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A Taxonomic Revision of *Schlechteranthus* subgenus *Microphyllus* (Ruschieae; Aizoaceae)

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Abstract—*Schlechteranthus* subgenus *Microphyllus* is a recently erected subgenus, which is revised here for the first time. The subgenus is comprised of nine succulent species, including a new species ***S. parvus***, and is endemic to the arid part of the Greater Cape Floristic Region. *Schlechteranthus* subgenus *Microphyllus* can be distinguished from subgenus *Schlechteranthus* by the smaller leaves (3.5–5.0 × 4–6 mm vs. 5–30 × 3.5–9.0 mm) and smaller capsules (2–6 × 2–6 mm vs. 6–11 × 4–9 mm), with seven to nine locules and small closing bodies that block one third of the locule (vs. 10 to 12 locules and closing bodies that block three quarters of the locule). Differences in leaf shape, degree of fusion, and arrangement, as well as inflorescence and spine structure were identified as important characters in distinguishing species in the subgenus. *Schlechteranthus parvus*, *S. pungens*, *S. spinescens,* and *S. stylosus* all share the presence of spines, caducous bracteoles, and cymose inflorescences. Maps illustrating species richness hotspots within a quarter degree square were produced for the genus and subgenera respectively. A key to the subgenera in *Schlechteranthus* and a comprehensive taxonomic treatment of subgenus *Microphyllus* is presented, including a key to the species, descriptions, figures illustrating diagnostic characters, and distribution maps.

Keywords—Distribution, Greater Cape Floristic Region, inflorescence structure, new species, papillate leaves, spines, succulent shrubs.

Schlechteranthus Schwantes is a genus of succulent shrubs included in the diverse and speciose tribe Ruschieae (Aizoaceae), with species endemic to the arid parts of the Greater Cape Floristic Region (Jürgens 1991; Hartmann 1996, 1998, 2001; Manning and Goldblatt 2012; Snijman 2013; Klak and Bruyns 2016). The genus is placed in the *Conophytum*-clade (Klak et al. 2013; Powell et al. 2016) and is distinguished from other genera in the clade by a combination of characters: a shrubby habit, leaves with a papillate epidermis and a prominent mucro, white to magenta cone-type flowers with stamens arranged in a cone, and 7- to 12-locular capsules with pointed expanding keels. The generic circumscription of *Schlechteranthus* was recently assessed, resulting in the expansion of the genus and erection of subgenus *Microphyllus* R. F. Powell (Klak and Bruyns 2016; Powell et al. 2016).

The phylogenetic analysis of Klak et al. (2013) placed *Schlechteranthus* sister to the previously recognised genus *Polymita* N. E. Br. An assessment of generic circumscription of these genera led to the expansion of *Schlechteranthus* to include *Polymita,* with a taxonomic revision for these species presented in Klak and Bruyns (2016). *Schlechteranthus* and *Polymita* were placed sister to *Octopoma subglobosum* (L. Bolus) L. Bolus in the tribal phylogeny produced by Klak et al. (2013), but as only two species of *Octopoma* N. E. Br. were sampled, generic relationships between these species were unclear.

Powell et al. (2016) expanded the phylogenetic sampling of *Octopoma* to include seven of the eight species, as well as the genus *Arenifera* A.G.J.Herre, which had not been sampled in any previous phylogenetic analyses. The results indicated that both *Octopoma* and *Arenifera* were polyphyletic, with five *Octopoma* and four *Arenifera* species placed sister to *Schlechteranthus* in the *Conophytum*-clade, while the type species of the genera were placed in the xeromorphic clade (Klak et al. 2013; Powell et al. 2016). The assessment of generic circumscriptions based on phylogenetic, morphological, and anatomical data of these species, specifically in relation to their sister genus *Schlechteranthus*, revealed two groups, which were recognised as subgenera (Powell et al. 2016). Subgenus *Schlechteranthus* includes species of *Schlechteranthus* and the previously recognised genus *Polymita,* while subgenus *Microphyllus* includes the species previously included in *Arenifera* and *Octopoma*. The subgenera are distinguished from one another by differences in epidermal cell shape, cuticle thickness, locule number, and variation in shrub, leaf, and capsule size (Powell et al. 2016).

The species of subgenus *Microphyllus* were previously included in *Eberlanzia* Schwantes, *Mesembryanthemum* L. and *Ruschia* Schwantes (Berger 1922; Bolus 1926, 1928, 1930, 1932; Brown 1930), but were subsequently moved into *Arenifera* based on the shared inflorescence structure, capsule shape, and presence of spines, and into *Octopoma* based on the shared 8-locular capsules (Hartmann 1996, 1998). The need for a taxonomic revision of these species was recognised even prior to the erection of the subgenus, with *Arenifera* and *Octopoma* identified as priority genera for taxonomic revision by Von Staden et al. (2013).

This study presents the first taxonomic revision for *Schlechteranthus* subgenus *Microphyllus* and includes the descriptions of nine species, including one new species, as well as a key to the species, notes on their ecology, and comprehensive distribution maps.

Materials and Methods

Examination of Morphological Characters—The complete collections of *Schlechteranthus* (160 specimens) housed at BOL, NBG (including SAM), and PRE were examined. In addition, all of the species of subgenus *Microphyllus* were studied in situ. During field visits, material was collected

for herbarium and living collections of each species. These specimens are housed as voucher specimens at NBG and form part of the living collection at Kirstenbosch Botanical Gardens (SANBI). The herbarium specimens and living collections were used for examination of leaf, floral, and capsule characters to compare and identify diagnostic morphological characters across the subgenus.

Phylogenetic Analyses—A molecular and morphological cladistic analysis for subgenus *Microphyllus* was conducted using the molecular phylogenetic data produced in Powell et al. (2016) and eight coded morphological characters for the morphological analyses. Both the molecular and morphological data was analysed for the species in *Schlechteranthus,* as well as for the outgroup taxon *Cheiridopsis denticulata* N. E. Br. *Cheiridopsis* was selected as the outgroup taxon as it was recovered sister to *Schlechteranthus* in Powell et al. (2016).

The molecular and morphological dataset was analysed separately using Bayesian inference in MrBayes v. 3.2.3 (Ronquist and Huelsenbeck 2003). The molecular data was analysed following Powell et al. (2016), with the combined plastid dataset partitioned into 10 partitions, with all parameters unlinked, the GTR + G + I model implemented (Huelsenbeck and Rannala 2004), and two simultaneous runs completed for 10^7 generations. For the morphological dataset, the standard model (Ronquist et al. 2011) was implemented and two simultaneous runs were completed for 1.5×10^6 generations. In both analyses, the split frequencies stabilised below 0.01 and suboptimal trees were discarded as the burn-in phase. A 50% majority-rule consensus tree was constructed from the remaining trees in the separate analyses and the posterior probability (PP) values are reported on the trees, respectively.

The maximum parsimony algorithm was implemented in PAUP* v. 4.0b4 (Swofford 2000) for both the molecular and morphological data separately, with characters equally weighted and unordered. A heuristic search with 1,000 random sequence additions, tree bisection-reconnection (TBR) branch-swapping and 10 trees held per replicate was performed. Internal support was assessed with 1,000 bootstrap (BS) replicates under the same search parameters. The strict consensus trees with bootstrap support values for the molecular and morphological data are presented, respectively, in Supplementary Figs. S1 and S2, available at the Dryad Digital Repository (Powell et al. 2017).

The morphological characters were coded manually with a polarised outgroup and were reconstructed onto the Bayesian inference consensus trees of both the molecular and morphological analysis using the parsimony trace character history function in Mesquite v. 3.04 (Maddison and Maddison 2015).

Distribution and Species Richness Maps—Data on the distribution of the species are presented as maps. These data were collected from the examined herbarium specimens as well as from field collections. The distribution for each species was recorded using the quarter degree reference system (Edwards and Leistner 1971; also outlined in Leistner and Morris 1976). The basic unit in this system is the one-degree square of latitude and longitude (a quarter degree square), which is designated by a degree reference number (i.e. degrees of latitude and longitude of the northwest corner) and the district name of that grid. This grid reference system was used to produce maps for each of the species in subgenus *Microphyllus.*

Species richness maps, indicating the number of species per quarter degree square (QDS) were produced for the genus as well as the subgenera. Distribution data for the species of subgenus *Schlechteranthus* was obtained from Klak and Bruyns (2016), while data for subgenus *Microphyllus* was collected from herbarium and field records. The distribution of the genus and subgenera were mapped separately in ArcMap (ESRI 2011). A QDS grid was overlaid onto the distribution data and the spatial join tool (ESRI 2011) was used to join the two datasets. The number of species per QDS was calculated for the genus and subgenera from the count data in the spatial join (ESRI 2011), and the data were presented on the maps accordingly.

Results

Taxonomy—The taxonomic revision of subgenus *Microphyllus* presented here recognised nine species, including one new species, *S. parvus.* The species were distinguished using a combination of characters, including differences in leaf shape (Table 1), degree of leaf fusion (Fig. 1), and leaf arrangement, as well as inflorescence and spine structure (Figs. 2, 3).

Phylogeny—Species of subgenus *Microphyllus* were recovered as monophyletic in both analyses (PP = 1, BS = 90 in the molecular tree; PP = 1, BS = 86 in the morphological tree). However, the topologies of the two phylogenies were incongruent, with very different species groupings (Fig. 4). Locule number and closing body size were recovered as a synapomorphic characters for the species of subgenus *Microphyllus* in both the morphological and molecular phylogenetic analyses (Fig. 4). The shared spiny inflorescence structure and caducous bracteoles of *S. parvus, S. pungens, S. spinescens,* and *S. stylosus* grouped these species together in the morphological phylogeny and these characters were recovered as synapormorphies for this clade (Fig. 4B).

The consistency index (CI) and retention index (RI) in the morphological phylogeny is greater than in the molecular phylogeny (CI = 0.94, BS = 0.76 in the molecular tree; CI = 1, RI = 1 in the morphological tree), while the tree length of the molecular phylogeny (tree length = 156) is much greater than the molecular phylogeny (tree length = 8) (Fig. 4).

Geographical Distribution—*Schlechteranthus* is distributed from Khubus to Clanwilliam (and an outlying population near Uniondale (*Fourcade 4370* (BOL)) with hotspots around Bitterfontein, Khubus, Kleinsee, Springbok, and Steinkopf (Fig. 5A). The distribution of subgenus *Schlechteranthus* extends from north of Khubus to just north of Bitterfontein, with only two hotspots north of Kleinsee (Fig. 5B). Subgenus *Microphyllus* has a much wider distribution range, from the border of Namibia southwards to Clanwilliam, with an eastern record at Uniondale (Fig. 5C). The highest species richness of subgenus *Microphyllus* is found around Bitterfontein (Fig. 5C), in contrast to subgenus *Schlechteranthus,* which does not occur as far south. There are minor hotspots for subgenus *Microphyllus* around Bitterfontein, Steinkopf, and between Steinkopf and Khubus (Fig. 5C).

Discussion

Habit—*Schlechteranthus* subgenus *Microphyllus* consists of woody shrubs or shrublets, some of which are markedly

Table 1. Table summarising important distinguishing characters for species of *Schlechteranthus* subgenus *Microphyllus.*

	Leaf shape (in outline)	Degree of leaf fusion	Bracteole persistent	Cymose inflorescence structure	Spinescent	Filamentous staminodes forming a complete series	Capsule top flattened at apex	Capsule base cup-shaped	Valve wings present
S. abruptus	lanceolate	¼	+	-	-	-	-	-	-
S. connatus	lanceolate	¼	+	-	-	-/+	-	+	-
S. inclusus	ovoid	¾	+	-	-	-	-	-	-
S. parvus	globose to subglobose	¾	-	+	+	+	-	-	-
S. pungens	oblong, sometimes ovoid	¼ – ⅓	-	+	+	-/+	-	-	+
S. spinescens	lanceolate	⅙ – ⅕	-	+	+	+	-	-	+
S. stylosus	ovoid	⅓ – ½	-	+	+	-/absent	-	-	-
S. subglobosus	globose	⅓	+	-	-	-	+	-	+
S. tetrasepalus	ovoid	⅔	+	-	-	absent	-	-	-

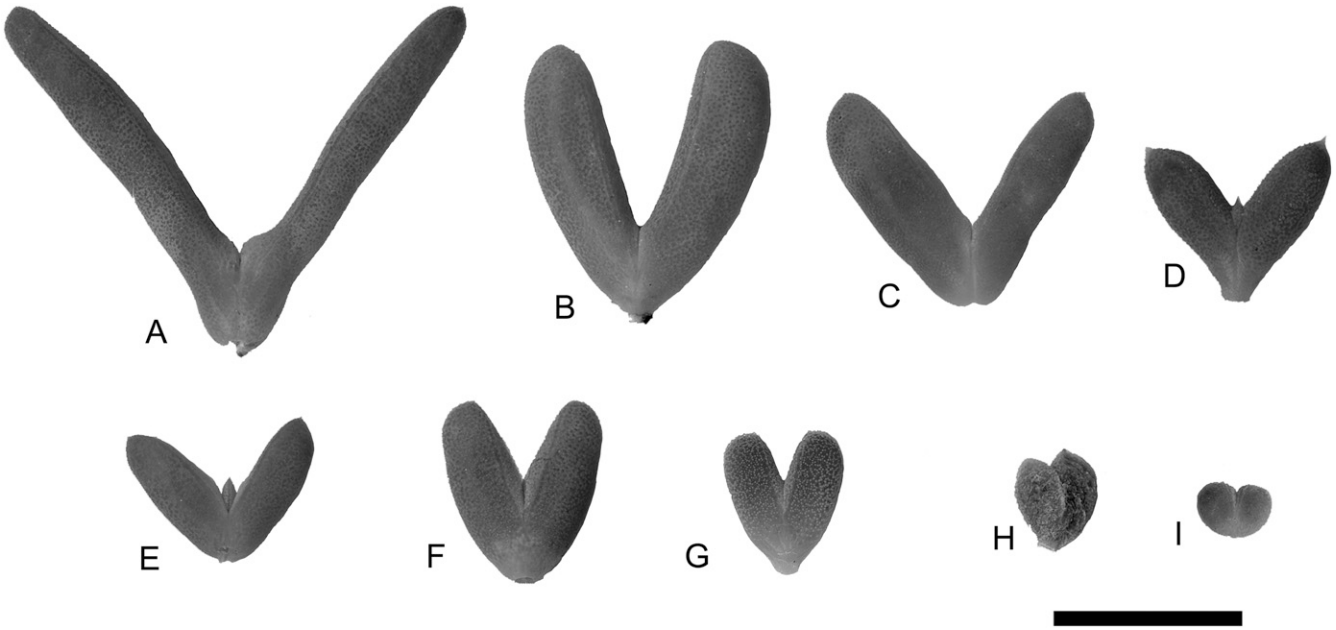

FIG. 1. Leaves of subgenus *Microphyllus,* illustrating the variation in leaf size and degree of fusion of the leaf pairs. A. *Schlechteranthus connatus, Powell 10* (NBG). B. *S. spinescens, Klak 2424* (BOL). C. *S. abruptus, Powell 5* (NBG). D. *S. subglobosus, Powell 33* (NBG). E. *S. pungens, Powell 28* (NBG). F. *S. inclusus, Powell 35* (NBG). G. *S. tetrasepalus, Klak 2411* (BOL). H. *S. stylosus, Powell 75* (NBG). I. *S. parvus, Powell 41*(NBG). Scale = 1 cm.

compact, including *S. connatus* (L. Bolus) R. F. Powell, *S. inclusus* (L. Bolus) R. F. Powell (Fig. 2H), *S. parvus,* and *S. tetrasepalus* (L. Bolus) R. F. Powell, only reaching 150 mm in height, while the larger shrubs, *S. pungens* (H. E. K. Hartmann) R. F. Powell and *S. stylosus* (L. Bolus) R. F. Powell, grow up to 400 mm tall. The species share an upright to spreading habit, although *S. connatus* is often decumbent. Although the shrubby habit (vs. caespitose) of species of *Schlechteranthus* has been coded in the morphological phylogeny (Fig. 4B) as a derived character, it is in fact the plesiomorphic character in the *Conophytum*-clade (Powell et al. 2017) and is only coded here as a derived state following the polarised outgroup method.

