, membranaceous, green or with the apex purple, margins scarious, often ciliate or fimbriate, acute, acuminate, or obtuse at the apex, glabrous or pubescent. Receptacle naked, slightly convex or planate,

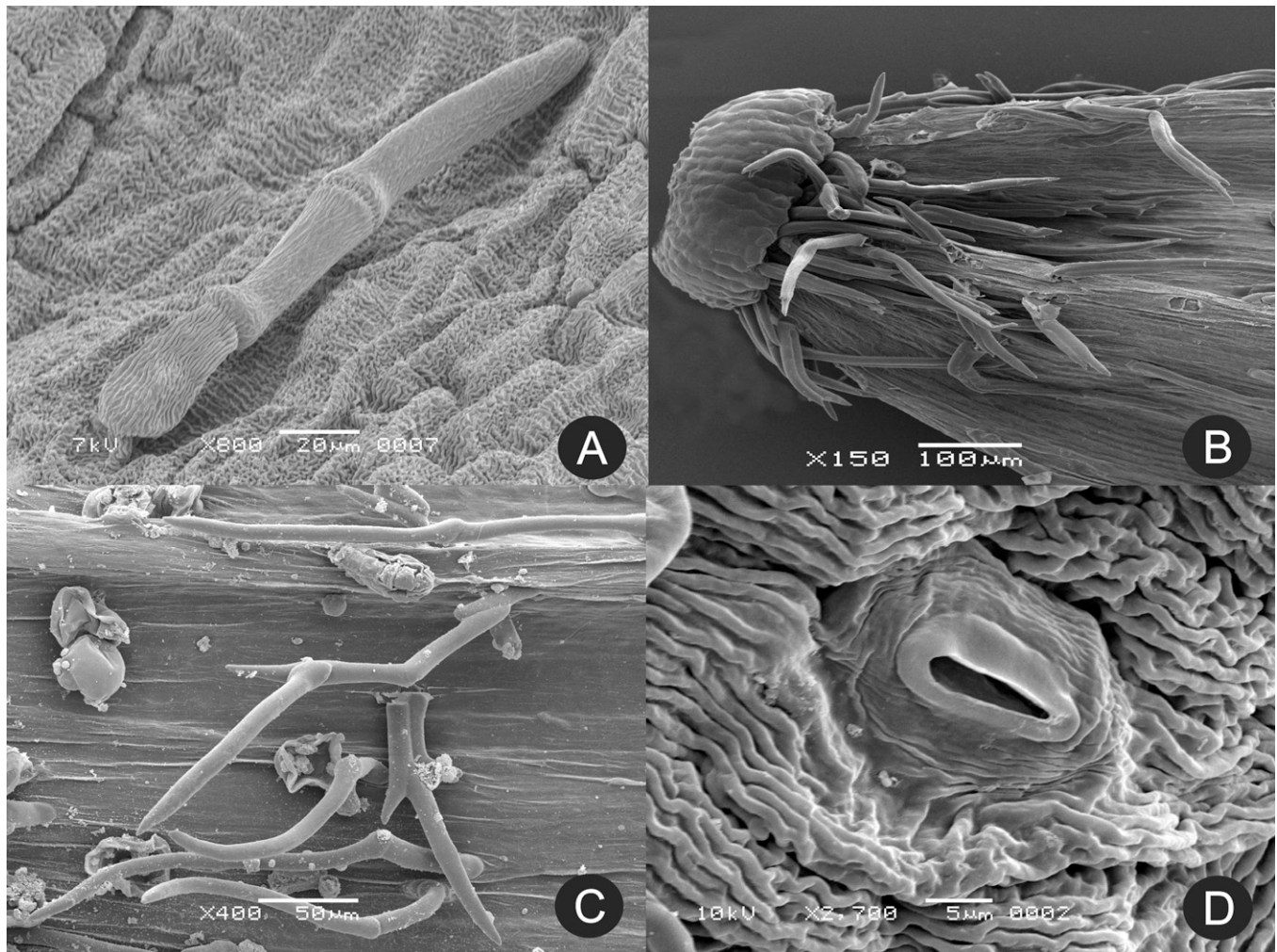


FIG. 6. SEM photographs of hairs and stomata in *Stomatanthus*. A. Simple filiform hair on the corolla of *S. africanus* (Schlieben 1233, P). B. Twin hairs on a fruit of *S. africanus*; note the distinctive carpodium at the base of the fruit (Compère 562, C). C. Ramose hairs on a fruit of *S. africanus* (Compère 562, C). D. Stoma on a corolla lobe of *S. africanus* (Schlieben 1233, P).

glabrous. Florets four to eight, bisexual, corollas white, funnellform or sub-funnelform, shortly five-lobed, tube with glandular and non-glandular hairs, lobes papillose, triangular, with stomata. Anthers with base rounded or obtuse, anther collar cylindrical, with transversely banded cells, the outer layers with thicker cell walls, anther appendages ovate, oblong, widely oblong, rounded, or truncate, emarginate at the apex. Style base not enlarged, covered with one to few-celled hairs, branches very long, linear, with papillose, sterile apical appendages, stigmatic areas in two, widely separated, marginal lines at the base of each style branch. Cypselae prismatic, five or six-ribbed, densely pubescent, with or without glandular hairs, with twin and ramose hairs, carpodium distinct, with cells oblong or sub-quadrate. Pappus white or

pale yellow, uniseriate, of 30–60, scabrous, capillary, persistent bristles with slender tips, apical cells rounded or acute. Pollen grains spheroidal, $P \times E = (16-20 \times 14-22) \mu\text{m}$, tricolporate, echinate.

Etymology—The generic name *Stomatanthus* derives from the Greek *stoma*, mouth, opening, and *anthos*, flower, and refers to the presence of stomata on the corolla lobes.

Distribution—The three species are endemic to Africa. One species has a widespread distribution from the northern sub-Saharan region throughout the entire continent to the south, except the Namibia desert. A second species grows in the southern Democratic Republic of Congo and northern Zambia, and the third species is a narrow endemic of the Kaffa Province in Ethiopia.

KEY TO THE SPECIES

1. Leaves 3.5–7 cm wide, cordate at the base; anthers with apical appendage truncate, emarginate at the apex 3. *S. meyeri*
1. Leaves 0.2–2.2 cm wide, cuneate or rounded at the base; anthers with apical appendage widely oblong or ovate, rounded at the apex 2
2. Leaves ovate, pubescent below; phyllaries of the involucre pubescent 1. *S. africanus*
2. Leaves oblong-lanceolate to linear, glabrous below; phyllaries of the involucre glabrous 2. *S. helenae*

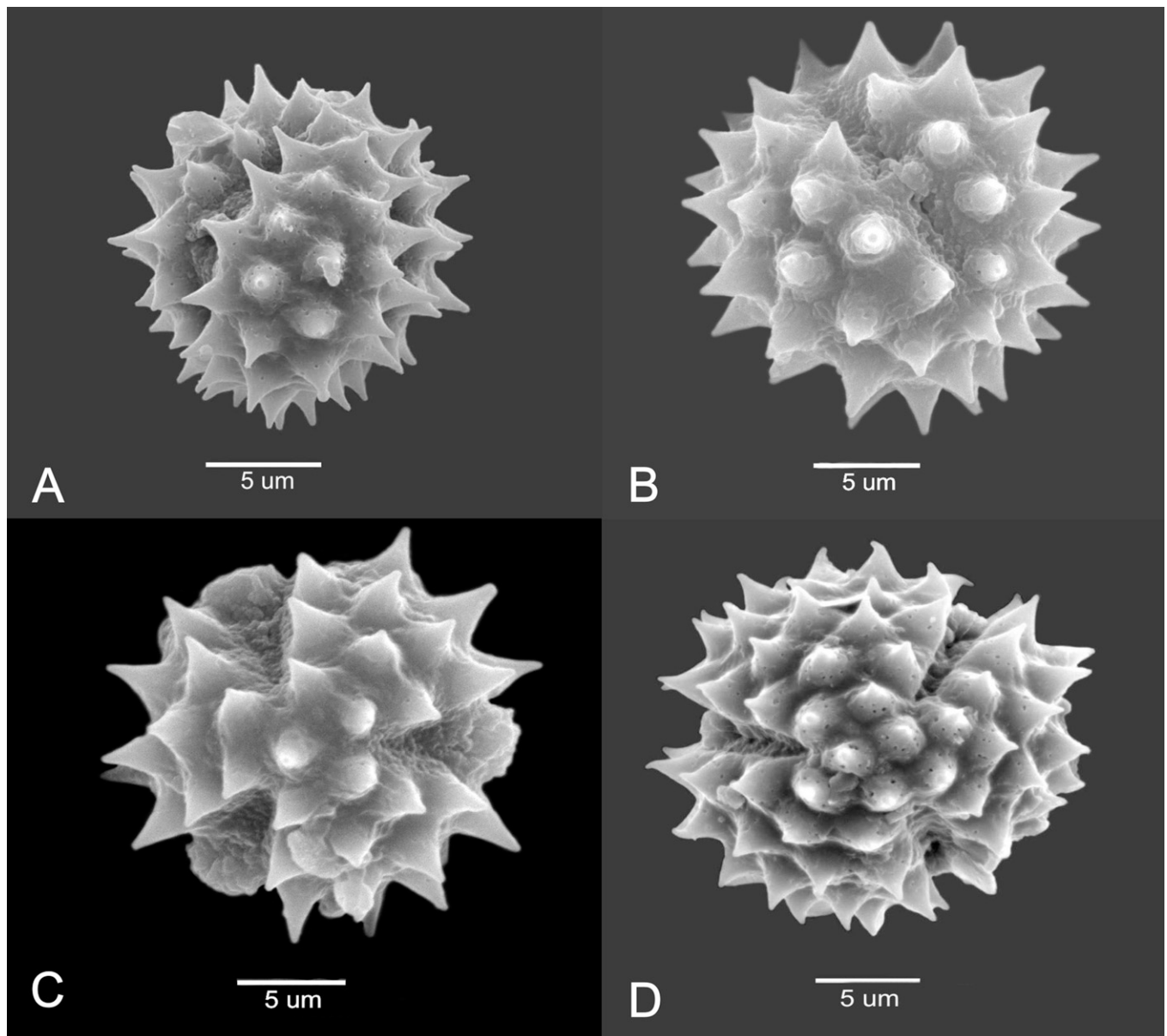


FIG. 7. SEM photographs of pollen grains of *Stomatanthes*. A. *Stomatanthes africanus* (Le Testu 2415, P), equatorial view. B–C. Pollen of *Stomatanthes helenae* (Duvoigneaud 4758 E1, BRLU). B. Equatorial view, showing the aperture with microperforate membrane. C. Polar view; note the granular membrane. D. *Stomatanthes meyeri* (Meyer 7966, US), polar view showing the spines densely distributed.

1. *STOMATANTHES AFRICANUS* (Oliv. & Hieron.) R. M. King & H. Rob., *Phytologia* 19: 430. 1970. *Eupatorium africanum* Oliv. & Hieron., *Fl. Trop. Africa* 3: 301. 1877.—TYPE: DEMOCRATIC REPUBLIC OF CONGO. Kasai-Occidental: Gumba, Niamniam Land, 5 Feb 1870, *Schweinfurth* 2897 [lectotype: K, designated by Smith (2005), photograph LP!; isotype: US, photograph LP!].

Eupatorium africanum Oliv. & Hieron. var. *vanmeelii* Lawairée, *Bull. Jard. Bot. État Bruxelles* 19: 220. 1949.—TYPE: DEMOCRATIC REPUBLIC OF CONGO. Katanga: Tugulu, 17 Nov 1846, *Van Meel* 155 (holotype: BR!).

Vernonia humilis C. H. Wright, *Kew Bull.*: 269. 1897.—TYPE: MALAWI. Mulanje: Mt. Mulanje, *McClounie* 30 (lectotype: K, here designated, photograph LP!).

Vernonia malosana Baker, *Kew Bull.*: 148. 1898.—TYPE: MALAWI. Zomba: Malosa and Zomba Mts., *Whyte s.n.* (holotype: K, photograph LP!).

Sub-shrubs 0.20–1.2 m tall, with xylopodium. Stems sometimes reddish. Leaves alternate, sub-opposite, or opposite, laxly arranged on stems, sessile or short-petiolate, petiole 4–6 mm long, blade 0.8–6.2 × 0.2–2.2 cm, membranaceous to sub-coriaceous, widely or narrowly ovate, base cuneate or rounded, apex acute, acuminate, or obtuse, margins entire, serrate, or irregularly lobulate, thickened, glabrous to puberulous above, with simple, non-glandular hairs mainly on the veins and sometimes glandular hairs on the blade beneath; venation acrodromous, rarely actinodromous. Heads in lax or dense cymes, forming a lax or dense, corymbiform inflorescence, peduncles 2–8 mm long, pubescent. Involucre

campanulate, 8–14 × 3–6 mm, one- or two-seriate; phyllaries five to seven, lanceolate to oblong-ovate, green or with the apex purple, pubescent, scarious and sometimes fimbriate at the margins, obtuse at the apex, outer phyllaries 3–5 mm long, inner phyllaries 4–10 mm long. Receptacle planate. Florets four or five, corollas 4.5–7.75 mm long, tube 3–5.25 × 0.3–0.9 mm, with glandular biseriate and non-glandular filiform hairs, lobes 0.5–0.88 × 0.35–0.55 mm. Anthers ca. 2 mm long, base obtuse, anther collar 0.28 × 0.35 mm, anther appendages ovate, rounded at the apex, 0.3–0.45 × 0.3–0.4 mm. Style shaft 6.5–7 mm long, style branches 3.5–4.12 mm long. Cypselae 3–4 mm long, densely pubescent (glandular biseriate, twin and ramose hairs), carpodium 0.12–0.18 × 0.24–0.30 mm, with cells mostly sub-quadrate but some oblong. Pappus 5–8 mm long with ca. 30 bristles, apical cells rounded. Pollen grains (Fig. 7A) spheroidal, $P \times E = (20 \times 22) \mu\text{m}$, tricolporate, echinate. Figure 8A–E.

Vernacular Names—Common names for this species are Kihangaza Umutanogá in Tanzania and Omuhaheka in Angola.

Phenology—Flowers throughout most of the year, except in the winter (June to September).

Distribution and Habitat—This species is widespread in central, east, west, and south continental Africa (Fig. 9) excluding deserts, semi-deserts, and rain forest areas, from (350-) 1,050–2,450 m. It occupies the biogeographic regions of woodland/savanna biomes (Udvardy 1975). The African savanna is a grassland ecosystem with trees sufficiently small or widely spaced so that the canopy does not close.

Notes—The syntype of *Eupatorium africanum*, Kirk s.n. (K), is cited in the protologue as growing in “Moramballa”, but this is a typographic error that corresponds to the locality Morrumbala in the riverside of the Zambesi River, in Mozambique.

Stomatanthes africanus usually forms dense populations and colonizes diverse ecological areas, becoming a weed of plantation crops.

Uses—This species is used for making brooms and brushes (Smith 2005), the leaves are used for oral treatments (mouth-wash), and the roots alleviate diarrhea, dysentery, and nasopharyngeal infections (Burkill 1985).

Conservation—The status of this species was proposed as least concern (LC) by Smith (2005), probably due to its wide geographical distribution.

Representative Specimens Examined—ANGOLA. Bengo Province: Golungo Alto, Oct 1855-Jan 1856, *Welwitsch* 3331 (P). Benguela Province: Cubal, Sep 1941, *Kulkues* 160 (M); Ganda, 18 Dec 1951, *Hess* 51/347 (M), id., 15 Dec 1933, *Hundt* 753 (P). Huambo Province: Huambo, 14 Oct 1971, *Barbosa et Silva* 12277 (M). Huila Province: Huila, Jan 1899, *Antunes* 642 (P); Lubango, *Humbert* 16193 (P). Kuando Kubango Province: Chissanda, 4 Oct 1946, *Gossweiler* 13686 (P). Luanda Province: Luanda, 1903–1904, *Gossweiler* 1197 (P). Lunda-Norte Province: Dundo, 18 Jun 1948, *Gossweiler* 14095 (P). Malanje Province: Malanje, *Young* 964 (S). BURUNDI. Karuzi Province: Karuzi, 29 Aug 1957, *Van der Ben* 1642 (US). Ruyigi Province: Kayangozi, 29 Oct 1966, *Lewalle* 1188 (M); Nyakazu Boma, 25 Sep 1974, *Reekmans* 3654 (M). CAMEROON. Adamaoua Province: Ngoum, 36 km N of Yoko, 9 May 1979, *Biholong* 441 (P); SW of Dang Haoussa, throughout the basin of Pangar, 18 Feb 1961, *Letouzey* 3503 (P). Centre Province: Bafia, 2 May 1978, *Ngameni Kamga* 158 (P). Est Province: Bertoua, 22 Jan 1960, *Letouzey* 2746 (P), id., 1962, *Vrcunisia Tchinye* 80 VT (P); Betaré Oya, 21 Feb 1960, *Breteler* 1081 (P), id., 4 Feb 1966, *Leeuwenberg* 7755 (P); Mboulai, 1 Feb 1965, *Raynal* 13363 (P). Littoral Province: 10 km W of Tonga, 30 km NW of Ndikiniméki, 13 Feb 1972, *Letouzey* 11217 (P, S). Nord Province: Banda, 29 Mar 1963, *Raynal* 10590 (P); Konon, 8 Feb 1977, *Fotius* 2599 (P); Ngaoundéré, 29 Jan 1978, *Fotius* 3010 (P), id., 20 Jan 1982, *Satabié* 619 (P); Poli, massif of Vokré, between Gagi and Ganamba, 15 Jan 1965, *Raynal*