Branches and Leaf Arrangement—Branches are up to 9(–13) mm in diameter, with the widest branches found in the very compact *S. tetrasepalus.* The upper branches are usually brown, but in *S. pungens* they are distinctively white, while in *S. spinescens* (L. Bolus) R. F. Powell they are often whitish-grey.

The leaves are usually crowded towards the tips of the branches in subgenus *Microphyllus,* however in *S. subglobosus* (L. Bolus) R. F. Powell the opposite leaf pairs are evenly spaced along the branches with visible internodes (Fig. 2E). In *S. inclusus* the leaves are decussate and tightly packed along the branch so that the internodes are not visible (Fig. 2G). In addition, the old blackened leaves remain on the branch in *S. inclusus* (Fig. 2G), in contrast to all the other species in the subgenus, where old leaves fall off the branch.

Leaves—The leaves in species of subgenus *Microphyllus* are triquetrous to broadly trigonous and mucronate (Fig. 1), although in *S. parvus* the mucro is not prominent. Leaves display various shapes in outline, including globose, ovoid, oblong to lanceolate (Fig. 1; Table 1). Leaf size ranges include 1.5–20.0 × 1.5–5.0 mm and the leaf pair bases are fused from a fifth to three quarters of the leaf length (Fig. 1; Table 1). Leaf color is usually green, ranging from bright to deep green and sometimes yellow-green. The leaves are slightly papillate, due to the epidermal cells forming blunt papillae, defined as low protuberances in the center of the epidermal cell (Opel 2005). These blunt papillae result in a slightly velvety appearance of the leaf, but never appear hairy to the naked eye. In *S. abruptus* (A. Berger) R. F. Powell, the protuberances are slightly extended, creating a trichome-like structure, which results in a prominently velvety leaf. The leaf surface of *S. subglobosus* is also slightly different from the rest of the species due to the stout, dome-shaped epidermal cells, which result in a rough leaf surface.

Inflorescence Structure—Flowers in species of subgenus *Microphyllus* are either solitary or arranged in cymose inflorescences (Table 1). The non-spiny species, i.e. *S. abruptus, S. connatus, S. inclusus, S. subglobosus,* and *S. tetrasepalus,* all share solitary flowers (Fig. 2C, F; Table 1), with the flowers on a central primary axis (most basal and central flowering stems representing the peduncle of the inflorescence or pedicel of solitary flowers in *Schlechteranthus*), as found in species of subgenus *Schlechteranthus* (Fig. 4B; Table 2; Appendix 1).

The central primary axis is sometimes prominently extended, ranging from one and a half times to 10 times longer than the capsule length (as found in *S. connatus* (Fig. 2C), *S. subglobosus,* and *S. tetrasepalus*). In the remaining species, as well as in species of subgenus *Schlechteranthus,* the central primary axis is proportionally equal to the length of the capsule (Fig. 4B; Table 2; Appendix 1).

The length of the central primary axis also affects the position of the bracteole, with the bracteole positioned more than halfway down the primary axis in *S. connatus* (Fig. 2C) and *S. tetrasepalus,* while in *S. abruptus* and *S. inclusus* the bracteoles are positioned at the base of the capsule (less than a quarter of the way down the primary axis (Fig. 2G)). The bracteoles of *S. subglobosus* are positioned the lowest, more than two thirds down the primary axis. Furthermore, in *S. inclusus,* the bracteoles are prominently cup-shaped (Fig. 2F). The bracteole is caducous in *S. parvus, S. pungens, S. spinescens,* and *S. stylosus* (Table 1), grouping these species in the morphological

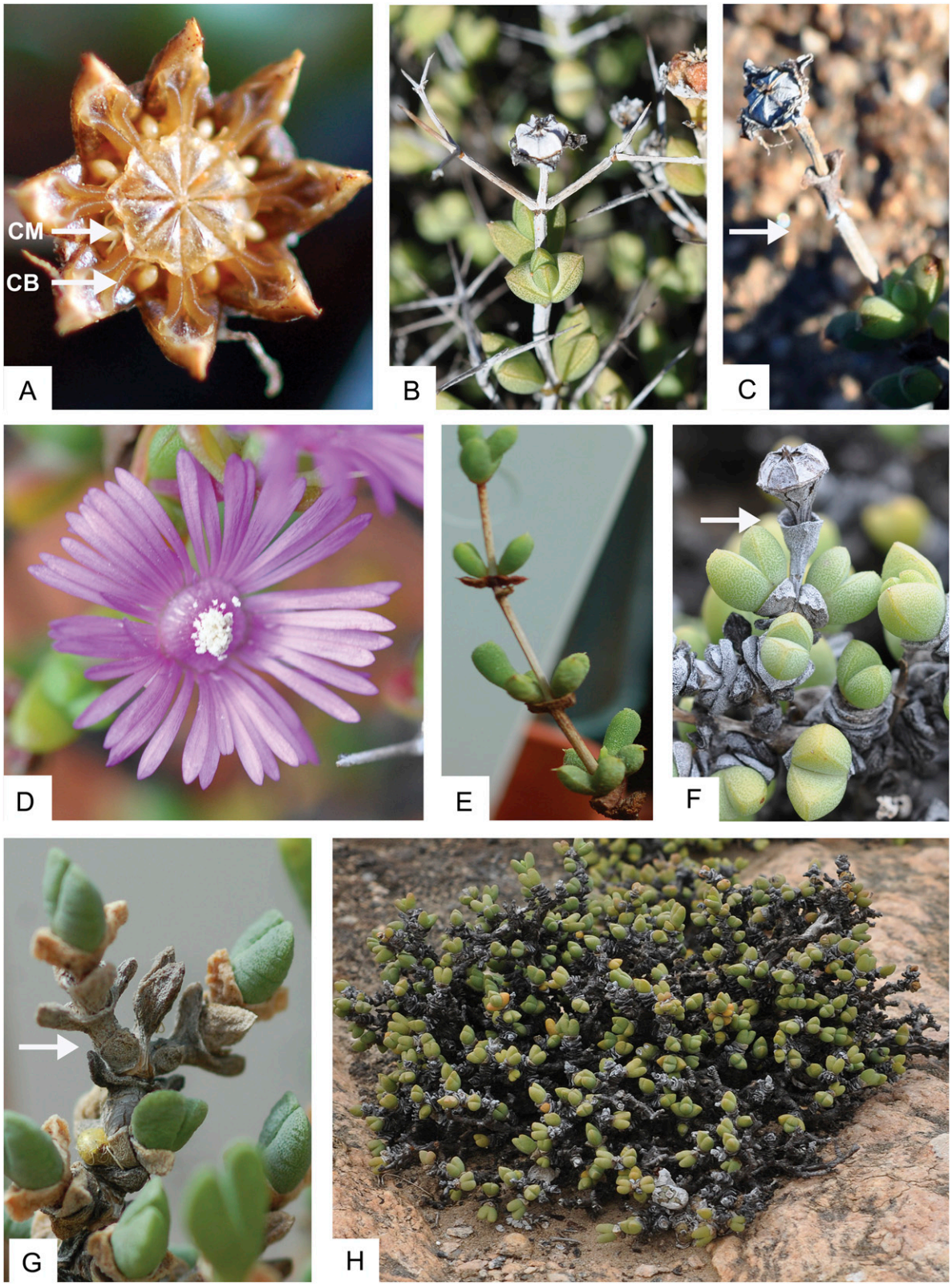

FIG. 2. A. Internal structure of capsules in subgenus *Microphyllus,* with arrows indicating closing bodies (CB) and covering membranes (CM). B. Spinescent inflorescence of *S. pungens* held above terminal leaf pair. C. Capsules of *S. connatus* on long central primary axis, arrow indicating the position of the bracteole. D. Magenta flower of *S. stylosus* with the stamens arranged in a cone in the centerof the flower, as is diagnostic of the genus *Schlechteranthus*. E. Evenly spaced leaves along the stem in *S. subglobosus*. F. Cup-shaped bracteole in *S. inclusus,* positioned at the base of the capsule. G. Old leaves that remain on stem in *S. inclusus.* H. Compact habit of *S. inclusus* found growing on a gneiss rocky outcrop along a river course. Photographs: R. F. Powell.

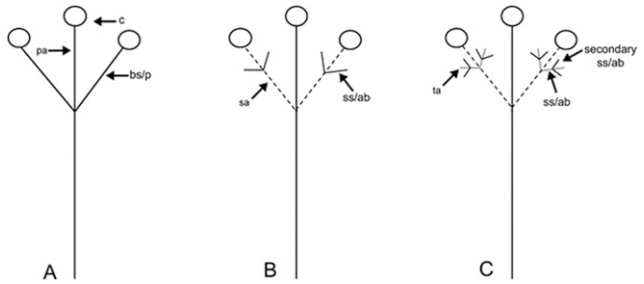

FIG. 3. Inflorescence structure and spine arrangement (spine type 2.2 of Hartmann and Stüber (1993)), in the spiny species *Schlechteranthus parvus, S. pungens, S. spinescens,* and *S. stylosus*. A. Inflorescence arranged in a simple cyme on the central primary axis (pa), with blunt spines (bs) derived from old pedicels (p) where capsules (c) have fallen off (spine ontogeny type 2 of Hartmann and Stüber (1993)), as found in *S. spinescens*. B. Inflorescence arranged in compound cyme on central primary axis and in simple cyme on secondary axes (indicated by dashed lines) with sharp spines (ss) derived from aborted buds (ab) (spine ontogeny type 1 of Hartmann and Stüber (1993)) on the two outer axes (as in *S. parvus* and *S. stylosus*), blunt spines also sometimes present where capsules have fallen off (spine ontogeny type 2 of Hartmann and Stüber (1993)). C. Inflorescence arranged in compound cyme on central primary axis, compound cyme on the secondary axes and in a simple cyme on the tertiary axes (ta) (indicated by dotted lines) as found in *S. pungens,* with sharp spines (ss) derived from aborted buds (ab) and blunt spines also sometimes present where capsules have fallen off.

phylogeny (Fig. 4B; Table 2; Appendix 1), although in the molecular phylogeny, these species are not recovered together in a clade (Fig. 4A).

Schlechteranthus parvus, S. pungens, S. spinescens, and *S. stylosus* share a cymose inflorescence with spines (Table 1). Both these characters, together with caducous bracteoles, are recovered as synapomorphies in the morphological phylogeny for these species in the subgenus (Fig. 4B; Table 2; Appendix 1). These species, however, do not form a clade in the molecular phylogeny, indicating the possible convergence of these characters (Fig. 4A). The convergence of spines is not unusual in the Aizoaceae, as spines are shown to have evolved numerous times in the Ruschioideae, such as in *Antimima* N. E. Br., *Drosanthemum* Schwantes and *Leipoldtia* L. Bolus, *Mestoklema* N. E. Br., and *Ruschia* Schwantes (Hartmann and Stüber 1993). Hartmann and Stüber (1993) studied spines of selected taxa of the Aizoaceae. Although *Schlechteranthus* was not included in the study, they discovered that, as in *Schlechteranthus,* the spines always occur as part of the dichasial inflorescence and are in a terminal position, in place of the pedicel (Hartmann and Stüber 1993). Two types of spine construction were defined, with the regular arrangement of spines in *Schlechteranthus* classifying the taxa into spine type 2 (Hartmann and Stüber 1993). In addition, two subtypes were defined for spine construction type 2 based on the relative position of the spines to the inflorescence (Hartmann and Stüber 1993). The position of the spines on the terminating younger branches of the inflorescences in the spiny *Schlechteranthus* species would include the species in spine construction subtype 2.2 (Hartmann and Stüber 1993). The arrangement and construction of the spiny dichasial inflorescence is closely related to the ontogeny of spines (Hartmann and Stüber 1993). In the study by Hartmann and Stüber (1993), two types of spine ontogeny were determined: one where the blunt spine is derived from the old pedicel (type 2) with an apparent abscission ring, as found in all spiny species of *Schlechteranthus* (only spine type in *S. spinescens*), and type 1, where the spine is derived from an aborted bud, as found in *S. parvus, S. pungens,* and *S. stylosus.*

In *S. spinescens,* the spines are arranged in a simple cyme on the central primary axis, with blunt spines derived solely from old pedicels where the capsules have fallen off (Fig. 3A; Table 2; Appendix 1). Although all the species share this spine type, this is the only spine formation found in *S. spinescens.* In *S. parvus, S. pungens,* and *S. stylosus* (Figs. 3B, C, 4; Table 2; Appendix 1), there are additional sharp spines derived from aborted axillary buds, which are arranged in compound cymes (Figs. 2B, 3B, C). In *S. parvus* and *S. stylosus*, the spines are arranged in a simple cyme on the secondary axes (Fig. 3B), while in *S. pungens,* the spines are arranged in a compound cyme on the secondary axes and in a simple cyme on the tertiary axes (Fig. 3C).