13023 (P); Wakwa, Jan 1964, *Piat* 109, 21957 (P). Ouest Province: Bambuto, May 1940, *Jacques Félix* 5490 (P); Bangwa, 30 Apr 1964, *de Wilde* 2354 (P); Fouban, Feb 1939, *Jacques Félix* 3111 (P). CENTRAL AFRICAN REPUBLIC. Autonomous Commune: Bangui, 21 Mar 1958, *Trochain* 10947 (P). Haute-Kotto Prefecture: Yalinga, 4 Feb 1921, *Le Testu* 2415 (P). Nana-Mambéré Prefecture: Baboua, 15 Jan 1964, *Descoings* 12705, 12715 (P); Bouar, *Audru* 3676 (P), id., Feb 1964, *Bille* 1565 (P), id., 2 Jan 1907, *Lenfant* 1098 (P). Ombella-M'Poko Prefecture: Bossembélé, 12 Jan 1964, *Descoings* 12556 (S). Ouaka Prefecture: Bambari, 24 Aug 1923, *Tisserant* 566 (P). CONGO. Cuvette-Ouest Region: Etoumbi, 7 Aug 1961, *Descoings* 8938 (P). Likouala Region: Impfondo District, Impfondo, 21 Feb 1963, *de Nere* 947 (S). Plateaux Region: Djambala District, Djambala, 1982, *Audru* 54744 (P). Pool Region: Kinkala District, Kinkala, 20 Jun 1964, *Bouquet* 132 (P); Pool District, Brazzaville, 11 Jun 1960, *Descoings* 5874 (P); Gamakala, 31 May 1963, *de Nere* 1307 (S); Maloukou, 1965, *Sita* 1162 (P). DEMOCRATIC REPUBLIC OF CONGO. Bas-Congo Province: Kisantu, 1930, *Panderyst* 24826 (US); Matadi, 10 Nov 1956, *Wagemans* 1158 (P); Mbanza-Ngungu, 8 Oct 1959, *Compère* 562 (C); without locality, 1930, *Vanderyst* 25033 (P). Katanga Province: Haut-Lomami District, Kafubu, 21 Nov 1927, *Guarré s.n.* (S); Lubudi, 7 Aug 1948, without leg. 1356 (BRLU); Mindingi, 1956, *Duigneaud et Timperman* 2190 E (BRLU); Mitwaba, 19 Aug 1949, *de Witte* 7343 (C); Lualaba District, Dilolo, 23 Aug 1956, *Duigneaud et Timperman* 2446 (BRLU); Kayuka, 13 Aug 1956, *Duigneaud et Timperman* 2309E (BRLU); Kisenge, 17 Aug 1956, *Duigneaud et Timperman* 2348 E (BRLU). Kinshasa Province: Kinshasa, 22 Jul 1957, *Robyns* 4384 (M). Nord-Kivu Province: Goma, 15 May 1959, *Leonard* 4235 (M); Lake Edward, *Humbert* 8272 bis. (P). Orientale Province: Haut-Uele District, Doruma, 1 Jan 1946, *Germain*. 808 (P). Tshopo District, Kanzenze, 1931, *de Witte* 561 (US). GABON. Ogooué-Ivindo Province: Bououé, 29 Aug 1957, *Anton-Smith* 301 (P). Ogooué-Lolo Province: Lastoursville, 18 Apr 1932, *Le Testu* 7453 (P). Ogooué-Maritime Province: Nyanga, 3 Jul 1919, *Le Testu* 2086 (P). ETHIOPIA. Southern Nations, Nationalities, and Peoples Regions (ex Illubabor): between Bure and Baro River, 17 Apr 1982, *Friis et al.* 2415 (C). GHANA. Brong-Ahafo Region: Wenchi District, Boku, 21 Mar 1953, *Morton* 8587 (M). GUINEA. Faranah Region: Faranah, Apr 1905, *Chevalier* 13192 (P). Kankan Region: Kankan, Dec 1903, *Pobéguin* 1001 (P). Kindia Region: Kindia, Dec 1937, *Jacques Félix* 2155 (P). Nzérékoré Region: Beyla, *Jacques Félix* 1541 (P); Monte Nimba, Feb 1946, *Schnell* 304 (P), id., Apr 1942, *Schnell* 1066 (P). IVORY COAST. Dix-Huit Montagnes Region: Sipilou, 16 Apr 1972, *Audru* 5012 (P), id., 26 Apr 1965, *Boudet* 2587 (P). Zanzan Region: Nassian, 20 Jan 1978, *César* 799 (P). KENYA. Rift Valley Province: without locality, 23 Jun 1949, *Bally* 356 (S). MALAWI. Central Region: Dedza District, Dedza, 21 Oct 1978, *Salubeni* 2357 (P). Nkhhotakota District, Nkhhotakota, 9 Sep 1946, *Brass* 17596 (US). Northern Region: Karonga District, Lupembe, 28 Feb 1931, *Schlieben* 1233 (P). Southern Region: Blantyre District, 1896, *Medley Wood* 6950 (U). Chiradzulu District, Zomba, 6 Nov 1984, *Nachamba* 159 (US). Mulanje District, Chambe, 3 Apr 1958, *Chapman* 577 (S). MOZAMBIQUE. Manica-Sofala Provinces: Chimanimani District, Chimanimani mountains, 27 Sep 1966, *Grosvenor* 200 (M). Zambezia Province: Lugela District, Lugela, 1 Jan 1948, *Faulkner* 174 (S). NIGERIA. Bamenda Province: Bamenda District, Bamenda, 6 Mar 1959, *Daramola* 40532 (P). SIERRA LEONE. Northern Province: Koinadugu District, Bintumani, 2 Jan 1966, *Adam* 22911 (P), id., 5 Jan 1966, *Adam* 22936 (P), id., 12 Jan 1966, *Adam* 23033 (P); Kabala, Mar 1965, *Adam* 8987 (M), id., 25 Nov 1965, *Adam* 22169 (P). SOUTH AFRICA. KwaZulu-Natal Province: Drakensberg, 20 Oct 1938, *Wall s.n.* (S). Limpopo Province: Modjadiskloof, 17 Sep 1959, *Scheepers* 690 (M); Pietersburg, Feb 1962, *Meruue* 41 (M). Mpumalanga Province: Lydenburg District, Buffelskloof Nature Reserve, 14 Nov 2004, *Venter* 10654 (NY). North West Province: Makapan, 29 Nov 1945, *Maguire* 2429 AA (M). SUDAN. Eastern Equatoria State: Imatong, 18 Feb 1982, *Friis et Voelsen* 938 (C). SWAZILAND. Hhohho District: Mbabane, 5 Nov 1959, *Campton* 89342 (M). TANZANIA. Iringa Region: Iringa Rural District, Iringa, 21 Oct 1962, *Lewis* 6068 (US); Kymbila, 19 Nov 1909, *Stolz* 102 (M), id., 31 Jan 1911, *Stolz* 490 (S), id., 1913, *Stolz* 2199 (M). Mufindi District, Ngwazi, 25 Sep 1987, *Lovett* 2265 (US). Njombe District, Kipengere, 14 Nov 1966, *Gillett* 17845 (M). Kagera Region: Kashasha, 10 Aug 1960, *Tanner* 5073 (M); Keza, Ngara, 24 Aug 1960, *Tanner* 5125 (M). Mbeya Region: Mbeya District, Mbeya, 24 Oct 1962, *Lewis* 6074 (US), id., 25 Nov 1989, *Lovett et Kayombo* 3521 (US). Morogoro Region: Mahenge, 15 Dec 1931, *Schlieben* 1552 (M, P). Rukwa Region: Sumbawanga, 28 Oct 1992, *Harder et al.* 1282 (P), id., 12 Oct 1965, *Richards* 20529 (P). UGANDA. Logisi District, Apr 1939, *Hazel* 725 (S). ZAMBIA. Copperbelt Province: Ndola, 23 Dec 1960, *Lindley* 36 (M). North-Western Province: Solwezi, Sep 1962, *Holmes* 1515 (M). ZIMBABWE. Manicaland Province: Mutare, 2 Nov 1967, *Mavi* 417 (M); Nyanga, 6 Dec 1930, *Fries et al.* 3456 (US). Mashonaland East Province: Marondera, 22 Sep 1945, *Julattay* 723 (M).

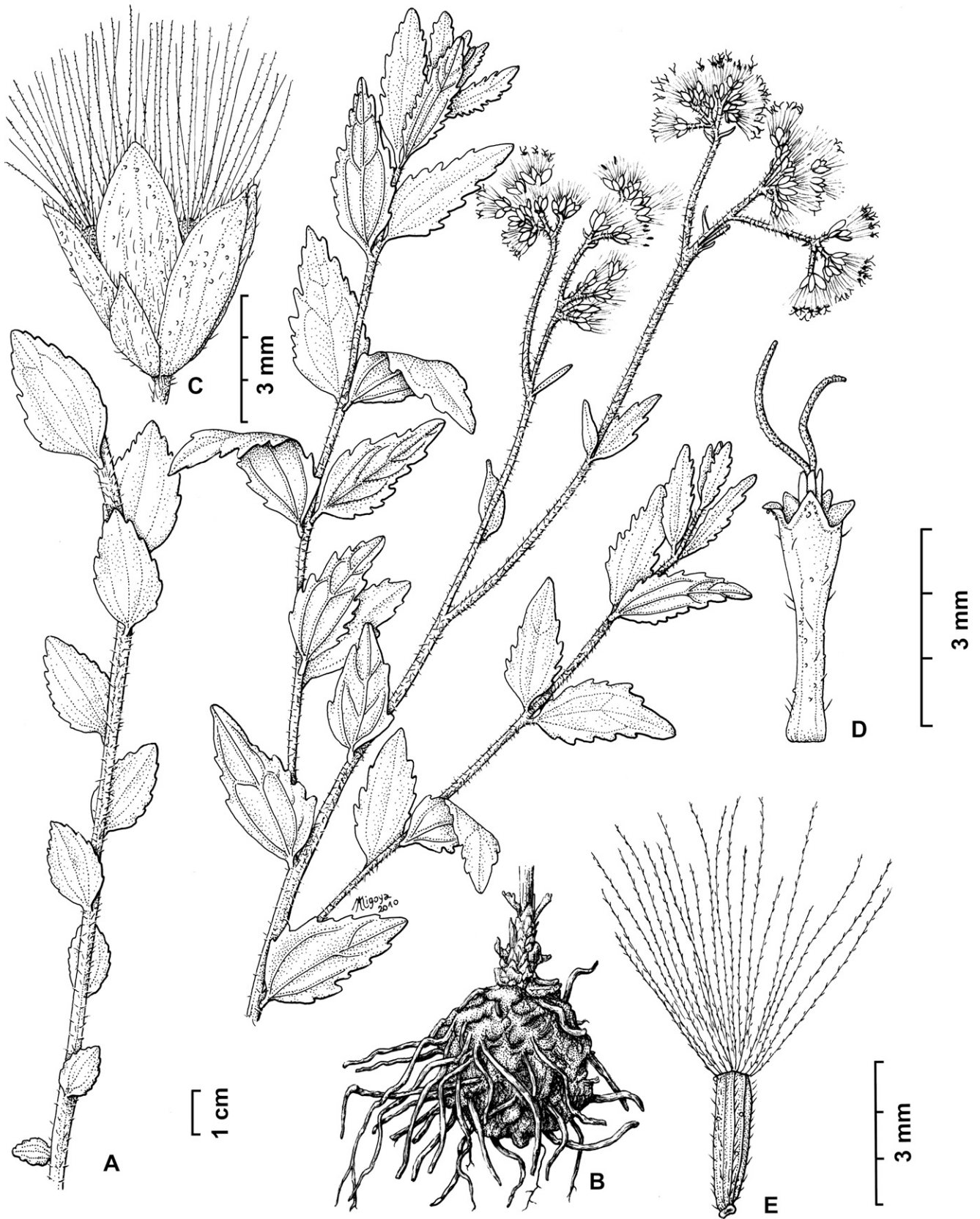


FIG. 8. *Stomatanthes africanus* (Oliv. et Hieron.) R. M. King et H. Rob. A. Apex of flowering branch. B. Xylopodium. C. Capitulum. D. Floret. E. Cypsel and pappus. Drawn from Jacques Félix 3111, P.