Floral Morphology—The calyx is green in all species, with four to six sepals and more or less equal petaloid staminodes, although the inner row is sometimes slightly shorter. The flowers are white to magenta and sometimes a combination thereof, i.e. magenta tips with a white central eye. Filamentous staminodes are occasionally absent (*S. tetrasepalus,* sometimes absent in *S. stylosus*) and the number of filamentous staminodes varies from a few (up to only 3) to many, in which case they form a complete series around the stamens (Table 1). *Schlechteranthus spinescens* and *S. parvus* have filamentous staminodes that form a complete series around the stamens, which is a useful character to distinguish *S. parvus* (Fig. 6A) from *S. stylosus.* Some species have few to many filamentous staminodes, such as *S. connatus* and *S. pungens,* forming a variable complete to incomplete series around the stamens (Table 1). The remaining species, *S. abruptus, S. inclusus, S. stylosus,* and *S. subglobosus,* always have only a few filamentous staminodes (sometimes absent in *S. stylosus*), forming an incomplete series around the stamens (Table 1). The stamens are always collected into a cone in the center of the flower (Fig. 2D), which is found in all species of *Schlechteranthus*. If filamentous staminodes are present (absent in some species), these surround the stamens and together then also form a cone. The flowers include six to nine stigmas, with the nectaries in a ring.

Capsule Morphology—The capsules are seven to nine locular (Fig. 2A) in subgenus *Microphyllus*, as opposed to the 10–12 locules found in subgenus *Schlechteranthus* (Powell et al. 2016). This character was recovered as a synapomorphy for subgenus *Microphyllus* in both the molecular and morphological phylogeny (Fig. 4; Table 2; Appendix 1). Capsule shape may be useful to distinguish some species in subgenus *Microphyllus*. The top of the capsule is usually convex, but sometimes only slightly so, with a somewhat flattened apex, as found in *S. subglobosus* (Fig. 7A; Table 1). The base of the capsule is funnel-shaped in all the species (Fig. 7A), with the exception of *S. connatus,* where the base is subglobose (Fig. 7B; Table 1). The subglobose base, in combination with the convex top, results in an almost globose capsule in *S. connatus*. The capsules possess complete covering membranes with small closing bodies that block a third of the locule (Figs. 2A, 7C). The small size of the closing bodies was recovered as a synapomorphy for this subgenus (Fig. 4; Table 2; Appendix 1). Closing rodlets are conspicuous in all species, with the rodlets protruding distally in *S. connatus* and *S. tetrasepalus.* Valve wings may be present or absent (Table 1), and if present, they are usually narrow (quarter to a third of the valve width). Valve wings are absent in *S. abruptus, S. connatus, S. inclusus, S. parvus,* and *S. stylosus.*

Phylogenetic Relationships—The monophyly of subgenus *Microphyllus* is supported by the seven to nine-locular capsules

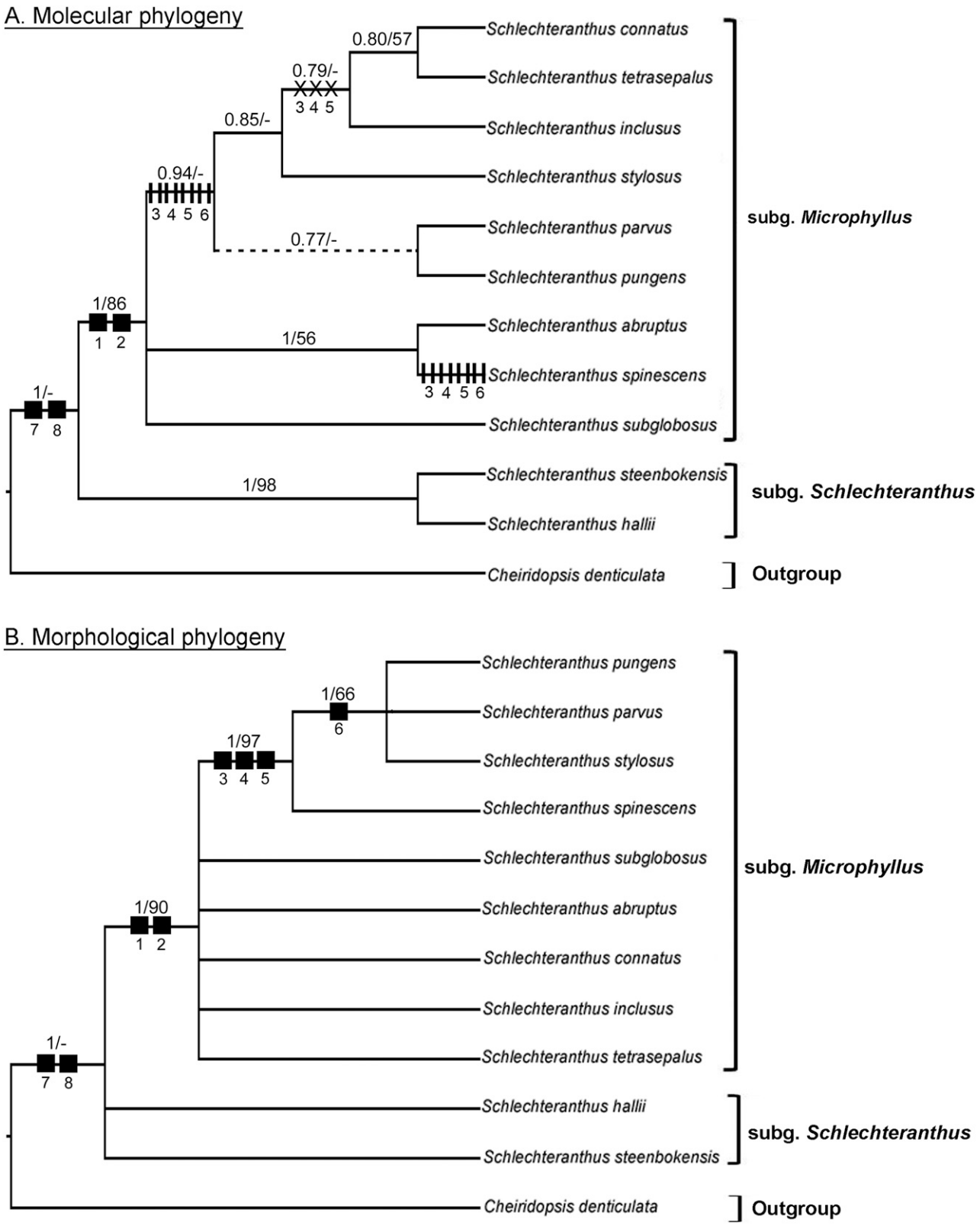

FIG. 4. A. Consensus tree from the Bayesian inference analysis from molecular plastid data (following Powell et al. 2016), tree length = 156, Consistency index (CI) = 0.94, Retention index (RI) = 0.76. B. Consensus tree from the Bayesian inference analysis from coded morphological characters (Table 2; Appendix 1) for species of subgenus *Microphyllus* and two species of subgenus *Schlechteranthus* as well as for *Cheiridopsis denticulata* (outgroup taxa); tree length = 8, Consistency index (CI) = 1.00, Retention index (RI) = 1.00. Posterior probabilities (PP) and bootstrap (BS) values are indicated above the branches. Black square = synapomorphy without reversal, parallel lines = convergence, X = loss. Character identification numbers are indicated below the symbols.

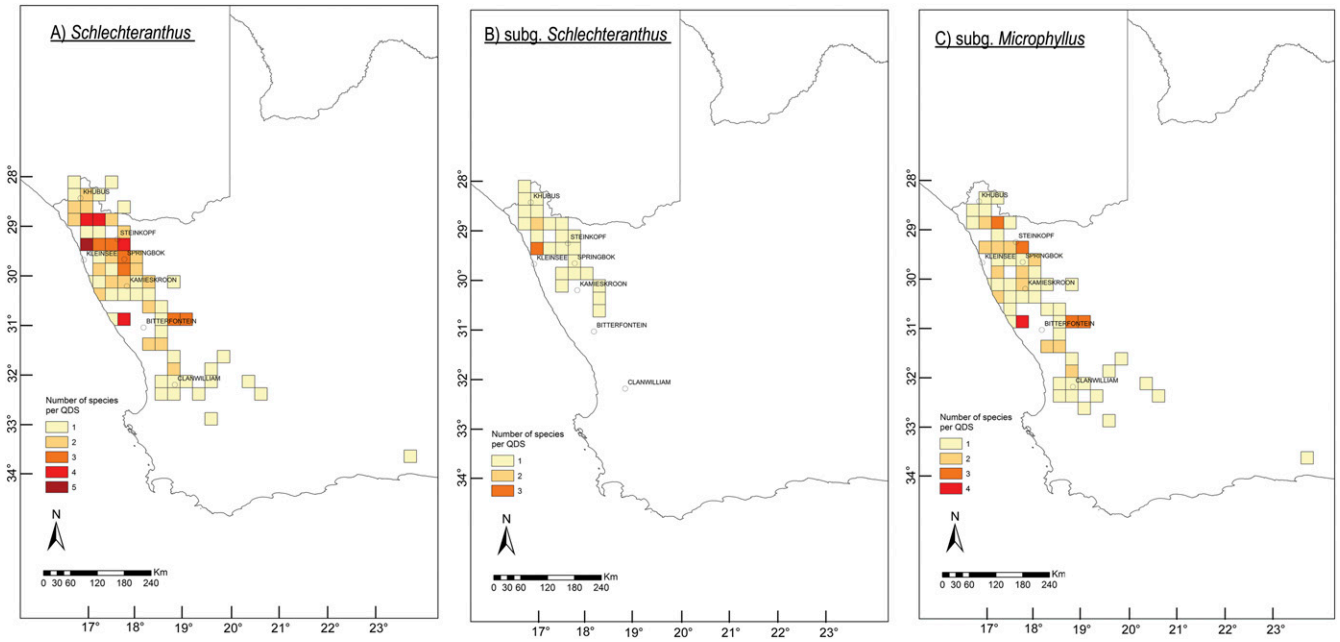

FIG. 5. Distribution and number of species per quarter degree square (QDS) (Edwards and Leistner 1971) in the Greater Cape Floristic Region, South Africa for: A. the genus *Schlechteranthus*; B. subgenus *Schlechteranthus;* C. subgenus *Microphyllus.*

with small closing bodies in both the morphological and molecular phylogenetic analyses (Fig. 4; Table 2; Appendix 1). The species of subgenus *Microphyllus* are grouped by strongly supported synapomorphic characters in the morphological phylogeny (Fig. 4B), while in the molecular analysis, no synapormorphic characters were recovered for the clades within subgenus *Microphyllus* (Fig. 4A). The clades recovered in the molecular analysis however indicate a slight distinction in geographical distributions of the species. The two species recovered in a well-supported clade, *S. abruptus* and *S. spinescens* (PP = 1, BS = 56), have a slightly more southern center of distribution (Fig. 8B, F) while the distributions of the majority of species (*S. connatus, S. inclusus, S. parvus, S. pungens, S. spinescens, S. stylosus, S. tetrasepalus*), recovered in a strongly supported clade (PP = 0.94), are centered in Namaqualand (Fig. 8A, C–E, G–I), as well as the remaining unresolved species (Fig. 4A), *S. subglobosus* (Fig. 8D).

In light of the incongruence between the two phylogenetic datasets, we have arranged the species in the taxonomic treatment according to the sequence suggested by the morphological analysis (Fig. 4B), so that morphologically similar taxa are arranged together, for ease of identification.

Taxonomic Treatment

Key to the Subgenera of Schlechteranthus

1. Capsules > 6 mm in diameter, with 10 to 12 locules, closing bodies blocking more than half of the locule; leaves ≥ 4.5 mm wide; epidermal cells anticlinally elongated, with calcium oxalate crystals deposited on the anticlinal walls . . . . . subg. *Schlechteranthus*
1. Capsules < 6 mm in diameter, with 7 to 9 locules, closing bodies blocking less than half of the locule; leaves ≤ 4.5 mm wide; epidermal cells isodiameteric without crystals on the anticlinal wall. . . . . subg. *Microphyllus*

Schlechteranthus subgenus Microphyllus R. F. Powell, Taxon 65: 259: 2016.—TYPE: *Schlechteranthus pungens* (H. E. K. Hartmann) R. F. Powell.

Arenifera A. G. J. Herre *sensu* H. E. K. Hartmann *p.p.* excluding type, Bradleya 14: 37. 1996.

Octopoma N. E. Br. *p.p.* excluding type, Gard. Chron. Ser. III. 87: 126, in clavi. 1930.

Low-growing, succulent, compact, upright to spreading shrub, often dome-shaped, 100–400 mm tall, with sparse to dense growth. Branches woody, decumbent or spreading to upright, branching from the base, up to 9(–13) mm in diameter, occasionally covered by persistent old leaves; upper branches brown, or whitish grey to white. Leaves triquetrous to fatly trigonous; globose, ovoid, oblong, or lanceolate in outline, 1.5–20.0 × 1.5–5.0 mm; margins thickened; leaf pairs fused for a fifth to three quarters of the length; mucronate, although mucro sometimes not prominent; slightly papillate, resulting in a slightly to prominently velvety, or rough leaf surface; bright green to deep green, sometimes yellow-green. Flowers solitary or in spinescent cymose inflorescences, spines formed either by old pedicels or aborted axillary buds; on central primary axis 10–55 mm long, equal to capsule length or up to 10 times longer; bracteole caducous or persistent, sometimes cup-shaped; flowers cone-type, with stamens collected into a cone; calyx lobes green, 4–6; petaloid staminodes ± equal, inner row sometimes shorter, white to magenta; filamentous staminodes absent or few to many, forming a complete or incomplete series around the stamens; stigmas six to nine, nectaries in a ring. Fruit a loculicidal capsule, with 7 to 9 locules, top prominently to slightly convex, base funnel-shaped, sometimes cup-shaped, 2.0–6.0 × 2.0–6.0 mm;

Table 2. Character matrix used for the morphological cladistic analyses for *Schlechteranthus*. Description of characters and character states are included in Appendix 1.