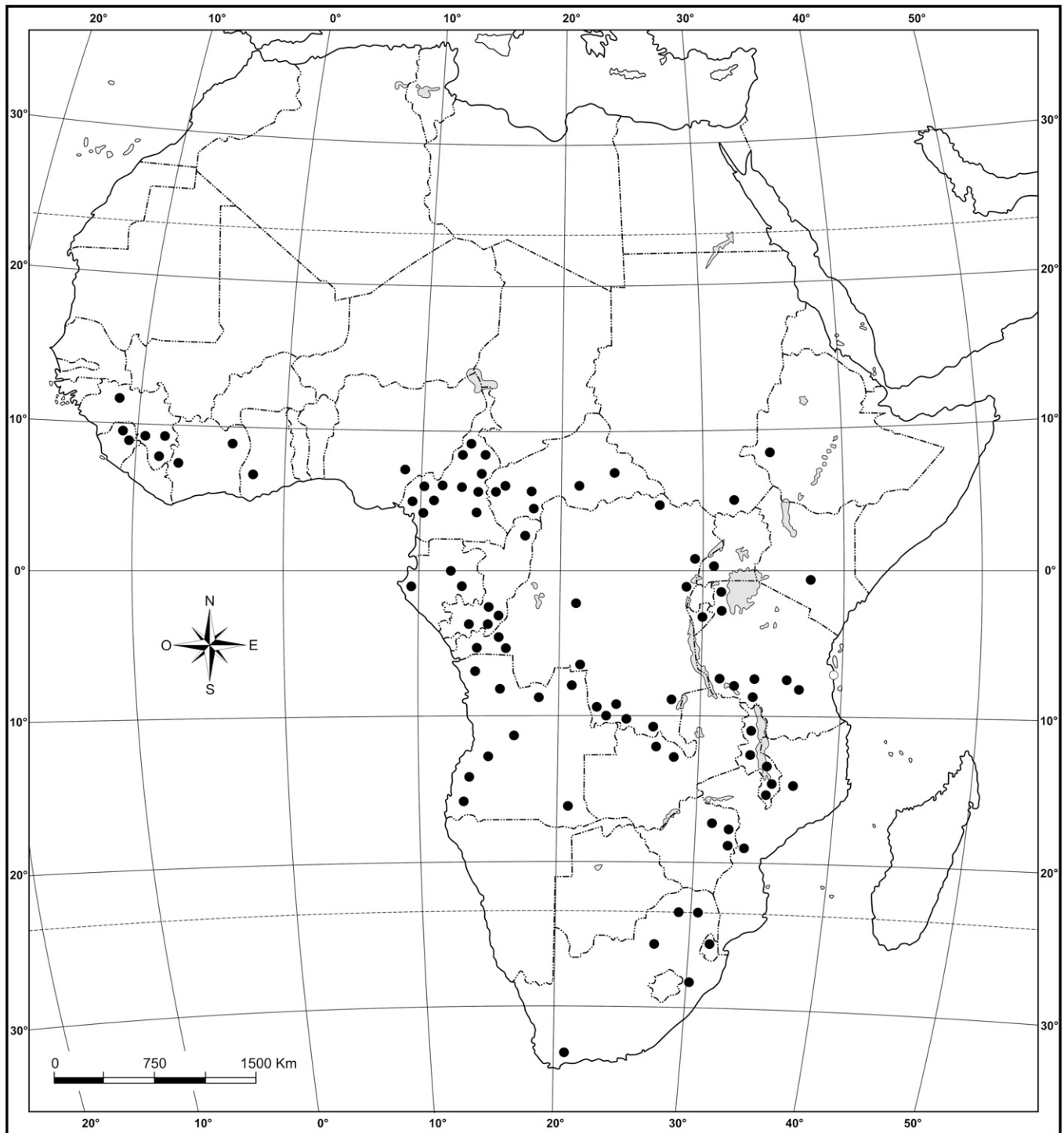


FIG. 9. Geographical distribution of *Stomatanthus africanus*.

2. *STOMATANTHES HELENAE* (Buscal. & Muschl.) Lisowski, *Fragm. Flor. Geobot. Suppl.* 1: 456. 1991. *Eupatorium helenae* Buscal. & Muschl., *Bot. Jahrb. Syst.* 49: 505. 1913.—
 TYPE: ZAMBIA. Copperbelt: Steppe zwischen Broken-Hill und Buana-Mucuba, 18 Jan 1910, *Aosta* 410 (holotype: B, destroyed). ZAMBIA. Copperbelt: Inter Ndola et Mufulira, Dembo, 30 Jan 1960, *Duwigneaud* 5313 [neotype: BRLU!, selected by Grossi (2011b)].

Perennial herbs or sub-shrubs 1.5 m tall, with xylopodium. Stems reddish. Leaves alternate or opposite, laxly arranged

on stems, sessile or short-petiolate, petiole 0.5–1.5 mm long, blade 3.5–8 × 0.5–1.5 cm, membranaceous to sub-coriaceous, oblong-lanceolate or elliptic-lanceolate, rarely linear, base cuneate, apex acute, margins strongly serrate, teeth thickened and rounded at the apex, slightly pubescent when young, becoming glabrous at maturity, with occasional, sparse and few, simple, non-glandular hairs along the margins beneath; venation acrodromous. Heads in lax or dense cymes, grouped into a lax corymbiform inflorescence, peduncles 2–12 mm long, densely pubescent. Involucre campanulate, 4–5 × 3 mm, 2–3-seriate; phyllaries six to eight, scarious

at the margins, glabrous, outer phyllaries 4 mm long, inner phyllaries 6 mm long, oblong, apex acute to acuminate, fimbriate along the margins. Receptacle slightly convex. Florets six to eight, corollas 4–6 mm long, tube 2–4 × 0.6–0.8 mm, with few glandular, biseriate hairs and abundant non-glandular, filiform hairs, lobes 0.6–0.8 × 0.45–0.6 mm. Anthers 1.8–2 mm long, base rounded, anther collar 0.3 × 0.18 mm, anther appendages widely oblong, rounded at the apex, 0.3 × 0.3 mm. Style shaft 6.5–7 mm long, style branches 3–3.5 mm long. Cypselae 3–4 mm long, densely pubescent (few twin-hairs and abundant ramose hairs), carpodium 0.1 × 0.25 mm, with cells sub-quadrate. Pappus 5–6 mm long with ca. 60 bristles, apical cells rounded. Pollen grains (Fig. 7B, C) spheroidal, $P \times E = (18 \times 20) \mu\text{m}$, tricolporate, echinate. Figure 10A–D.

Phenology—Flowers throughout most of the year, except in the winter (June to September).

Distribution and Habitat—This species is restricted to southern Democratic Republic of Congo and northern Zambia (Fig. 11). *Stomatanthes helenae* inhabits open forests and savannas, from 1,000–2,000 m. It grows in the central Zambezi Miombo woodlands ecoregion (White 1983), characterized by the Miombo trees (*Brachystegia* Benth., *Julbernardia* Pellegr., *Isoberrinia* Craib & Stapf, of the Fabaceae family). *Stomatanthes helenae* grows in the wet miombo woodlands of northern Zambia, which receive more than 1,000 mm rainfall per year. Canopy height is usually greater than 15 m, reflecting deeper and moister soils, which create favorable growth conditions for very rich vegetation (Abdallah and Monela 2007).

Conservation—Proposed here as endangered (EN) according to the IUCN (2001) criteria and subcriteria B₂ ab (iii), i.e. the area of occupancy is estimated to be less than 500 km², severely fragmented, and there is a continuing decline in the extent and/or quality of the habitat.

Representative Specimens Examined—DEMOCRATIC REPUBLIC OF CONGO. Bandundu Province: 13 km E of Mukumbi, *Duwigneaud* 4795 (BRLU); between Swambo and Mukumbi, *Duwigneaud* 3345 (BRLU). Haut Katanga Province: Kundelungu Plateau, 3 km S of the source west of Lutshipuka, 4 Nov 1969, *Lisowski et al.* 7716 (BR, POZG), id., near Barrera, *Lisowski et al.* 7401 (POZG), id., road Gombela-Barrera, *Lisowski* 57129 (POZG). Katanga Province: Kolwesi District, Delcomine, 14 Dec 1959, *Duwigneaud* 4572 (BRLU); Fungurume, *Duwigneaud* 3462 (BRLU); 25 km W of Kolwezi, 11 Dec 1959, *Duwigneaud* 4503 (BRLU). Likasi District, Kakontwe, *Duwigneaud et Timperman* 2027 (BRLU); Kamwali, 19 Jan 1960, *Duwigneaud* 5118 (BRLU); Mitonte, *Duwigneaud* 3006 (BRLU); Tantara, 23 Dec 1959, *Duwigneaud* 4758 E1 (BRLU). Lualaba District, Bianco-Lualaba, *Hombé s.n.* (BR). Lubumbashi District, Luapula valley, near Kiniana, *Lisowski* 288 (POZG); Lubumbashi, 1 Oct 1961, *Poelman* 50 (BR), id., *Salésiens* 128 (BR); surroundings of Lubumbashi, near the farm “Sept sources”, *Lisowski* 57128 (POZG); Welgelegen, 1912, *Corbisier* 582 (BR). Tanganika District, Marungu Plateau, env. of Kasiki above ravine Kafufe, 1 Apr 1971, *Lisowski et al.* 11948 (POZG), id., Pepa, Aug 1946, *Thienpont* 85 (BR); between Mindigi and Menda, 13 km N of Menda, *Duwigneaud et Timperman* 2079 (BRLU), id., 5 Dec 1959, *Duwigneaud* 4416E, 4417 (BRLU); Menda, *Duwigneaud* 3317, id., 6 Dec 1959, *Duwigneaud* 4446 (BRLU); Muhila Mount, S of mount Kiseni, *Lisowski* 57130 (POZG). ZAMBIA. Copperbelt Province: Ndola District, Between Ndola and Mufulira, Dembo, 1 Jan 1960, *Duwigneaud* 5313E (BRLU).

3. *STOMATANTHES MEYERI* R. M. King & H. Rob., *Kew Bull.* 30: 463. 1975.—TYPE: ETHIOPIA. Kaffa: 30 km S along Omonaadda road, after turnoff of Jimma road, at Little Ghibbie River, 7°31'N, 37°23'E, 2,200 m, 10 Jan 1962, *Meyer* 7966 (holotype: US!; isotype: K, photograph LP!).

Sub-shrubs 1–3 m tall, without xylopodium. Stems sometimes reddish. Leaves densely arranged on stems, with blade

3–5.5 × 3.5–7 cm, sub-coriaceous, ovate, sub-triangular, margins thickened, serrate or crenate, base cordate, apex acute, pubescent below, with abundant non-glandular, filiform hairs and few glandular, biseriate hairs beneath; venation actinodromous; basal leaves alternate, petiole 5–10 mm long, upper leaves sub-opposite, sub-sessile. Heads in dense cymes, grouped into a dense corymbiform inflorescence, peduncles 2–7 mm long, densely pubescent. Involucre cylindrical, 5–8 × ca. 2 mm, 3–4-seriate; phyllaries 10–15, oblong, apex obtuse, scarious at the margin, slightly pubescent, outer phyllaries 3–4 mm long, inner phyllaries 6–10 mm long. Receptacle slightly convex. Florets ca. five, corollas 5–6 mm long, tube 3–3.5 × 0.9 mm, with glandular biseriate hairs and few non-glandular, filiform hairs, lobes 0.7–0.75 × 0.5 mm. Anthers 2 mm long, base obtuse, anther collar 0.3 × 0.2 mm, anther appendages oblong, emarginate at the apex, 0.3 × 0.2 mm. Style shaft 7–8.5 mm long, style branches 3.5 mm long. Cypselae 1.8–3 mm long, pubescent (glandular biseriate, twin, and ramose hairs), carpodium 0.3 × 0.48 mm, with cells oblong and sub-quadrate. Pappus 6–6.25 mm long with ca. 40 bristles, apical cells acute. Pollen grains (Fig. 7D) spheroidal, $P \times E = (16 \times 14) \mu\text{m}$, tricolporate, echinate. Figure 12A–D.