Species	1	2	3	4	5	6	7	8
S. abruptus	1	1	0	0	0	0	1	1
S. connatus	1	1	0	0	0	0	1	1
S. hallii	0	0	0	0	0	0	1	1
S. inclusus	1	1	0	0	0	0	1	1
S. parvus	1	1	1	1	1	1	1	1
S. pungens	1	1	1	1	1	1	1	1
S. spinescens	1	1	1	1	1	0	1	1
S. steenbokensis	0	0	0	0	0	0	1	1
S. stylosus	1	1	1	1	1	1	1	1
S. subglobosus	1	1	0	0	0	0	1	1
S. tetrasepalus	1	1	0	0	0	0	1	1

covering membranes complete; closing bodies small, blocking ⅓ of locule; closing rodlet conspicuous, sometimes protruding distally; valve wings narrow, ¼ to ⅓ of valve width, sometimes absent. Seeds obovate to pear-shaped; smooth to slightly pustulate.

Diagnostic Characters—Subgenus *Microphyllus* can be distinguished from subgenus *Schlechteranthus* by the smaller leaves (3.5–5.0 × 4–6 mm vs. 5–30 × 3.5–9.0 mm), smaller capsules (2–6 × 2–6 mm vs. 6–11 × 4–9 mm), with only seven to nine locules (vs. 10 to 12 locules) and small closing bodies that block a third of the locule (vs. larger closing bodies that block three quarters of the locule). In addition, the epidermal cells are isodiametric with no crystals deposited on the anticlinal wall, whereas in subgenus *Schlechteranthus* the epidermal cells are anticlinally elongated with calcium oxalate crystal deposits on the anticlinal walls. The epidermal cells of subgenus *Microphyllus* form blunt papillae which are found throughout the epidermis, but concentrated around the stomata, while in subgenus *Schlechteranthus*, the papillate epidermal cells are only found surrounding the stomata. *Schlechteranthus holgatensis* is an exception in subgenus *Schlechteranthus*, as it is densely papillate throughout the leaf surface. Nine species are currently recognised in subgenus *Microphyllus* and six species in subgenus *Schlechteranthus* (Klak and Bruyns 2016).

Species of subgenus *Microphyllus* may be confused with other species of Ruschioideae which also have multilocular capsules and spines, as found in *Leipoldtia*, however, species of subgenus *Microphyllus* are distinguished from these species by the mucronate leaves, narrow valve wings (broad in *Leipoldtia*), small or large closing bodies (always large in *Leipoldtia*), and seven- to nine-locular capsules (10-locular capsules in *Leipoldtia*).

Ecology—The species occur in a wide range of ecological habitats such as gentle rocky slopes, alluvial banks, and rocky soils, and on a number of geologies including calcrete, gneiss, quartz, red loamy sand, sandstone, and shale. The species flower from mid-winter to spring, i.e. August to October.

Key to the Species of Subgenus *Microphyllus*

1. Flowers solitary; bracteole persistent on central primary axis, old pedicels or aborted axillary buds not forming spines; valve wings absent or very narrow, up to a quarter of valve width . . . 2
   2. Leaves markedly globose in outline; leaves positioned at regular intervals along the branch; capsules slightly convex, flattened at apex; branches upright to spreading; leaves usually bright green . . . **4. *S. subglobosus***
   2. Leaves ovoid to lanceolate in outline; leaves crowded towards the tips of the branches or stacked tightly along the branch; capsules convex, not flattened at apex; branches decumbent or upright to spreading; leaves green to dark green, never bright green . . . 3
      3. Central primary axis one and a half to 10 times longer than capsule length; capsules often held in a row above the terminal leaf pairs; bracteoles more than a third of the way down the primary axis . . . 4
         4. Leaves ovoid in outline, < 5 mm long, opposite leaf pairs fused two thirds of the length; capsule bases funnel-shaped; branches upright . . . **3. *S. tetrasepalus***
         4. Leaves lanceolate in outline, > 8 mm long, opposite leaf pairs fused for a quarter of the length; capsule bases rounded; branches decumbent . . . **5. *S. connatus***
      3. Central primary axis equal in length to capsule length; capsules not held in a row above terminal leaf pairs; bracteoles usually at base of capsules but always less than a quarter of the way down the primary axis . . . 5
         5. Leaves decussate, with old leaves persisting on branch; opposite leaf pairs fused for three quarters of the length, ovoid in outline, ≤ 11 mm long . . . **1. *S. inclusus***
         5. Leaves opposite, crowded towards the tips of the branch, with old leaves falling off branch; opposite leaf pairs fused for a quarter of the length, lanceolate in outline, ≥ 12 mm long . . . **2. *S. abruptus***
1. Flowers in cymose inflorescences; bracteoles caducous on central primary axis, old pedicels or aborted axillary buds forming spines; valve wings narrow, up to a third of the valve width . . . 6
   6. Blunt spines derived solely from old pedicels where capsules have fallen off; inflorescences in simple cymes . . . **6. *S. spinescens***
   6. Sharp spines derived from aborted axillary buds; inflorescences in compound cymes . . . 7
      7. Spines arranged in compound cyme on secondary axes; upper branches white; opposite leaf pairs fused for a quarter to a third of the length . . . **7. *S. pungens***
      7. Spines arranged in simple cyme on secondary axes; upper branches brown; opposite leaf pairs fused for a third to three quarters of the length . . . 8
         8. Leaves ovoid in outline, prominently mucronate, leaf pairs fused for less than or equal to half of the length; filamentous staminodes few, not forming a complete series around the stamens; large shrub to 400 mm tall . . . **8. *S. stylosus***
         8. Leaves subglobose to globose in outline, not prominently mucronate, leaf pairs fused for more than or equal to half of the length; filamentous staminodes many, forming a complete series around the stamens; shrublet to 150 mm tall . . . **9. *S. parvus***

1. Schlechteranthus inclusus (L. Bolus) R. F. Powell, Taxon 65: 259. 2016. *Mesembryanthemum inclusum* L. Bolus, Ann. Bolus Herb. 4: 40. 1926. *Octopoma inclusum* (L. Bolus) N. E. Br., Gard. Chron. 3: 126. 1930; Hartmann, Bradleya 16: 72. 1998; Hartmann, Ill. Handb. Succ. Pl. Aizoaceae 2: 190. 2001; Klak in Snijman, Pl. Gr. C.F.R. 2: 219. 2013. *Ruschia restituta* G. D. Rowley, nom. nov. non. *Ruschia inclusa* L. Bolus, Natl. Cact. Succ. J. 33: 8. 1978.—TYPE: SOUTH AFRICA. Northern Cape Province: slopes overlooking the sea, south of Hondeklip Bay, Namaqualand [3017DA], 1924, *Pillans sub BOL 17758* (lectotype, designated by Hartmann (1998): BOL!, isosyntype: K-image!).

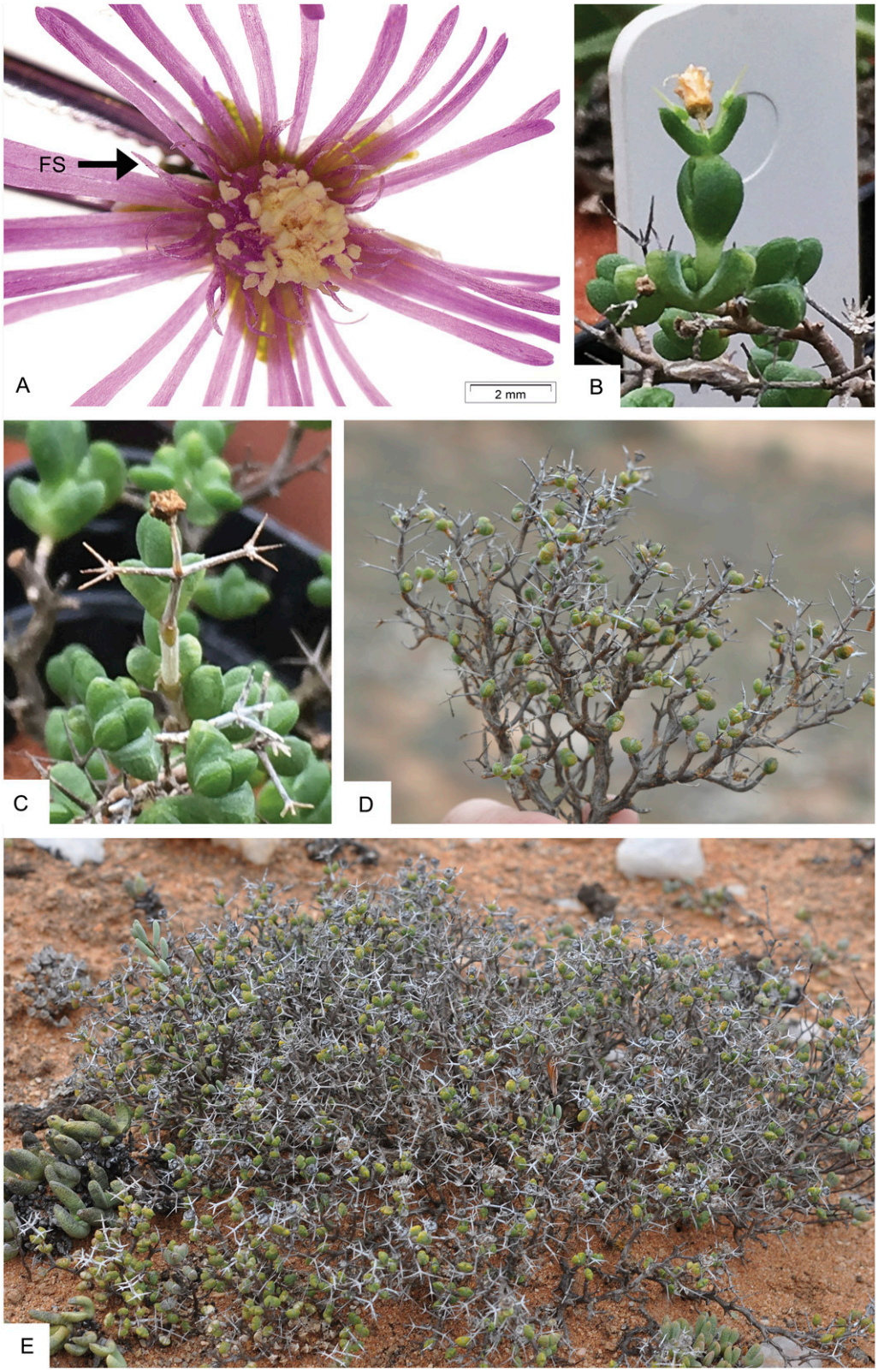

FIG. 6. A new species of *Schlechteranthus*, *S. parvus*. A. Flower of *S. parvus* with many filamentous staminodes (FS), forming a complete series around the stamens. B. Old flower of *S. parvus*, with spines developing from aborted apical buds. C. Spine arrangement in compound cyme in *S. parvus*. D. Branch of *S. parvus* cut at base to illustrate small size and spines. E. *Schlechteranthus parvus* in habitat, illustrating the small size of the species and display of dense spines.

Dense upright shrublets, to 100 mm tall. Branches to 8 mm in diameter; upper branches brown; leaves present along the branch, prominently stacked, with old black leaves remaining on branch. Leaves triquetrous, ovoid in outline; 4.0–11.0 × 3.0–3.5 mm; leaf pairs fused for ¾ of length; mucro prominent; slightly velvety; green, often blackened at base. Flowers solitary, on central primary axis to 11 mm long, equal proportionally to capsule length, bracteoles persistent, present

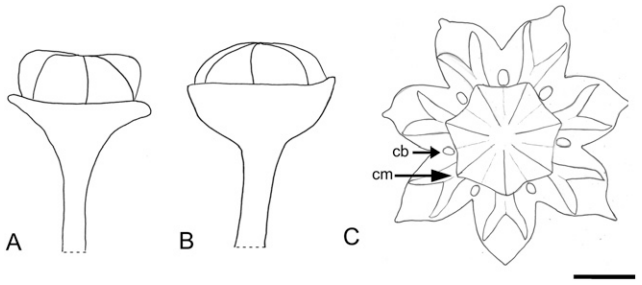

FIG. 7. Capsule shape and structure in subgenus *Microphyllus*. A. Capsule with flattened apex and funnel-shaped base, as found in *S. pungens*. B. *Schlechteranthus connatus* with convex top and subglobose base. C. Internal capsule structure found in subgenus *Microphyllus* (*S. connatus*), arrows indicating the closing bodies (cb) and covering membranes (cm). Scale = 1 cm.

less than ¼ way down axis, prominently cup-shaped, often holding capsule base; spines absent; filamentous staminodes few, forming an incomplete series around the stamens. Fruit 8-locular; top slightly convex, base funnel-shaped; 4.0 × 3.0 mm; closing rodlets conspicuous; valve wings absent. Figure 9.

Diagnostic Characters—This species is easily distinguished by the decussate leaves stacked along the branch and the old blackened leaves that remain on the branch (Fig. 2G). However, it may be confused with *S. tetrasepalus*, which shares a compact habit and leaf pairs with a high degree of fusion (Fig. 1F, G). *Schlechteranthus inclusus* is, however, further distinguished by the short central primary axis which is equal in length to the length of the capsule, and the cup-shaped bracteoles (primary axis at least one and a half times longer than capsule, leaves crowded towards the tip of the branches, with old leaves falling off, and bracteoles not cup-shaped in *S. tetrasepalus*).

Distribution and Ecology—This species has a coastal distribution, found on the west coast of South Africa between Kleinsee and the Groen River mouth (Fig. 8A). *Schlechteranthus inclusus* is associated with a range of geologies including calcrete, granite, and gneiss, but always in shallow soil. The distribution of this species is closely linked to alluvial habitats, often occurring on rocky patches in or alongside river courses. It flowers from August to September.

Additional Specimens Examined—South Africa. NORTHERN CAPE: 2917 (Springbok): Namaqualand, Kleinsee, Farm Drooge Kraal 180, lower south-eastern slopes of Naroegas se Berg, below trig beacon (–AD), *Desmet and Smale 3284* (NBG). 3017 (Hondeklipbaai): east of Koingnaas, on south slope (–AB), *Klak 474* (BOL); South of Koingnaas along road to Hondeklip Bay, at Swartlintjiesrivier (–AB), *Klak 2359* (BOL); Close to turnoff to Hondeklipbaai from Kleinsee (–AB), *Powell 35* (NBG); Spoegrivier cave, on rocks above the river (–AD), *Klak 1836* (BOL); Nama'land, two miles north of Kamieskroon (–BB), *Littlewood sub KGB 584/59* (BOL); Gemsbokvlei, 10 miles east of Port Nolloth (–BC), *Van Heerde 27400* (BOL); North of Flamink Berg, Walle Kraal, Namaqualand (–BC), *Pillans 17911* (BOL); South of Groenrivier mouth, near the lighthouse (–DC), *Klak 1832* (BOL); Cape Province, Namaqualand, six miles north of Garies (–DD), *Hall sub NBG 1016/60* (BOL); Garies District, farm Tweerivier (–DD), *Klak 2411* (BOL). Precise locality unknown: South border of Little Namaqualand, *Peers sub NBG 1394/33* (BOL).

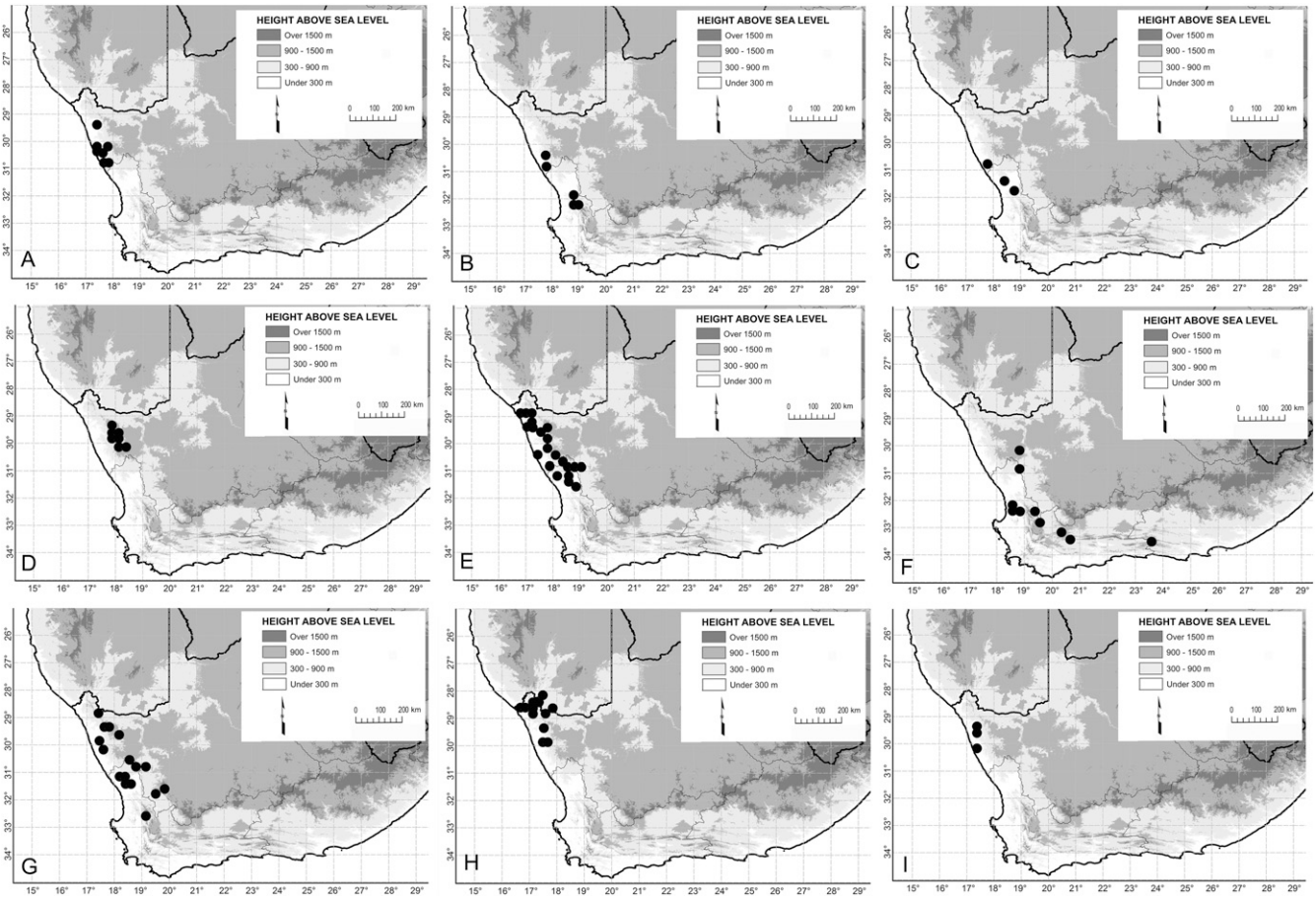

FIG. 8. Known geographical distributions of the species in subgenus *Microphyllus*. A. *Schlechteranthus inclusus*. B. *S. abruptus*. C. *S. tetrasepalus*. D. *S. subglobosus*. E. *S. connatus*. F. *S. spinescens*. G. *S. pungens*. H. *S. stylosus*. I. *S. parvus*.

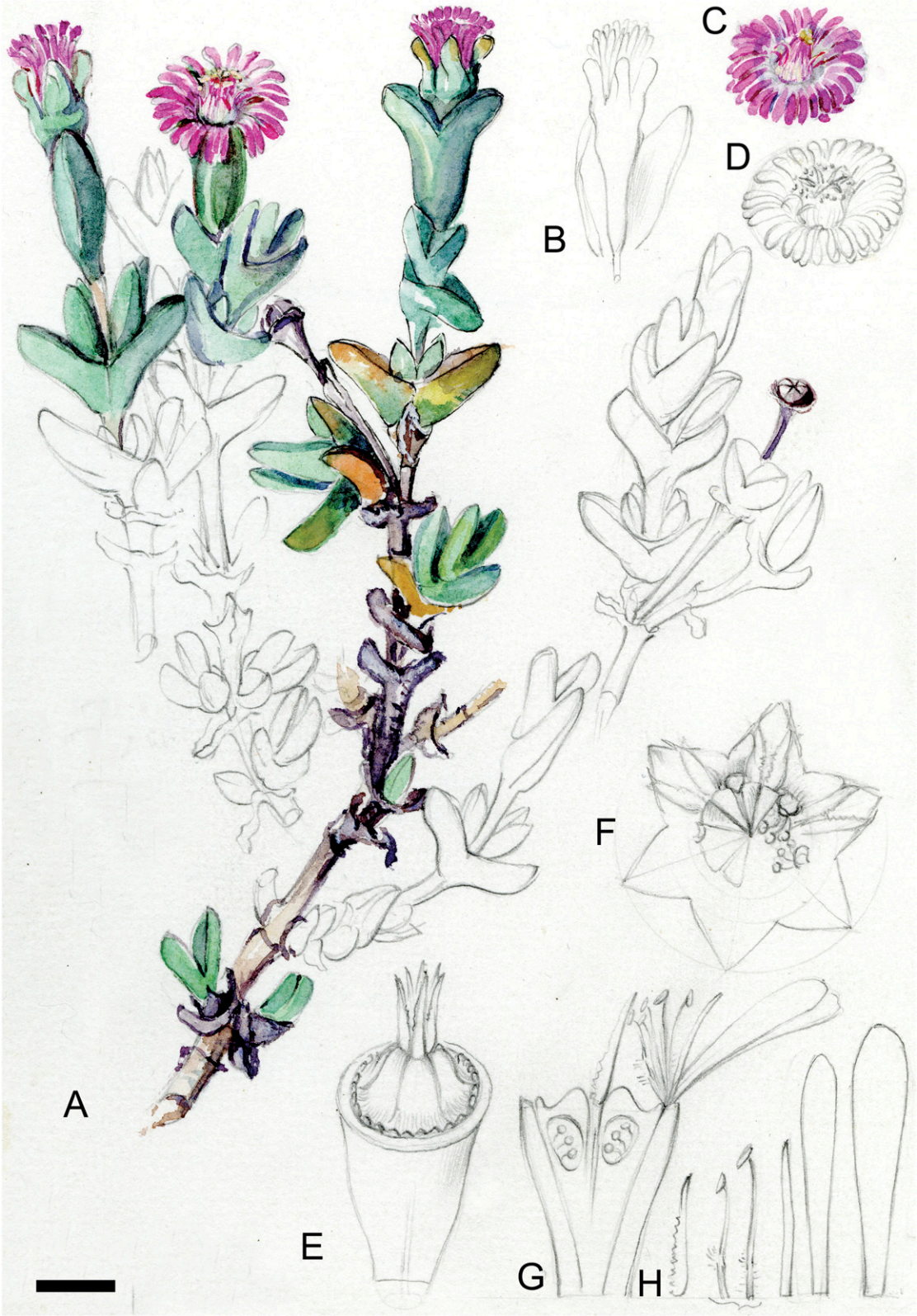

FIG. 9. Drawing of type material for *S. inclusus* (*Pillans sub BOL 17758* (BOL)). A. Habit and leaf arrangement of *S. inclusus*. B. Terminal opposite leaf pair with flower in bud. C. Flower with stamens and filamentous staminodes collected in a cone in the center of flower, as is diagnostic for the genus. D. Flower with arrangement of stamens loosely arranged in a cone, typically found near the end of the flowering season. E. Flower with all staminodes removed showing the nectaries arranged in a ring. F. Open capsule with small closing bodies and complete covering membranes. G. Longitudinal section of flower showing the arrangement of the style, stamens, and petaloid staminodes. H. Floral components illustrating the style, stamens, filamentous staminodes, and petaloid staminodes. Scale: A–D = 10 mm; E, G = 3.3 mm; F, H = 2.5 mm. Artist B. Carter.

2. SCHLECHTERANTHUS ABRUPTUS (A. Berger) R. F. Powell, Taxon 65: 259. 2016. *Mesembryanthemum abruptum* A. Berger, Bot. Jahrb. Syst. 57: 638. 1922. *Octopoma abruptum* (A. Berger) N. E. Br., Gard. Chron. 3: 126. 1930; Hartmann, Bradleya 16: 72. 1998; Hartmann, Ill. Handb. Succ. Pl. Aizoaceae 2: 189. 2001; Klak in Manning and Goldblatt, Pl. Gr. C.F.R. 1: 296. 2012. *Ruschia abrupta* (A. Berger) G. D. Rowley, Natl. Cact. Succ. J. 33: 8. 1978.—TYPE: SOUTH AFRICA. Western Cape Province: Brandewynrivier, between Clanwilliam and Calvinia [3118DD], Oct 1897, *R. Schlechter 10828* (holotype: GRA–image!; isotypes: BOL!; BR–image!, K–image!, S–image!, WAG–image!). [Note: Powell et al. (2016) erroneously cited the BOL specimen as holotype. However, the original description cited a specimen housed at GRA, and therefore it is correctly cited here as the holotype.]

Ruschia rupigena L. Bolus, Notes Mesembryanthemum 3: 520. 1935. *Ruschia rupicola* L. Bolus, Notes Mesembryanthemum 2: 415. 1933, *nomen illegit.* non Schwantes Z. Sukkulentenk. 2: 187. 1926. *Octopoma rupigena* (L. Bolus) L. Bolus J. S. African Bot. 33: 306. 1967; Hartmann, Bradleya 16: 73. 1998; Hartmann, Ill. Handb. Succ. Pl. Aizoaceae 2: 190. 2001; Klak in Manning and Goldblatt, Pl. Gr. C.F.R. 1: 297. 2012.—TYPE: SOUTH AFRICA. Western Cape Province: near Pakhuis, Clanwilliam Div., common on rocks between Pakhuis and Buishoekfontein [3218BB], Sep 1933, *L. Bolus sub NBG 1504/33* (holotype: BOL!; isotype: PRE-image!).

Sparse, upright to spreading shrub, to 250 mm tall. Branches to 9 mm in diameter; upper branches brown; leaves crowded towards tips of branches, old leaves not remaining on the branch. Leaves triquetrous, lanceolate in outline; 12.0–20.0 × 2.5–5.0 mm; leaf pairs fused for ¼ of length; mucro prominent; prominently velvety as a result of extended papillae of epidermal cells; green. Flowers solitary; on central primary axis to 11 mm long, equal proportionally to capsule length, bracteoles persistent, present less than ¼ way down axis; spines absent; filamentous staminodes few, forming an incomplete series around the stamens. Fruit 8-locular; top slightly convex, base widely funnel-shaped; 5.0 × 3.5 mm; closing rodlets conspicuous; valve wings absent. Figure 10.

Diagnostic Characters—*Schlechteranthus abruptus* is most likely to be confused with *S. connatus* as the species share a similar leaf shape and size, but can be distinguished by the shape of the capsule, which has a funnel-shaped base (capsule base subglobose in *S. connatus*) and the primary axis which is also not lengthened (prominently lengthened in *S. connatus*). The bracteole position in *S. abruptus* is also distinct, as it is almost always found at the base of the capsule, but no more than a quarter of the way down the primary axis (more than half way down the primary axis in *S. connatus*). *Schlechteranthus abruptus* can also be distinguished by its prominently velvety leaf surface, which is unique to this species in the subgenus, and otherwise only found in *S. holgatensis* Klak in subgenus *Schlechteranthus* (Klak and Bruyns 2016).

Distribution and Ecology—*Schlechteranthus abruptus* is found in the area between Clanwilliam and Garies (Fig. 8B). The species is found on shallow rocky sandstone soils and flowers from July to August.

Additional Specimens Examined—South Africa. WESTERN CAPE: 3017 (Hondeklipbaai): north of Garies, Kys (–BD), *Klak 468* (BOL); Klip Vlei, between Kamieskroon and Garies, Namaqualand (–DD), *Thorne 49957* (SAM). 3218 (Clanwilliam): inter Pakhuis et Nardouw (–BB), *Leipoldt s.n.* (BOL). 3219 (Wuppertal): Klipfontein, north of Boontjieskloof (–AA), *Esterhuysen 32204* (BOL); On Pakhuis Pass, just before turnoff to Wuppertal (–AA), *Powell 5* (NBG); Pakhuis, near turnoff to Wuppertal (–AA), *Klak 433* (BOL). Precise locality unknown: near Clanwilliam, *L. Bolus sub BOL 23833* (BOL).