Phenology—Flowers in the summer (December to March).

Distribution and Habitat—Known only from the type collection.

Endemic to southwestern Ethiopia (Kaffa Province; Fig. 11), in open, grassy areas and road margins, at 2,200 m. The southwestern zone has few remaining natural forests in Ethiopia. The dominant vegetation type is the moist Afromontane forest with mean annual rainfall between 1,800–2,300 mm and annual mean temperature of 15–22°C (Hundera 2007).

Conservation—Proposed here as critically endangered (CR) according to the IUCN (2001) criteria and subcriteria B₁ ab(ii, iv) c(ii,iii) ; D₂, i.e. the extent of occurrence less than 100 km², known only in one locality, and there is inferred a continuing decline in the area of occupancy and in the extent of occurrence.

Excluded Taxa—*Stomatanthes zambiensis* is excluded here because it has verticillate phyllotaxis and lacks ramose hairs. The remaining species also have some morphological features that deviate from those of *Stomatanthes*, including paniculiform inflorescences and the hair types on the cypselae. The exact generic placement of these species must await further work on the entire tribe Eupatorieae.

Stomatanthes corumbensis (B. L. Rob.) H. Rob., *Phytologia* 20: 336. 1970. *Eupatorium corumbense* B. L. Rob., *Contr. Gray Herb.* 104: 15. 1934.—TYPE: BRAZIL. Matto Grosso do Sul: Urucum, Corumbá, Apr 1927, *D. Smith* 94 (holotype: NY!).

Stomatanthes dentatus (Gardner) H. Rob., *Phytologia* 20: 336. 1970. *Eupatorium dentatum* Gardner, *London J. Bot.* 6: 443. 1847.—TYPE: BRAZIL. Goyas: Villa de Arrayas, Mar 1840, *Gardner* 3833 (holotype: BM!; isotypes: B, K, US, photographs GH!).

Stomatanthes dictyophyllus (DC.) H. Rob., *Phytologia* 20: 336. 1970. *Eupatorium dictyophyllum* DC., *Prodr.* 5: 153. 1836.—TYPE: BRAZIL. São Paulo: São Paulo, Nov 1833, *Lund* 853 (holotype: G, photograph LP!).

Stomatanthes hirsutus H. Rob., *Phytologia* 20: 336. 1970.—TYPE: BRAZIL. Federal District: Gama, cerrado by

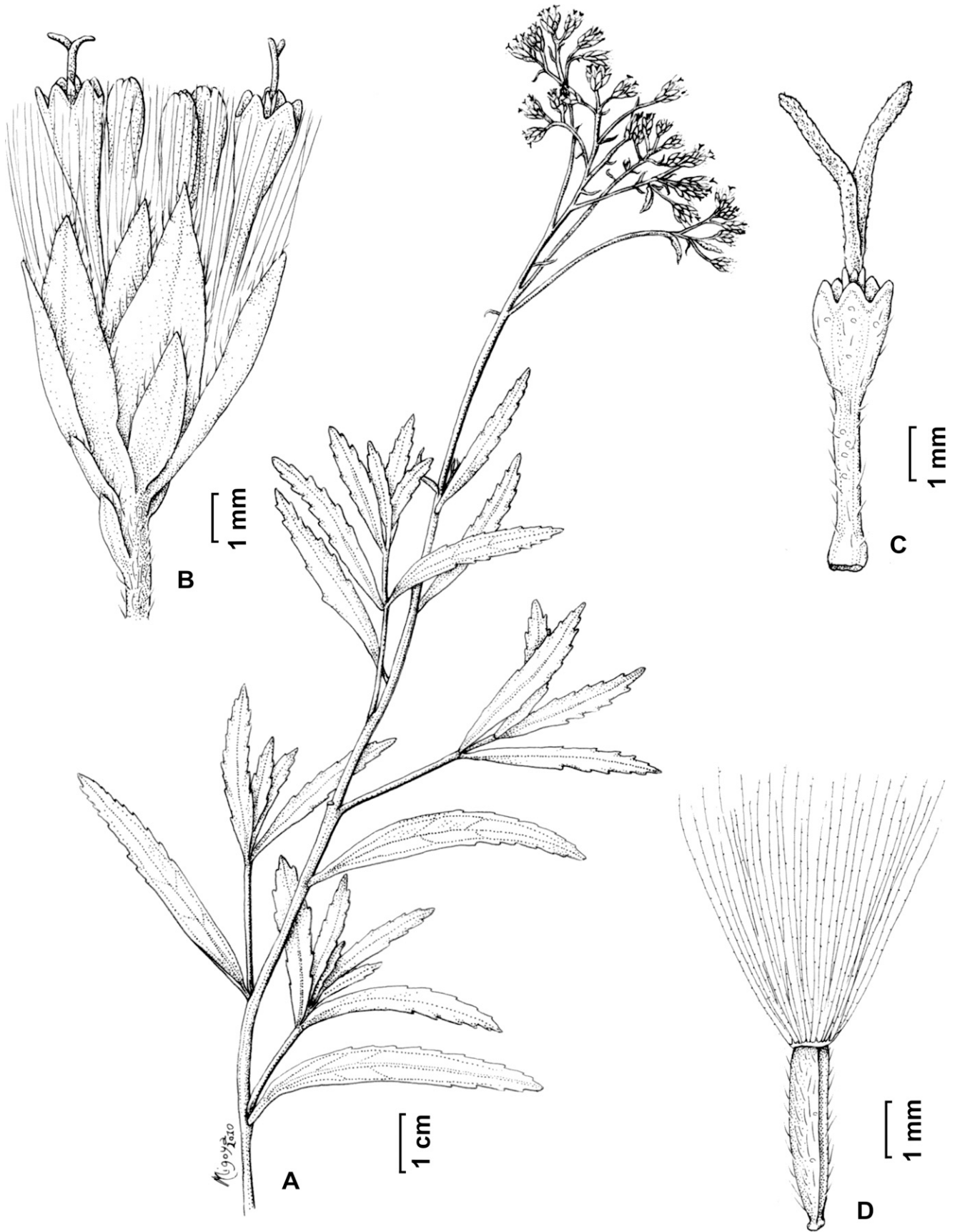


FIG. 10. *Stomatanthes helena* (Buscal. & Muschl.) Lisowski. A. Apex of flowering branch. B. Capitulum. C. Floret. D. Cypsel and pappus. Drawn from DuVigneaud 4446, BRLU.

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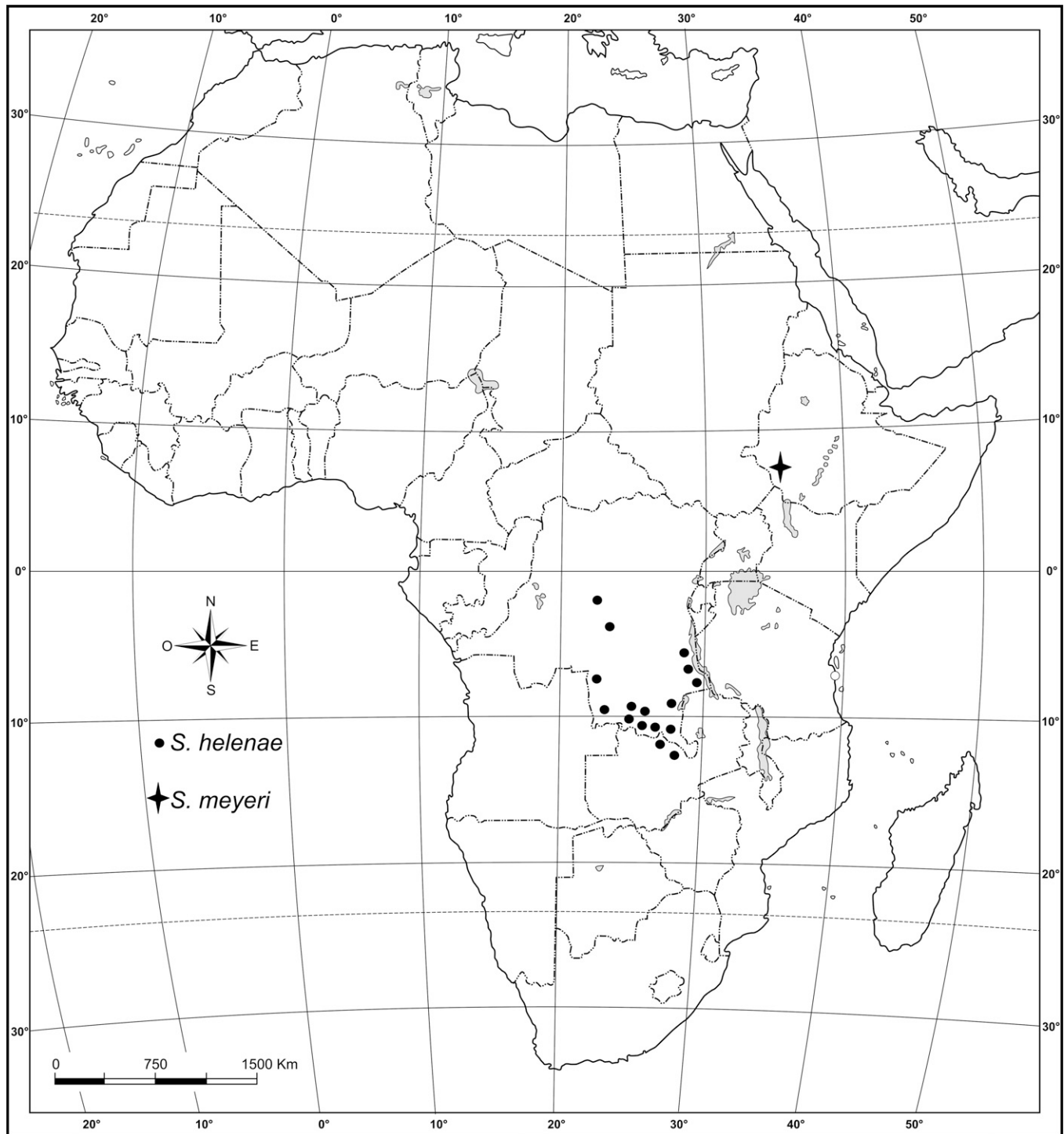


FIG. 11. Geographical distribution of *Stomatanthes helenae* and *Stomatanthes meyeri*.

Rio Gama (field A-43), 7 Mar 1965, L. B. Smith 15063 (holotype: US!; isotype: NY!).

Stomatanthes loefgrenii (B. L. Rob.) H. Rob., *Phytologia* 20: 337. 1970. *Eupatorium loefgrenii* B. L. Rob., *Contr. Gray Herb.* 104: 18. 1934.—TYPE: BRAZIL. São Paulo: São Jose dos Campos, Löfgren 120 (holotype: S!; isotype: GH, photograph LP!).

Stomatanthes oblongifolius (Spreng.) H. Rob., *Phytologia* 20: 337. 1970. *Conyza oblongifolia* Spreng., *Syst. Veg. Fl.*

Peruv. Chil. 3: 512. 1826.—TYPE: BRAZIL. Ad fl. magnum Amer. austr., Rio Grande, *Sello s.n.* (holotype: B, destroyed, photograph F 16311 in LP!; isotypes: C!, K, P!, photograph LP!).

Stomatanthes pernambucensis (B. L. Rob.) H. Rob., *Phytologia* 20: 337. 1970, comb. illeg. *Eupatorium pernambucense* B. L. Rob., nom. illeg., *Contr. Gray Herb.* 90: 31. 1930.

Stomatanthes pinnatipartitus (Sch. Bip. ex Baker) H. Rob., *Phytologia* 20: 337. 1970. *Eupatorium pinnatipartitum* Sch.

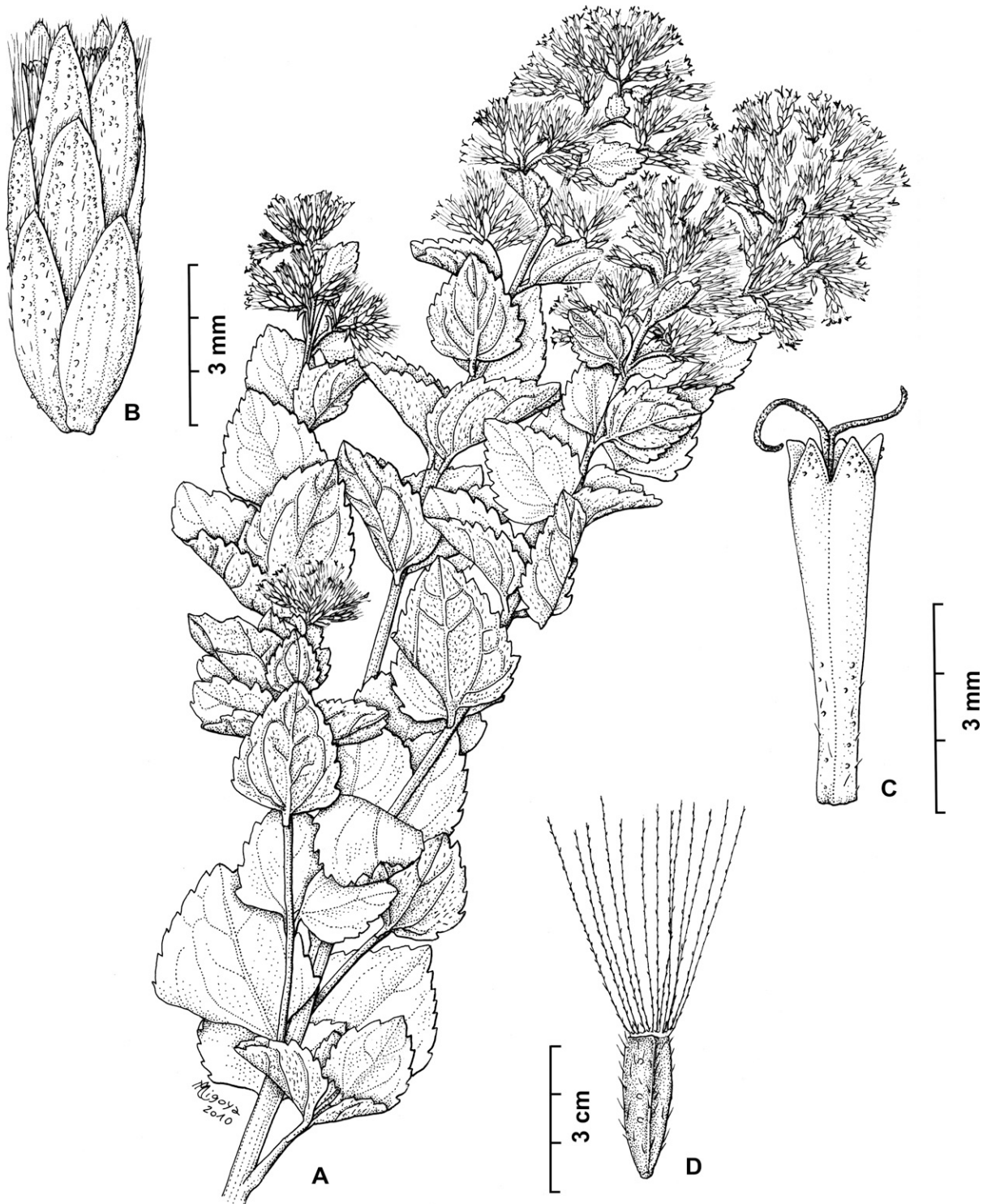


FIG. 12. *Stomatanthes meyeri* R. M. King & H. Rob. A. Apex of flowering branch. B. Capitulum. C. Floret. D. Cypsel and pappus. Drawn from Meyer 7966, US.

Bip. ex Baker, Fl. Brasil. 6 (2): 338. 1876.—TYPE: BRAZIL. Matto Grosso: Cuiabá, in campis regiones Oreadum, *Manso 106* (syntype: BR); Minas Gerais: Caldas, *Regnell 236* (syntypes: C!, P!, S!); between Villa Franca and Cachoeira, *Burchell 5539* (syntype: K); between Tejuco and Veraba legitima, *Burchell 5797* (syntypes: GH!, K).

Stomatanthes polycephalus (Sch. Bip. ex B. L. Rob.) H. Rob., Phytologia 20: 337. 1970. *Eupatorium polycephalum* Sch.

Bip. ex B. L. Rob., Contr. Gray Herb. 77: 30. 1926, based on the original description of *Eupatorium bracteatum* Gardner, Fl. Brasil. 6 (2): 338, 1876.—TYPE: BRAZIL. Minas Gerais: Minas Gerais, Sep-Oct 1834, *Riedel 418* (holotype: P!).

Stomatanthes reticulatus M. A. Grossi & J. N. Nakaj., Ann. Bot. Fennici 46: 443. 2009.—TYPE: BRAZIL. Minas Gerais: São Roque de Minas, Parque Nacional Serra da Canastra,

estrada São Roque de Minas- Sacramento, 5 Oct 1994, Nakajima et al. 513 (holotype: HUFU!; isotypes: LP!, SPFI!, UEC!, US!).

Stomatanthes subcapitatus (Malme) H. Rob., *Phytologia* 20: 337. 1970. *Eupatorium bracteatum* Gardner var. *racemosa* Baker, *Fl. Brasil.* 6 (2): 339. 1876.—TYPE: BRAZIL. Rio Grande do Sul: Rio Pardo, *Riedel 488* (syntype: LE, photograph LP!). BRAZIL. Without locality, *Sello 697* (syntypes: BR, P).

Stomatanthes trigonus (Gardner) H. Rob., *Phytologia* 20: 337. 1970. *Eupatorium trigonum* Gardner, *London J. Bot.* 6: 446. 1847.—TYPE: BRAZIL. Goiás: upland campos, Oct 1839, *Gardner 3270* (holotype: BM; isotypes: NY!, P!).

Stomatanthes warmingii (Baker) H. Rob., *Phytologia* 20: 337. 1970. *Eupatorium warmingii* Baker, *Fl. Brasil.* 6 (2): 339. 1876.—TYPE: BRAZIL. Minas Gerais: ad Lagoa Santa, *Warming 364* (syntype: C!), *Warming 366* (syntype: C!), *Warming s.n.* (syntype: P!).

Stomatanthes zambiensis R. M. King & H. Rob., *Kew Bull.* 30(3): 465. 1975.—TYPE: ZAMBIA. Northern Province: Mporokoso District, Mporokoso-Kawimbe, 7 Jan 1960, *Richards 12084* (holotype: K!, photograph GH!, LP!).

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APPENDIX 1. Characters and character states used in the cladistics analysis of the genus *Stomatanthus*. See Supplemental Table 1 for codification of character states.

1. Leaf disposition: (0) alternate or opposite (1) verticillate. **2. Leaf petiole:** (0) present (1) absent or very short (2) absent or present. **3. Blade shape:** (0) ovate or obovate (1) elliptic or orbicular (2) oblong or linear. **4. Blade partition:** (0) entire (1) lobulate or pinnatifid (2) pinnatifid or pinnatisect. **5. Blade margin:** (0) entire (1) crenate, dentate, or serrate (2) sometimes entire, or dentate, or crenate or serrate. **6. Blade base:** (0) attenuate (1) rounded (2) cuneate (3) cordate. **7. Blade apex:** (0) acute or acuminate (1) obtuse or rounded (2) acute or rounded. **8. Adaxial blade pubescence:** (0) absent (1) tomentose or tomentulose (2) hirsute. **9. Abaxial blade pubescence:** (0) absent (1) tomentose or tomentulose (2) hirsute. **10. Blade glandular hairs:** (0) absent (1) present. **11. Blade venation:** (0) pinnate camptodromous, occasionally actinodromous (1) trinerved