3. SCHLECHTERANTHUS TETRASEPALUS (L. Bolus) R. F. Powell, Taxon 65: 259. 2016. *Ruschia tetrasepala* L. Bolus, Notes Mesembryanthemum 2: 373. 1932. *Octopoma tetrasepalum* (L. Bolus) H. E. K. Hartmann, Bradleya 16: 74. 1998; Hartmann, Ill. Handb. Succ. Pl. Aizoaceae 2: 190. 2001; Klak in Snijman, Pl. Gr. C.F.R. 2: 219. 2013.—TYPE: SOUTH AFRICA. Western Cape Province: between the town and Sout River [3118DD], Apr 1932, *Luckhoff sub BOL 20203* (holotype: BOL!).

Dense upright shrublet, to 130 mm tall. Branches to 7(–13) mm in diameter; upper branches brown; leaves crowded towards tips of branches, old leaves not remaining on the branches. Leaves triquetrous, ovoid in outline; 3.0–5.0 × 1.5–4.0 mm; leaf pairs fused for ⅔ of length; mucro prominent; slightly velvety; green. Flowers solitary; on central primary axis to 13 mm long, at least 1½ times longer than capsule length, bracteoles persistent, present more than ⅓ way down axis; spines absent; filamentous staminodes absent. Fruit 7- to 8-locular; top convex, base funnel-shaped; ca. 5.5 × 4.0 mm; closing rodlets conspicuous, protruding distally; valve wings absent.

Diagnostic Characters—This species is most similar to *S. inclusus* in its compact habit, leaves with a high degree of fusion (Fig. 1F, G), and solitary flowers, but is distinguished by the longer central primary axis, which is at least one and a half times longer than the capsule, often resulting in the capsules held in a row above the terminal leaf pairs (primary axis equal in length to capsule and capsules not held in a row in *S. inclusus*). In *S. tetrasepalus,* the old leaves do not remain on the branch, leaving branches bare, while in *S. inclusus,* the old leaves remain on the branch.

Distribution and Ecology—This species occurs on gravel sandstone patches on alluvial banks of the Groen River (Fig. 8C) and in the Knersvlakte in quartz. *Schlechteranthus tetrasepalus* flowers in September.

Additional Specimens Examined—South Africa. WESTERN CAPE: 3017 (Hondeklipbaai): Tweeriviere, Groen River (–DD), *Bruyns 10856* (BOL). 3118 (Vanrhynsdorp): Knersvlakte, Farm Moedverloor (–AD), *Klak 933, Klak 2418* (BOL).

4. SCHLECHTERANTHUS SUBGLOBOSUS (L. Bolus) R. F. Powell, Taxon 65: 259. 2016. *Ruschia subglobosa* L. Bolus, Notes Mesembryanthemum 1: 140. 1928. *Mesembryanthemum reductum* (L. Bolus) N. E. Br., Gard. Chron. 3: 33. 1930. *Octopoma subglobosa* (L. Bolus) L. Bolus, J. S. African Bot. 29: 49. 1963; Hartmann, Bradleya 16: 73. 1998; Hartmann, Ill. Handb. Succ. Pl. Aizoaceae 2: 190. 2001; Klak in Snijman, Pl. Gr. C.F.R. 2: 219. 2013.—TYPE: SOUTH AFRICA. Northern Cape Province: hills on north side of O'kiep, Little Namaqualand [2917DB], Oct 1926, *Pillans 5844* (holotype: BOL!).

Sparse spreading shrub, to 200 mm tall. Branches to 4 mm in diameter; upper branches brown; leaves positioned at regular intervals along the branches, old leaves not remaining on the branches. Leaves fatly trigonous, markedly globose in outline; 2.5–9.0 × 1.5–3.0 mm; leaf pairs fused for ⅓ of length; mucro very prominent as result of leaf shape; rough, as a result of stout dome-shaped epidermal cells; bright green. Flowers solitary; on central

FIG. 10. Drawing of type material for *S. abruptus* (*Bolus sub NBG 1504/33* (BOL)). A. Closed capsule of *S. abruptus*. B. Open flower with stamens and filamentous staminodes collected in a cone. C. Flowering branch of *S. abruptus*. D. Habit and leaf arrangement of *S. abruptus*. E. Longitudinal section of flower showing the arrangement of the style, stamens, and petaloid staminodes. F. Enlarged top part of leaf illustrating the velvety leaf surface. G. Floral components illustrating the style, stamens, filamentous staminodes, and petaloid staminodes. H. Open capsule with small closing bodies and complete covering membranes. I. Flower with all staminodes removed showing the nectaries arranged in a ring. Scale: A–D = 10 mm; E–I = 2.5 mm. Artist B. Carter.

primary axis to 25 mm long, at least five times longer than capsule length, bracteoles persistent, present more than ⅔ way down axis; spines absent; filamentous staminodes few, forming an incomplete series around the stamens. Fruit 7- to 8-locular; top slightly convex, flattened at the apex, base narrowly funnel-shaped; ca. 4.0 × 2.5 mm; closing rodlets conspicuous; valve wings narrow, up to ¼ width of valve. Figure 11.

Diagnostic Characters—*Schlechteranthus subglobosus* is a distinct species and, although it shares a globose leaf shape with *S. parvus* (Fig. 1D, I), the leaf pairs are only fused for a third of the length with a very prominent mucro (fused for a quarter of the length with obscure mucro in *S. parvus*) and the flowers are solitary (flowers in cymose inflorescence in *S. parvus*). The leaves of *S. subglobosus* are regularly spaced along the branch (Fig. 2E), which is similar to *S. inclusus*, while the rest of the species in the subgenus have the leaves crowded towards the tips. In *S. subglobosus,* however, the leaves are positioned at regular intervals along the branch with the internodes visible between the leaves (Fig. 2E), while in *S. inclusus* the leaves are tightly packed and decussate, with no visible internodes (Fig. 2G). *Schlechteranthus subglobosus* can further be distinguished from the other species in the subgenus by its bright green leaves with a rough surface and very prominent mucro as a result of the fatly trigonous leaf shape, while the leaves in the remaining species are triquetrous green to dark green leaves, with a slightly velvety to velvety leaf surface and a prominent mucro (obscure in *S. parvus*) in the rest of the subgenus).

Distribution and Ecology—*Schlechteranthus subglobosus* has a narrow distribution with a specific habitat, found only on gentle rocky slopes, usually gneiss, on hills between Springbok and Kamieskroon (Fig. 8D). The species flowers from August to September.

Additional Specimens Examined—South Africa. NORTHERN CAPE: 2917 (Springbok): On road between Goodhouse and Concordia (–BD), *Powell 33* (NBG); Namqualand, Ratelpoort (–BD), *Hall,* sub *NBG 1770/48* (BOL); Three km east of Nababeep and one and a half km north of Divide copper mine (–DB), *Hilton-Taylor 2080* (BOL); Two km east of Springbok, O'kiep (–DB), *Klak 2418* (BOL); Namaqualand, near Springbok (–DB), *L. Bolus* sub BOL 19008 (BOL); Khamieskroon District, Ybeep (–DD), *Bruyns 7610* (BOL); Namaqualand District, Kamiesberg mountain range at pass on Droëdap road (–DD), *Burgoyne 11265* (NBG); Little Namaqualand, three miles south of Mesklip (–DD), *Salter 4598* (BOL); Little Namaqualand, Mesklip (–DD), *Esterhuysen 7769* (BOL); Namaqualand, Farm De Draay 346 (–DD), *Le Roux 4126b* (NBG). 2918 (Gamoep): Springbok District, Kweekfontein (–CA), *Bruyns 8240* (BOL); Namaqualand District, On road from Gamoep to Springbok, two km before farm Silverfontein (–CC), *Klak 753* (BOL); Nuwedam, Springbok (–CC), *Bruyns 9146* (BOL). 3018 (Kamiesberg): One km north of Rooidoringkloof turn-off (-AA), *Klak 866* (BOL); Southeast of Hôsabees in 'Pypmaker se Poort', road to Gamoep (–AB), *Hilton-Taylor 2239* (BOL). Precise locality unknown: Bushmanland, *SUG 8917* (BOL).

5. SCHLECHTERANTHUS CONNATUS (L. Bolus) R. F. Powell, Taxon 65: 259. 2016. *Ruschia connata* L. Bolus, Notes Mesembryanthemum 1: 139. 1928. *Mesembryanthemum connatum* (L. Bolus) N. E. Br., Gard. Chron. 3: 32. 1930. *Octopoma connatum* (L. Bolus) L. Bolus, J. S. African Bot. 29: 49. 1963; Hartmann, Bradleya 16: 72. 1998; Hartmann, Ill. Handb. Succ. Pl. Aizoaceae 2: 189. 2001; Klak in Snijman, Pl. Gr. C. F.R. 2: 219. 2013.—TYPE: SOUTH AFRICA. Northern Cape Province: Springbok (2917) between Doornpoort and Brakfontein [2917], Jul 1927, *Pillans 5794* (holotype: BOL!).

Ruschia conjuncta L.Bolus, Notes Mesembryanthemum 2: 239. 1931. *Octopoma conjunctum* (L.Bolus) L.Bolus J. S. African Bot. 32: 128. 1966. *Type:* South Africa, Northern Cape Province: Rietkloof, Knersvlakte [3018DC], Oct 1930, *Matthews 19381* (holotype: BOL!).

Sparse low-growing decumbent to upright shrub, to 100 mm tall. Branches to 7 mm in diameter; upper branches brown; leaves crowded towards tips of branches, old leaves not remaining on the branches. Leaves triquetrous, lanceolate in outline; 8.0–20.0 × 1.5–5 mm; leaf pairs fused for ¼ of length; mucro prominent; slightly velvety; green. Flowers solitary; on central primary axis to 55 mm long, at least three times longer than length of capsule, bracteoles persistent, present more than ½ way down axis; spines absent; filamentous staminodes few to many, forming an incomplete to complete series around the stamens. Fruit 8-locular; top prominently convex, base cup-shaped, resulting in capsule appearing subglobose; ca. 6.0 × 6.0 mm; closing rodlet conspicuous, protruding distally; valve wings absent. Figure 12.

Diagnostic Characters—*Schlechteranthus connatus* may be confused with *S. abruptus* as they share a similar leaf shape and size, but is distinguished by the longer central primary axis, which is at least three times longer than the capsule (Fig. 2C), and bracteoles persistent, present more than half way down the axis (primary axis equal to length of capsule and bracteole mostly at base of capsule in *S. abruptus*). The capsule itself is also markedly globose in *S. connatus* (Figs. 2C, 7B), as a result of the subglobose base and convex top, whereas in *S. abruptus* the base of the capsule is funnel-shaped and the top not prominently rounded. *Schlechteranthus connatus* also lacks the prominently velvety leaf surface of *S. abruptus,* and is only slightly velvety.

Distribution and Ecology—*Schlechteranthus connatus* is widespread in northern Namaqualand extending from the Richtersveld southwards into the Knersvlakte (Fig. 8E). It is generally found on rocky soil associated with gneiss or quartz and sometimes occurs in red loamy sand. The species flowers from September to October.

Additional Specimens Examined—South Africa. NORTHERN CAPE: 2816 (Oranjemund): Richtersveld, five km westwards along Holgat river from Eksteenfontein turn-off, along Kuboos-Lekkersing road (–DD), *Klak 1504* (BOL). 2817 (Vioolsdrif): Six km south of Eksteenfontein (–CC), *Bruyns 9106* (BOL); Eksteenfontein, Pypfontein (–CC), *Bruyns 9132* (BOL); Richtersveld, 15 km east of Eksteenfontein, on road to Vioolsdrif (–CD), *Klak 1513* (BOL); Klipbokberge, Richtersveld (–CD), *Stellenbosch University Gardens 9289* (BOL); Doornriver, Richtersveld, Little Namaqualand (–CD), *Hort. Stellenbosch 8792* (BOL). 2917 (Springbok): 24 km north of Grasvlakte on road to Eksteenfontein (–AB), *Bruyns 9104* (BOL); 19 km south of Port Nolloth on road to Grootmis, Kwagganap River (–AC), *Klak 2397* (BOL); South-East of Naroegas (–AD), *Klak 1499* (BOL); between Bulletrap and the N7 (–BD), *Powell 10* (NBG); Two km towards Nigramoep (–DA), *Klak 927* (BOL); Springbok, Drie Draai (–DD), *Bruyns 9152* (BOL). 3017 (Hondeklipbaai): south of Kran se vlei, Hondeklip Bay (–AD), *Klak 899* (BOL); Grootvleipass, near Kamieskroon (–BB), *Klak 1853* (BOL); ca. 1 km north of Kamieskroon hotel (–BB), *Klak 1871* (BOL); Six miles south of Garies, Namaqualand (–DD), *Acocks 15102* (BOL); Garies District, farm Tweerivier (–DD), *Klak 2410* (BOL); Garies District., farm Tweerivier, near Groenrivier (–DD), *Klak 2403* (BOL). 3018 (Kamiesberg): Kamiesberg, northern slopes of Weeskindpeak, 8 km southwest of Leliefontein (–AC), *Helme 3226* (BOL); Klipbok, Knersvlakte (–CB), *Bruyns 5372* (BOL); Garies District, Farm Keurbos (–CB), *Klak 1263* (BOL); Rietkloof, Knersvlakte (–DC), *National Geographic-IPC Tour 119* (BOL); Garies, farm Stofkrall (–DD), *Klak 1525* (BOL). 3019 (Loeriesfontein): Loeriesfontein, entrance to Donkiedam (–CC), *Bruyns 10859* (BOL). WESTERN CAPE: 3118 (Vanrhynsdorp): Komkans Bitterfontein (–AA), *Bruyns 12806* (BOL); Near Goerap, along road to Rietfontein (–AA), *Klak 2299* (BOL); Knersvlakte, Kareeberg, on farm Kareeberg (–BA), *Klak 2284b* (BOL); Knersvlakte, Vanrhynsdorp div., farm Arizona (–BC), *Klak 632* (BOL); Knersvlakte, Rooiberg, S of Nuwerus (–BC), *Desmet 1805* (NBG) Farm Quaggaskop, Vanrhynsdorp (–BC), *Klak*