acrodromous. **12. Stem pubescence:** (0) absent (1) present. **13. Inflorescence density:** (0) lax (1) dense. **14. Inflorescence type:** (0) corymbiform cymes (1) paniculiform cymes. **15. Number of florets per capitula:** (0) four or five (1) six to eight (2) more than eight. **16. Peduncle pubescence:** (0) absent (1) present. **17. Involucre shape:** (0) cylindrical (1) hemispherical (2) campanulate. **18. Phyllaries series length:** (0) eximbricate (one- or two-seriate, phyllaries almost equally long) (1) sub-imbricate (2- or more-seriate, phyllaries of different length) (2) imbricate (3-more-seriate, phyllaries very unequally long). **19. Phyllaries pubescence:** (0) absent (1) present. **20. Phyllaries venation:** (0) non-prominent and non-banded (1) prominent with two or three dark bands. **21. Phyllaries apex:** (0) obtuse, rounded, or truncate (1) acute to acuminate (2) caudate. **22. Receptacle shape:** (0) planate (1) slightly convex (2) conspicuously convex. **23. Corolla shape:** (0) funnellform (tube narrow and limb widened) (1) campanulate (tube and limb narrow). **24. Corolla pubescence:** (0) absent (1) present. **25. Corolla hairs type:** (0) exclusively glandular (1) glandular and simple uniseriate (2) glandular and twin hairs. **26. Corolla lobes stomata:** (0) absent (1) present. **27. Corolla color:** (0) exclusively white (1) white, pink, or lilac. **28. Corolla lobes papillae:** (0) absent (1) present on both sides (2) present on one side. **29. Anther appendage shape:** (0) well-developed, ovate-oblong, rounded at the apex (1) reduced, very wide, truncate at the apex. **30. Anther collar:** (0) with thickened cells (1) without thickened cells. **31. Anther base:** (0) rounded or obtuse (1) caudate. **32. Style base:** (0) glabrous (1) pubescent. **33. Stylopodium:** (0) absent (1) present. **34. Style branches apex:** (0) linear to spatulate (1) clavate. **35. Style branches papillae shape:** (0) non-apiculate (1) apiculate. **36. Cypsela ribs number:** (0) four to six (1) more than six. **37. Cypsela carpodium shape:** (0) symmetrical, well developed (1) asymmetrical, well developed (2) reduced to absent. **38. Cypsela carpodium cells shape:** (0) sub-quadrate (1) oblong (2) sub-quadrate and oblong. **39. Cypsela carpodium cell walls:** (0) not or scarcely thickened (1) thickened (2) thickened only in the outer layers. **40. Cypsela hairs type:** (0) twin hairs and glandular (1) exclusively twin hairs (2) exclusively glandular (3) twin hairs, ramose, and few glandular (4) mostly glandular and few twin hairs. **41. Cypsela base:** (0) not stipitate (1) stipitate. **42. Pappus bristles apical cells apex:** (0) exclusively rounded (1) exclusively acute (2) rounded and acute. **43. Pappus bristles type:** (0) scabrid (1) plumose (2) sub-plumose.

APPENDIX 2. Taxa studied and specimens examined with vouchers. The analyzed specimens of *Stomatanthus africanus*, *S. helena*, and *S. meyeri* are cited in the "Representative specimens examined" section of the main text.

Austroeupatorium inulifolium (Kunth) R. M. King & H. Rob. ARGENTINA. Buenos Aires: Isla Martín García, 28 Mar 1997, *Hurrel et al.* 3548 (LP); ruta Poplar, 16 Mar 2000, *Delucchi* 2337 (LP); Punta Lara, 26 Mar 1932, *Cabrera* 2094 (LP); Pereyra Iraola, 7 Apr 1967, *Crisci* 64 (LP); Córdoba: Salsipuedes, *Dawson* 19 (LP); 2 km E de Arroyito, 2 May 1971, *Krapovickas et al.* 18525 (LP); Corrientes: Paso de los Libres, 24 Mar 1948, *Palacios* & *Cuezo* 2219 (LP); Jujuy: Palpalá, 16 Apr 1969, *Cabrera* & *Fabris* 19932 (LP). BRAZIL. Santa Catarina: Anitápolis, Palhoca, 2 Apr 1953, *Klein* 469 (LP); Itajaí, 14 Apr 1962, *Klein* 2892 (LP). *Austroeupatorium laetevirens* (Hook. & Arn.) R. M. King & H. Rob. ARGENTINA. Chaco: Colonia Benítez, 7 Jun 1933, *Schulz* 259 (LP); Fontana, May 1938, *Meyer* 3209 (LP); Corrientes: estancia Santa Teresa, 26 Apr 1952, *Pedersen* 1697 (LP); BRAZIL. Minas Gerais: Viçosa, 12 May 1964, *Vidal* 190 (LP); Paraná: Guaira, Sete Quedas, 22 Apr 1968, *Hatschbach* 19103 (LP); Rio Barigui, Curitiba, 17 Mar 1971, *Hatschbach* 26562 (LP). *Campuloclinium macrocephalum* (Less.) DC. ARGENTINA. Córdoba: La Falda, 16 Mar 1939, *Dawson* 431 (LP); La Granja, Alta Gracia, 2 Dec 1937, *Birabén* 58 (LP); Mina Clavero, 10 Jan 1967, *Fabris* 6760 (LP); Sierra Grande, entre San Antonio y Copina, 1 Feb 1936, *Rodrigo* 459 (LP); Misiones: Ruta 201, Apóstoles, 8 Dec 1986, *Xifreda* & *Maldonado* 386 (LP); Salta: La Caldera, 18 Jan 1968, *Cabrera* 19091 (LP); Pampa Grande, 2 May 1942, *Hunziker* 1808 (LP); PARAGUAY. Caaguazú: 5 km W of Caaguazú, road 2, 8 Feb 1966, *Krapovickas et al.* 12496 (LP); Sierra de Amambay, Mar 1934, *Rojas* 6896 (LP); Yaguarón, Mt. Oratorio, 31 Jan 1966, *Krapovickas et al.* 12267 (LP). *Eupatorium cannabinum* L.: DENMARK. Helsingør, 6 Aug 1953, *Pedersen* 2417 (LP); ENGLAND. Surrey: Chertsey Bridge, 8 Aug 1971, *Cabrera* 22788 (LP); GERMANY. Schonhauser Park, Aug 8 1971, *Kurtz s.n.* (CORD); SWEDEN. Västergötland: Göteborgs archipelago, Vinga, Aug 1911, *Belfrage s.n.* (LP). *Eupatorium dubium* Willd. ex Poir. U. S. A. Connecticut: Salem, 23 Aug 1936, *Weatherby* & *F. Weatherby s.n.* (LP); Rhode Island: Tuckertown Road, South Kingstown, 25 Aug 1929, *Collins s.n.* (LP). *Eupatorium purpureum* L. U. S. A. Pennsylvania: Alleghany Co., Falls River Valley, Glenshaw, 27 Aug 1921, *Jennings s.n.* (LP); Virginia: Cabell Co., 2 miles from Huntington, Four-pole Valley, 22 Aug 1938, *Gilbert s.n.* (LP); Clarendon, 22 Aug 1928, *Blake* 10655 (LP).

Gyptis commersonii Cass. ARGENTINA. Buenos Aires: Coronel Suarez, abra del Pantanos Viejo, 14 Dec 1979, *Pertusi 150* (LP); Saavedra, Abra del Hinojo, 13 Dec 1979, *Pertusi 141* (LP); Tornquist, Sierra de la Ventana, ruta 76, 300 m al W de la intersección de la ruta 76 y la ruta a Ventana, 2 Dec 1979, *Proyecto Ventania 973* (LP); Corrientes: Curuzú Cuatiá, ruta 12, 9 km E de Perugorria, 29–31 Oct 1974, *Tressens et al. 627* (LP); Monte Caseros, 25 Oct 1950, *Nicora 5486* (LP); Entre Ríos: Colón, Parque Nacional El Palmar, 15 Nov 2003, *Cocucci et al. 2950* (CORD); Concordia, Salto Grande, 12 Oct 1968, *Cabrera et Sagastegui 19283* (LP); BRAZIL. Paraná: Laranjeira do Sul, 7 Nov 1963, *Pereira et Hatschbach 7735* (LP); URUGUAY. Colonia: Riachuelo, 15 Nov 1936, *Cabrera 3920* (LP); Durazno: Río Negro, Dec 1934, *Legrand 334* (LP). *Hatschbachella polyclada* (Dusen ex Malme) R. M. King & H. Rob. BRAZIL. Paraná: Campo Grande, 1 Feb 1904, *Dusén 3938* (M); near Jaguariava, 25 Mar 1916, *Dusén 18010* (C); Pirai do Sul, serra das Fumas, 30 Mar 1957, *Hatschbach 3659* (LP); Rio dos Papagaios, Palmeira, 24 Mar 1988, *Silva et Hatschbach 506* (C); Rio Grande do Sul: Porto Alegre, Ponta Grossa, Fazenda Escola, ICN 127570 (ICN). *Hatschbachella tweediana* (Hook. & Arn.) R. M. King & H. Rob. ARGENTINA. Corrientes: estancia Fortín del Iberá, 19 Apr 1969, *Pedersen 9101* (LP); ruta 12, 32 km W de Ituzaingó, 14 Apr 1974, *Krapovickas et al. 25387* (LP); 14 km E de San Luis del Palmar, camino a Herlitzka, 29 Jan 1972, *Mroginski et al. 527* (LP); Entre Ríos: Diamante, 15 Dec 1960, *Burkart 22321* (LP); Santa Elena, 14 Mar 1962, *Burkart et al. 23537* (LP); Misiones: Loreto, 29 Jan 1946, *Montes 1837* (LP); Posadas, 12 Apr 1930, *Rodriguez 174* (LP); BRAZIL. Paraná: São Judas Tadeu, Guarapuava, 24 Feb 1988, *Hatschbach et Ribas 51898* (C); PARAGUAY. San Pedro: Colonia Primavera, 21 Apr 1957, *Woolston 815* (LP); URUGUAY. Colonia: Riachuelo, 10 Feb 1934, *Cabrera 2830* (LP); Maldonado: cerro Pan de Azúcar, 18 May 1937, *Rosengurt 1842* (LP). *Stomatanthes corumbensis* (B. L. Rob.) H. Rob. BRAZIL. Matto Grosso do Sul: Urucum, Corumbá, Apr 1927, *Smith 94* (NY). *Stomatanthes dentatus* (Gardner) H. Rob. BRAZIL. Federal District: Brasília, Aug 1961, *Macedo 73* (RB); Goiás: Ponte Alba, 20 Aug 1994, *Glaziou. 21640* (P); Matto Grosso: Alto Araguaia, Rio Araguaia, 21 Jul 1974, *Hatschbach 34671* (US); Chapada dos Guimarães, Rio Mutuca, 30 km al NE de Cuiabá, 12 Jul 1984, *Mori et al. 16697* (NY, US); Município de Cuiabá, Cuiabá-Jaciara, 71 km al E de Cuiabá, 9 km al O de São Vicente, 15 Jul 1984, *Mori et al. 16832* (NY); Minas Gerais: Belo Horizonte, 8 Aug 1942, *Evangelista de Oliveira 991* (RB); Lagoa Santa, *Warming 361, 362* (C, P); Pará: Santa Ana, Jul-Aug 1834, *Riedel 419* (P), *Riedel 1301* (P); Rio de Janeiro: São Gonçalo, 25 Jul 1984, *Mori et al. 16979* (NY); São Paulo: São José dos Campos, 28 Aug 1962, *Mimura 520* (US). *Stomatanthes dyctiophyllus* (DC.) H. Rob. BRAZIL. Federal District: área del Cristo Redentor-DF, 16 Aug 1988, *Azevedo 93* (US); Cuenca del Río São Bartolomeu, 21 Aug 1980, *Herlinger et al. 5341* (NY); D.F., 5 Sep 2000, *Santos et al. 498* (US); Parque Ecológico das Sucupiras, 25 Sep 2004, *Correia et Passos 10* (HUFU); Goiás: Anápolis, 21 Jul 1952, *Macedo 3568* (RB); Caldas Novas, Rio Quente, 8 Oct 1986, *Kummrow 2827* (C); Cristalina, 9 Oct 1963, *Cobra et Oliveira 254* (RB); Município Alto Paraíso, Chapada dos Veadeiros, 28 Sep 1975, *Hatschbach et Kummrow 37237* (C, LP); São João de Aliança, 18 Aug 1974, *Macedo 5355* (US); Matto Grosso do Sul: Município Caracol, Rodovia Bela Vista a Caracol, próximo ao Rio Caracol, 12 Mar 2004, *Hatschbach et al. 77030* (BHCB); Rio Brillante, 16 Feb 1970, *Hatschbach 23684* (RB); Minas Gerais: Município Santa Luzia, Lagoa Santa, *Warming et Lund s.n.* (C); Município Várzea da Palma, Rodovia Pirapora-Corinto, 10 km al O de Várzea da Palma, 20 Oct 1999, *Hatschbach et al. 69343* (HUFU); Ressaquinha, 12 Sep 1964, *Pereira 9155* (RB); Serra das Sete Voltas, Parque Nacional da Serra da Canastra, São Roque de Minas, 25 Sep 1996, *Romero et Nakajima 3732* (LP); São Paulo: Franca, 14 Nov 1934, *Lund s.n.* (C); Moji-Guaçu, Reserva Florestal Fazenda Campininha, cercano a Pádua Sales, 20 Sep 1956, *Kuhlmann 3929* (RB); Tocantins: Taguatinga, 9 Sep 1965, *Irwin et al. 8118* (NY, US). *Stomatanthes hirsutus* H. Rob. BRAZIL. Brasília: Gama, 20 Mar 1964, *Pereira 9038* (LP, M); Goiás: Município Cristalina, Cristalina, 10 Dec 1967, *Duarte 10130* (M, US); ruta para Cachoeira do Arrojado, 24 Jan 1988, *Hatschbach et Cordeiro 51814* (BR, C, NY, S); Serra dos Cristais, 5 Apr 1973, *Anderson 8242* (NY, US); Minas Gerais: Município de Delfinópolis, ruta hacia "Casinha Branca Condomínio de Pedras", 12 Mar 2003, *Pacheco et al. 520* (HUFU); São Roque de Minas, Parque Nacional da Serra da Canastra, 23 Feb 1997, *Romero et al. 3963* (HUFU). *Stomatanthes loefgrenii* (B. L. Rob.) H. Rob. BRAZIL. São Paulo: São José dos Campos, *Löfgren 120* (S). *Stomatanthes oblongifolius* (Spreng.) H. Rob. ARGENTINA. Entre Ríos: entre Concepción del Uruguay y Colón, 15 Dec 1957, *Burkart 20540* (SI);

Misiones: Apóstoles, 13 Oct 1977, *Cabrera et al. 28714* (SI); BRAZIL. Minas Gerais: Ipanema, 23 Apr 1881, *Glaziou 12876* (P); Paraná: Município Arapotí, Fazando do Lobo, 22 Mar 1968, *Hatschbach 18879* (C, LP); Parque Nacional de Itapuã, Morro do Araçá, *Pinheiro 485* (ICN); Rio das Perdizes, 21 Mar 1968, *Hatschbach 18825* (C); Rio Grande do Sul: Cruz Alta, 4 Mar 1923, *Malme 770* (S); Giruá, Granja Sodol., Mar 1964, *Hagelund 2043* (ICN); Morro Agudo, Porto Alegre, 25 May 1976, *Hagelund 10351* (C); Pelotas, 17 Mar 1984, *Pedersen 13832* (C, MO, NY); PARAGUAY. Alto Paraguay: Sierra de Maracayú, 1898–1899, *Hassler 5778* (BM, K); Caaguazú: Caaguazú, 1905, *Hassler 9161* (C, US); Curupicai-ti, Estancia Primera, Apr 1927, *Rojas 5032* (M, LP); URUGUAY. Maldonado: Cerro de las Ánimas, *Chebaroff 3835* (LP, SI); Sierra de Los Caracoles, Estancia Campo Chico, 23 Apr 2006, *Bonifacio 2247* (SI); Rivera: Tranqueiras, 25 Mar 1918, *Herter 2216* (S); Tacuarembó: Bañado de Rocha, Mar 1944, *Chebaroff 10917* (LP). *Stomatanthes pernambucensis* (B. L. Rob.) H. Rob. BRAZIL. Pernambuco: Rio Meta, Sep 1839, *Gardner 2900* (BM).

Stomatanthes pinnatipartitus (Sch.Bip. ex Baker) H. Rob. BRAZIL. Minas Gerais: Catiara, 27 Aug 1950, *Duarte 2971* (NY, RB); Poços de Caldas, 16 Jul 1981, *Yamamoto et al. 1087* (HUFU); próximo a Guarita de Sacramento, Sacramento, 29 Jun 1994, *Romero et Nakajima 1087* (HUFU); Saco, 27 Aug 1980, *Leitas Filho et al. 19* (HUFU); Serra do Pico, 12 Apr 1879, *Glaziou 11035a* (BHCB, P); Uberaba, 19 Jun 2003, *Da Silva s.n.* (HUFU); Uberlandia, 22 Jul 1956, *Macedo 4568* (US). *Stomatanthes polycephalus* (Sch.Bip. ex B. L. Rob.) H. Rob. BRAZIL. Bahia: Bom Jesus da Lapa, 25 Sep 1963, *Santos et Castellanos 24336* (LP, M, RB); Minas Gerais: Jardim Botânico Belo Horizonte, 25 Aug 1932, *Barreto 362* (RB); Joaquim Felício, Serra do Cabral, 9 Mar 1996, *Lewinsohn et al. 96622* (US); Município Grão Mogol, Serra do Calixto, 11 km do Francisco Sá, 14 Oct 1988, *Harley et al. 25023* (BHCB, M); Santana do Riacho, 6 Nov 1981, *Pinto 365/81* (RB); Sete Lagoas, 5 Oct 1967, *Silva 133* (RB). *Stomatanthes reticulatus* M. A. Grossi & J. N. Nakaj. BRAZIL. Minas Gerais: Base do morro após o Curral de Pedras, 8 Dec 1994, *Romero et Nakajima 1495* (HUFU, LP); Estrada São Roque-Sacramento, após a Torre de observação, 18 Oct 1997, *Romero et al. 4781* (HUFU); Estrada para a Serra da Chapada, 14 Oct 1997, *Romero et al. 4592* (HUFU); São Roque de Minas, Parque Nacional da Serra da Canastra, 3 km da sede administrativa, 20 Nov 1996, *Romero et al. 3787* (HUFU); Vale do Rio São Francisco, 7 Dec 1994, *Nakajima et Romero 686* (HUFU). *Stomatanthes subcapitatus* (Malme) H. Rob. BRAZIL. Paraná: Jaguariava, 22 Oct 1910, *Dusén 10734* (NY, S, US); Turma, 20 Oct 1914, *Dusén 15682* (GH, S); Villa Velha, 27 Nov 1908, *Dusén 7213* (S); PARAGUAY. Amambay: Cabecera Aquidabán, Sierra de Amambay, Sep 1933, *Rojas 6347* (LP); Cerro Torin, Sierra de Amambay, Sep 1921, *Rojas 3948* (LP). *Stomatanthes trigonus* (Gardner) H. Rob. BOLÍVIA. Beni: estancia Villa Camba, 39 km al N del Río Yata, lado E de la ruta a Riberalta, 4 km hacia el Río Benicito, 13 Oct 1995, *Hanagarth et Rosales 71* (US); Santa Cruz: Parque Nacional Noel Kempff Mercado, cerca de Los Fierros, 1 Jul 1993, *Saldias et al. 2854* (US); BRAZIL. Bahia: Município de Correntina, Velha da Galinha, 12 km abajo de las cascadas de Furnaça, Rio Corrente, 27 Aug 1995, *Mendoza et al. 2407* (US); Brasília: Agua Limpia, 30 km S of Universidad de Brasília, 9 Jul 1976, *Davis et Shepherd 60027* (NY); Chapada da Contagem, ca. 20 km NE of Brasília, 27 Oct 1965, *Irwin et al. 9584* (NY, US); Reserva Ecológica de IBGE, cercano a Río Taquara 20 Sep 1999, *Fonseca et Alvarenga 2121* (US); Goiás: Município de Niquelândia, Granja Engenho, ca. a 11 km de Niquelândia/Dois Irmãos, 13 Aug 1997, *Fonseca et al. 1523* (US); Mato Grosso: ca. 75 km N de Xavantina, Oct 1964, *Irwin et Soderstrom 6693* (NY); Chapada dos Guimarães, 19 Oct 1973, *Prance et al. 19198* (NY); Matto Grosso do Sul: Base Camp, 26 Oct 1968, *Harley et al. 10858* (NY); Município Nova Andradina, Casa Verde, 10 Nov 1973, *Hatschbach et Kocziacki 33004* (C, M, NY, P, US); Santa Ana da Chapada, 8 Oct 1902, *Malme 2404 a* (S); Minas Gerais: Aguas Santas, 23 Aug 1887, *Glaziou 17077* (P); Município Ituiutaba, 14 Nov 1948, *Macedo 1382* (BM, NY, S); ruta BR-050, 15–20 km W de Uberaba, 13 Oct 1990, *Hatschbach et Silva 54498* (C); São Paulo: Moji-Guaçu, Reserva Forestal (Campininha), Pádua Sales, 30 Oct 1957, *Handro 734* (NY). *Stomatanthes warmingii* (Baker) H. Rob. BRAZIL. Minas Gerais: Município Santa Luzia, Lagoa Santa, 5 Aug 1933, *Barreto 8344* (BHCB); Serra de Catiara, 23 Aug 1950, *Duarte 2928* (RB). *Stomatanthes zambiensis* R.M. King & H. Rob. ZAMBIA. Northern Province: Abercorn District, Kambole, 1 Jan 1964, *Richards 18908* (K, US); Mporokoso District, Mporokoso-Kawimbe, 7 Jan 1960, *Richards 12084* (K, photograph GH, LP).