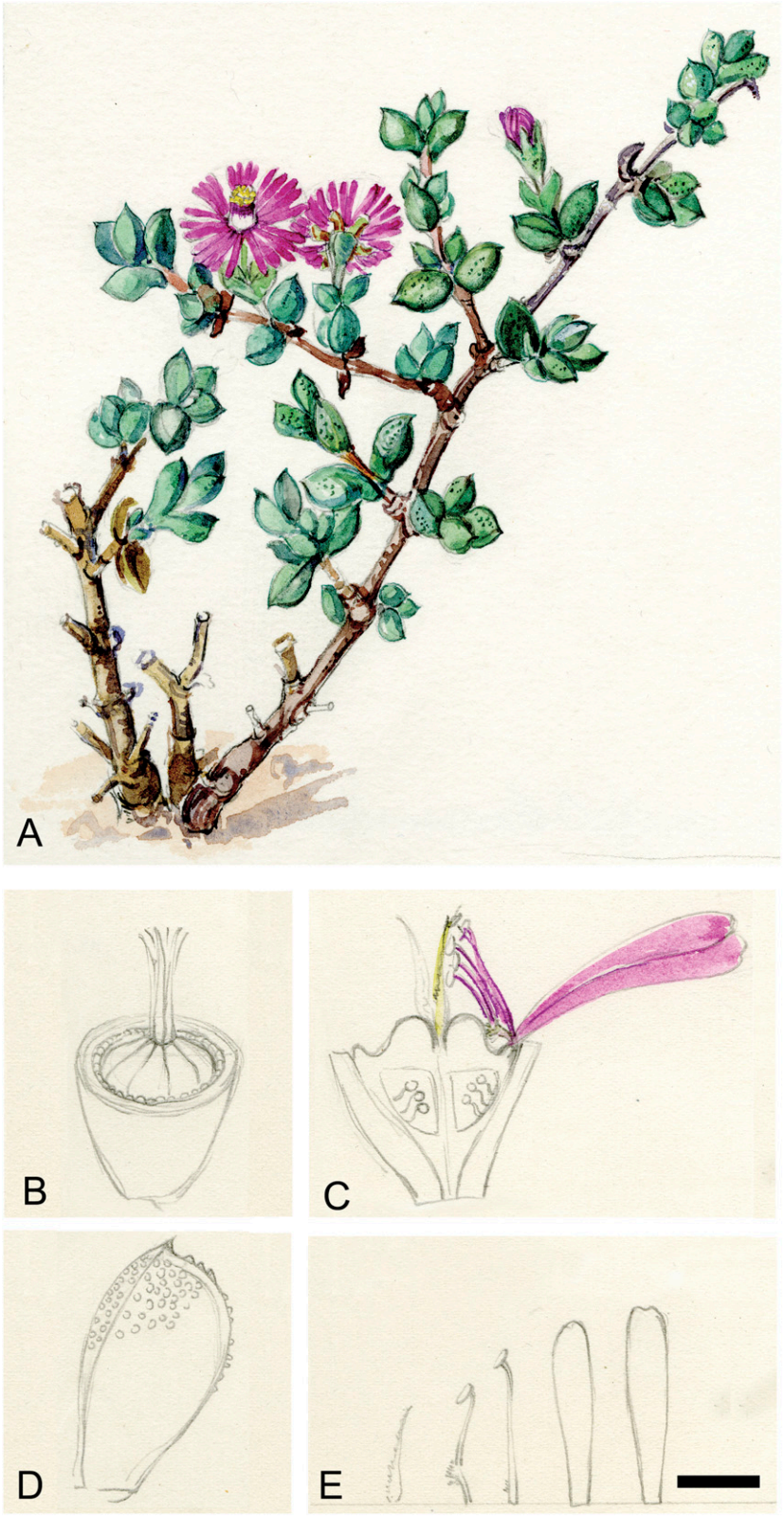

FIG. 11. Drawing of type material for *S. subglobosus* (*Pillans 5844* (BOL)). A. Habit and leaf arrangement of *S. subglobosus*. B. Flower with all staminodes removed showing the nectaries arranged in a ring. C. Longitudinal section of flower showing the arrangement of the style, stamens, and petaloid staminodes. D. Enlarged leaf of *S. subglobosus* illustrating the dome-shaped epidermal cells. E. Floral components illustrating the style, stamens, filamentous staminodes, and petaloid staminodes. Scale: A = 10 mm; B–C = 2 mm; D–E = 2.5 mm. Artist B. Carter.

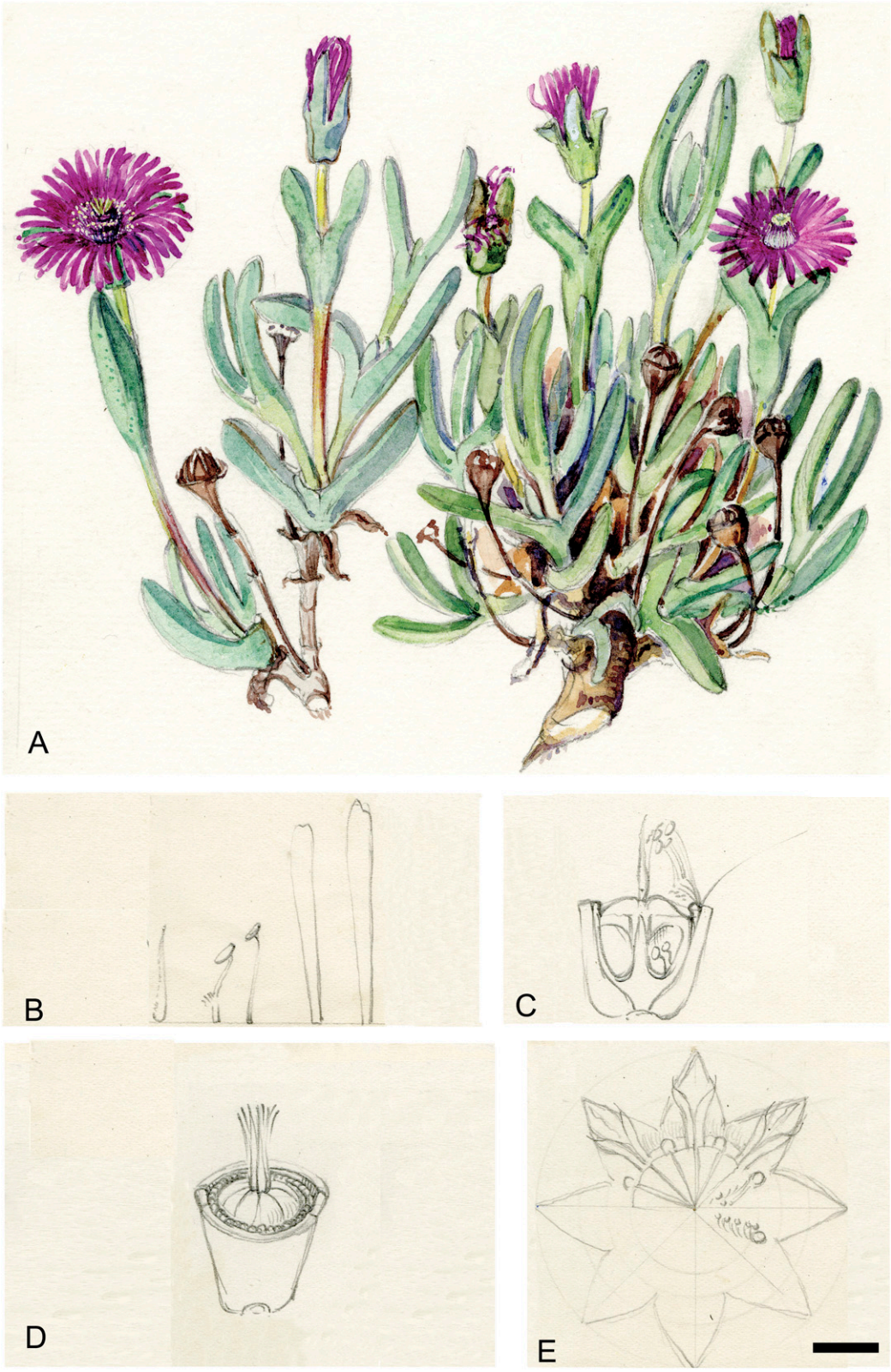

FIG. 12. Drawing of type material for *S. connatus* (*Pillans 5794* (BOL)). A. Habit and leaf arrangement of *S. subglobosus*. B. Floral components illustrating the style, stamens, filamentous staminodes, and petaloid staminodes. C. Longitudinal section of flower showing the arrangement of the style, stamens, and petaloid staminodes. D. Flower with all staminodes removed showing the nectaries arranged in a ring. E. Open capsule with small closing bodies and complete covering membranes. Scale: A = 10 mm; B–D = 3.3 mm; E = 2.5 mm. Artist B. Carter.

1452 (BOL); Zandkraal, Vanrhynsdorp (–DB), *Acocks 14859* (BOL). Precise locality unknown: Between Garies and Kamieskroon, *L. Bolus 24220* (BOL).

6. SCHLECHTERANTHUS SPINESCENS (L. Bolus) R. F. Powell, Taxon 65: 259. 2016. *Ruschia spinescens* L. Bolus, Notes Mesembryanthemum 2: 175. 1930. *Arenifera spinescens* (L. Bolus) H. E. K. Hartmann, Bradleya 14: 38. 1996; Hartmann, Ill. Handb. Succ. Pl. Aizoaceae 1: 69. 2001; Buys in Snijman, Pl. Gr. C.F.R. 2: 178. 2013.—TYPE: SOUTH AFRICA. Western Cape Province: Whitehill near Matjiesfontein, Laingsburg [3320BC], Oct 1929, *Compton sub BOL 19081* (holotype: BOL!).

Sparse upright to spreading shrub, to 200 mm tall. Branches to 8 mm in diameter; upper branches often whitish to grey; leaves crowded towards tips of branches, old leaves not remaining on the branches. Leaves triquetrous, lanceolate in outline, 3.0–13.0 × 2.0–3.0 mm, leaf pairs fused for a ⅙ to a ⅕ of the length; mucro prominent; slightly velvety; deep green. Flowers in simple cymose inflorescence; central primary axis to 15 mm long, equal proportionally to capsule length, bracteoles caducous; spines present, arranged in simple cyme, formed by old pedicels where capsules have fallen off, held at obtuse angle, blunt, mostly elevated above terminal leaf pair, but also present below terminal leaf pair; filamentous staminodes many, forming a complete series around the stamens. Fruit 7- to 8-locular; top convex, base narrowly funnel-shaped, 2.5 × 2.0 mm; closing rodlet conspicuous; valve wings narrow, up to ⅓ width of valve. Figure 13.

Diagnostic Characters—*Schlechteranthus spinescens* is most similar to *S. pungens* as they have similar leaf shapes in outline (Fig. 1B, E) and overlap in distribution (Fig. 8F, G). However, *S. spinescens* can be easily recognised by the different arrangement of spines and spine formation. In *S. spinescens*, the spines are arranged in a simple cyme with blunt spines derived from old pedicels where the capsules have fallen off (Fig. 3A), while in *S. pungens* the spines are arranged in a compound cyme, with sharp spines derived from aborted axillary buds (Fig. 3C).

Distribution and Ecology—This species occurs in the Western Cape and Namaqualand, and is the only species in the subgenus to extend into the Little Karoo towards Uniondale (Fig. 8F). Plants grow in a range of soils, including quartzite, shale, and sand, but generally in shallow soils. This species flowers in October.

Additional Specimens Examined—South Africa. NORTHERN CAPE: 3018 (Kamiesberg): Namaqualand, Varsche River Extension, Vanrhynsdorp, quartz lag gravel patch between Preekstoelkop and N7 (–BB), *Desmet and Ellis 1345* (NBG); 35 miles west of Loeriesfontein (–DD), *Lavis 162* (BOL). WESTERN CAPE: 3218 (Clanwilliam): On sand flat near Calvinia road, about two miles out of Clanwilliam (–BA), *Galpin s.n.* (BOL); Namaqualand, Wolwenes, Knersvlakte, Heuweltjie veld to west of N7 (–BC), *Desmet and Ellis 1498* (BOL); Rondegat, Clanwilliam (–BD), *Esterhuysen s.n.* (BOL). 3219 (Wuppertal): Syfering, west of Elandsvlei (–AD), *Klak 1370* (BOL); Cederberg, farm Ramkraal (–AD), *Klak 953* (BOL); Skitterykloof (–DC), *Klak 2424* (BOL). 3320 (Montagu): Six km west of Matjiesfontein, farm Aasvoelbos (–AB), *Klak 1685* (BOL). 3323 (Willowmore): along road to Willowmore, Uniondale (–DA), *Fourcade 4370* (BOL).

7. SCHLECHTERANTHUS PUNGENS (H. E. K. Hartmann) R. F. Powell, Taxon 65: 259. 2016. *Arenifera pungens* H. E. K. Hartmann, Bradleya 14: 37. 1996; Hartmann, Ill. Handb. Succ. Pl. Aizoaceae 1: 69. 2001; Buys in Snijman, Pl. Gr. C.F.R. 2: 178. 2013.—TYPE: SOUTH AFRICA. Western Cape Province: Vanrhynsdorp [3118], Mar 1988, *Hartmann, Dehn, Gölling, Rust and Stüber 25739* (holotype: HBG–image!).

Large upright to spreading shrub, often dome-shaped, to 400 mm tall. Branches to 4 mm in diameter; upper branches white; leaves crowded towards tips of branches, old leaves not remaining on the branches. Leaves triquetrous, mostly oblong, sometimes ovoid in outline, 3.0–6.0 × 2.0–2.5 mm, leaf pairs fused for ¼ to ⅓ of length; mucro prominent; slightly velvety; dark green. Flowers in compound cymose inflorescences; central primary axis to 13 mm long, equal proportionally to capsule length, bracteoles caducous; spines present, arranged in compound cyme, secondary axes with spines arranged in compound cyme, tertiary axes with spines arranged in simple cyme; spines derived from aborted axillary buds and less frequently from old pedicels; spines branching at an angle $< 45°$, sharp, elevated above terminal leaf pair; filamentous staminodes few to many, forming an incomplete to complete series around stamens. Fruit 7- to 8-locular; top convex, base funnel-shaped, 2.0–3.0 × 4.0–4.5 mm; closing rodlet conspicuous; valve wings very narrow, up to ⅓ width of valve.

Diagnostic Characters—*Schlechteranthus pungens* is most similar to *S. stylosus,* as both species are large shrubs (up to 400 mm tall) with spines derived from aborted axillary buds (Fig. 3), but *S. pungens* differs with longer (3.0–6.0 mm) mostly oblong leaves (Fig. 1E) in outline (shorter (1.5–2.0 mm) and ovoid (Fig. 1H) in *S. stylosus*). Although the spines are derived in a similar manner to *S. stylosus*, the spines in *S. pungens* are arranged in a compound cyme on the secondary axes (Fig. 3C), while in *S. stylosus* the spines are arranged in a simple cyme on the secondary axes (Fig. 3B).

Schlechteranthus pungens and *S. spinescens* share a similar leaf shape (Fig. 1B, E) and their distributions overlap (Fig. 8F, G). However, *S. pungens* is distinguished by the spines that are arranged in a compound cyme and are derived from aborted axillary buds (Fig. 3C) (spines arranged in simple cyme and derived from old pedicels where capsules have fallen off in *S. spinescens* (Fig. 3D)).

Distribution and Ecology—This species has a wide distribution, occurring from Hondeklipbaai southwards to Calvinia (Fig. 8G) and is found on low slopes, growing in very rocky soils. *Schlechteranthus pungens* flowers in September.

Additional Specimens Examined—South Africa. NORTHERN CAPE: 2817 (Vioolsdrif): Namaqualand District, Richtersveld, south-west of Helskloof Valley between hills where road splits (–CD), *Burgoyne 11105* (PRE). 2917 (Springbok): Steinkopf, west of Steinkopf (–BC), *Klak 925* (BOL); between Bulletrap and the N7 (–BD), *Powell 12* (NBG); Namaqualand District, six km on second Komaggas road W of Springbok (–CD), *Burgoyne 11235* (PRE). 2918 (Gamoep): 26 km east of Springbok, farm Smorenskadu (–CA), *Klak 2358* (BOL). 3017 (Hondeklipbaai): Namaqualand, Kookfontein, north-northeast of Soebatsfontein (–BA), *Desmet 400* (NBG). 3018 (Kamiesberg): 23 miles east of Kliprand (–DA), *Stayner sub KGB 1208/62* (BOL); 35 miles west of Loeriesfontein, Calvinia (–DD), *Stayner 1970* (BOL). 3019 (Loeriesfontein): Loeriesfontein, Donkiedam Farm (–CC), *Klak 1285* (BOL); Loeriesfontein District, Donkiedam Farm (–CC), *Klak 1291* (BOL). WESTERN CAPE: 3118 (Vanryhnsdorp): Bitterfontein, Komkans (–AA), *Bruyns 12804* (BOL); Nuwerus, on farm Aurora (–AB), *Bruyns 7583* (BOL); Two km south of Nuwerus (–AB), *Bruyns 9093* (BOL); Namaqualand, Farm Moedverloor 208 (–AD), *Desmet and Ellis 1459* (NBG); Namaqualand, Droesand, Rooipan, Knersvlakte (–BC), *Desmet and Ellis 1508* (NBG); Zout Rivier Bridge (–BC), *Matthews sub NBG 282/38* (BOL); Knersvlakte, farm Arizona, behind old farmhouse shed (–BC), *Klak 1450* (BOL). 3119 (Calvinia): Blaukrantz pass (–DB), *Pearson 3909* (BOL); South-western corner of Elandsberg (–DC), *Bruyns 9180* (BOL). 3219 (Wuppertal): Bossiesberg, Calvinia (–BA), *Bruyns 7568* (BOL).

8. SCHLECHTERANTHUS STYLOSUS (L. Bolus) R. F. Powell, Taxon: 259. 2016. *Ruschia stylosa* L. Bolus, Notes Mesembryanthemum 1: 144. 1928. *Mesembryanthemum styliferum* (L. Bolus) N. E. Br., Gard. Chron. 3: 32. 1930, nom. nov. non *M. stylosum* (L. Bolus) N. E. Br. *Eberlanzia stylosa* (L. Bolus) L. Bolus, Notes Mesembryanthemum 3: 387. 1958. *Arenifera*

FIG. 13. Drawing of type material for *S. spinescens* (*Compton sub BOL 19081* (BOL)). A. Habit and leaf arrangement of *S. spinescens*. B. Enlarged flower in bud. C. Enlarged leaf, showing the fused opposite leaf pairs. D. Open capsule with small closing bodies and complete covering membranes. E. Flower with all staminodes removed showing the nectaries arranged in a ring. F. Longitudinal section of flower showing the arrangement of the style, stamens, and petaloid staminodes. G. Floral components illustrating the style, stamens, filamentous staminodes, and petaloid staminodes. Scale: A = 10 mm; B–C = 5 mm; D = 2.5 mm; E = 3.3 mm; F–G = 2 mm. Artist B. Carter.

stylosa (L. Bolus) H. E. K. Hartmann, Bradleya 14: 38. 1996; Hartmann, Ill. Handb. Succ. Pl. Aizoaceae 1: 70. 2001; Buys in Snijman, Pl. Gr. C.F.R. 2: 178. 2013.—TYPE: SOUTH AFRICA. Northern Cape Province: Hills NE of Arris Drift [2816DA], Jul 1927, *Pillans 5742* (holotype: BOL!).

Ruschia armata L. Bolus, Notes Mesembryanthemum 1: 145. 1928. *Mesembryanthemum armatum* (L. Bolus) N. E. Br., Gard. Chron. 3: 32. 1930. *Eberlanzia armata* (L. Bolus) L. Bolus, Notes Mesembryanthemum 3: 387. 1958.—TYPE: SOUTH AFRICA. Northern Cape Province: between Brakfontein and Oograbies Mt., Little Namaqualand [2917AA], Oct 1926, *Pillans 5789* (holotype: BOL!).

Dense spreading shrub, often dome-shaped, to 400 mm tall. Branches to 7 mm in diameter; upper branches brown; leaves crowded towards tips of branches, old leaves not remaining on the branches. Leaves triquetrous, ovoid in outline, 1.5–2.0 mm × 2.0–2.5 mm, leaf pairs fused for ⅓ to ½ of length; mucro prominent; slightly velvety; yellow-green to deep green. Flowers in compound cymose inflorescences; central primary axis to 8 mm long, equal proportionally to capsule length, bracteoles caducous; spines present, arranged in compound cyme, secondary axes with spines arranged in simple cyme; spines derived from aborted axillary buds and less frequently from old pedicels; spines branching at ± 45°, sharp, elevated above terminal leaf pair; filamentous staminodes few to absent, forming an incomplete series around the stamens. Fruit 7- to 9-locular; top convex, base funnel-shaped, ca. 4.0 × 3.0 mm; closing rodlet conspicuous; valve wings absent. Figure 14.

Diagnostic Characters—*Schlechteranthus stylosus* may be confused with *S. parvus* as they have a similar leaf size with a high degree of fusion (Fig. 1H, I) and the same spine arrangement (Fig. 3B). However, *S. stylosus* can be distinguished by the few filamentous staminodes which do not form a complete series around the stamens (many filamentous staminodes which form a complete series in *S. parvus*). The leaves are also ovoid in outline in *S. stylosus* (subglobose in *S. parvus*) with a very prominent mucro (mucro obscure in *S. parvus*). *Schlechteranthus stylosus* is also typically a larger shrub (up to 400 mm in height) compared to *S. parvus* (up to 150 mm in height).

Schlechteranthus stylosus may be confused with *S. pungens*, as both species are large shrubs with spines derived from aborted axillary buds (Fig. 3), but *S. stylosus* is distinguished by the ovoid leaves in outline (mostly oblong in *S. pungens*) and spines arranged in a simple cyme on the secondary axes (Fig. 3B) (spines arranged in compound cyme on secondary axes in *S. pungens* (Fig. 3C)).

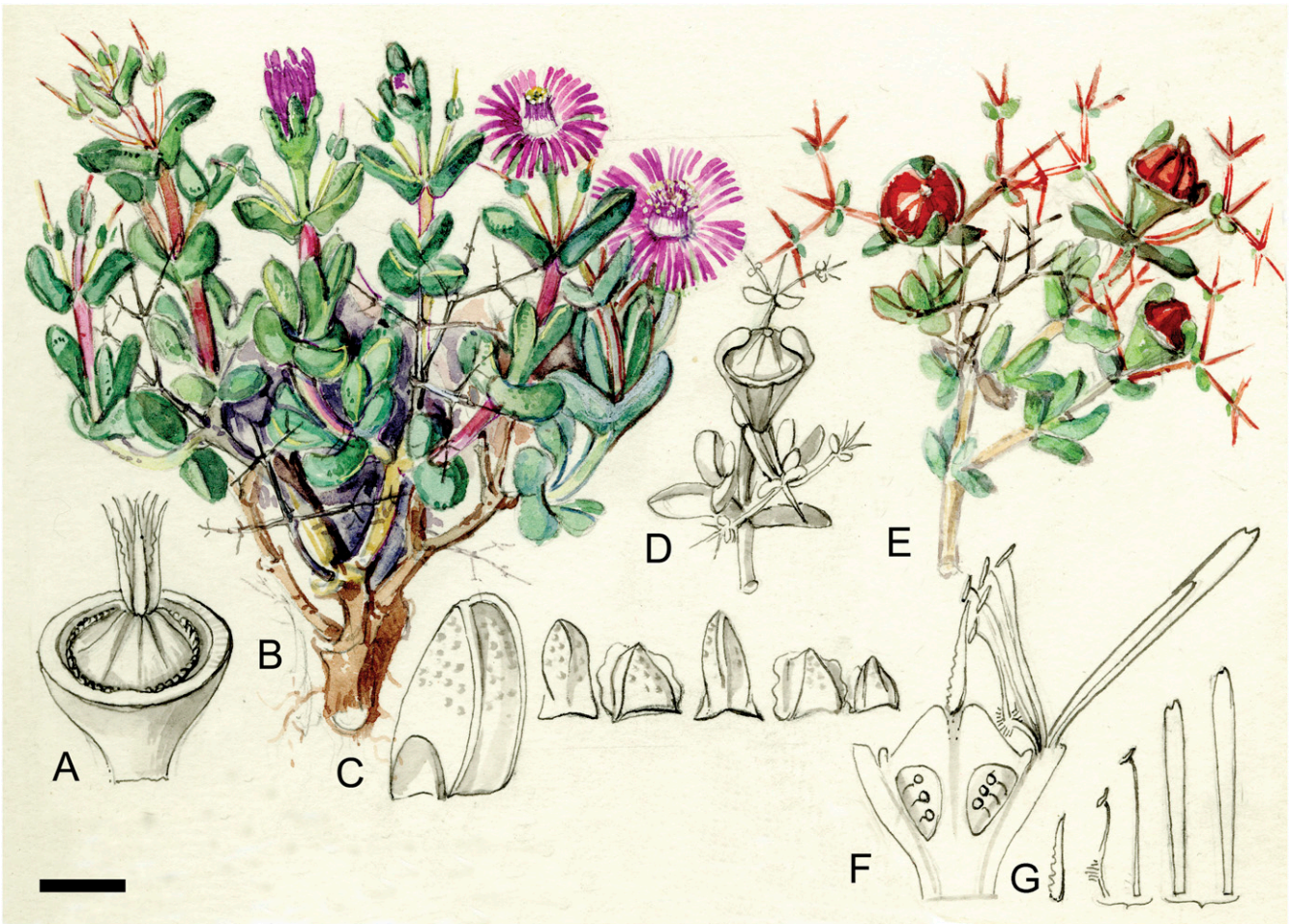

FIG. 14. Drawing of type material for *S. stylosus* (*Pillans 5789* (BOL)). A. Flower with all staminodes removed showing the nectaries arranged in a ring. B. Habit and leaf arrangement of *S. stylosus*. C. Enlarged leaf and components of calyx. D. Spine development from aborted axillary buds and cymose inflorescence. E. New growth with early stages of development of spines and capsules. F. Longitudinal section of flower showing the arrangement of the style, stamens, and petaloid staminodes. G. Floral components illustrating the style, stamens, filamentous staminodes, and petaloid staminodes. Scale: A = 2.5 mm; B = 10 mm; C = 5 mm; D–E = 10 mm; F–G = 3.3 mm. Artist M. Page.

Distribution and Ecology—*Schlechteranthus stylosus* is distributed widely in northern Namaqualand, occurring from the Richtersveld to just south of Springbok (Fig. 8H). The species is found solely on rocky quartzite soils, generally on flats, but sometimes found on the lower slopes of hills. This species flowers from August to September.

Additional Specimens Examined—South Africa. NORTHERN CAPE: 2816 (Oranjemund): Arris drift (–DA), *Hall sub NBG 116/53* (BOL); Sendelings Drift (–DB), *Hall s.n.* (BOL). 2817 (Vioolsdrif): On pass up the Vandersterberg towards Koeskopfontein (–AC), *Powell 75* (NBG); Grasdrif, Richtersveld (–AD), *Williamson 3267* (BOL); Richtersveld between Helskloof se Hek and Eksteenfontein (–CA), *Williamson 3304* (BOL); Gelykberg, Richtersveld (–CA), *Hall s.n.* (BOL); Lekkersing, five km north of Uitspanpoort (–CC), *Bruyns 9123* (BOL); Cape Prov. Nama'land, Richtersveld, Rooiberg middlemost (–CD), *NBG 423/61* (BOL); Rooiberg, Richtersveld (–CD), *NBG 432/62* (BOL); ± 15 km north of Kosies (–DC), *Bruyns 9252*. 2917 (Springbok): About 12 km W of Bulletrap (–BC), *Klak 1255* (BOL); Springbok area on road to Komaggas; ± five km from Namaqua National Park gate (–CD), *Burgoyne 11799* (PRE).

9. **Schlechteranthus parvus** R. F. Powell & Klak, sp. nov.—TYPE: SOUTH AFRICA. Northern Cape Province: Komaggas, alongside road between Koingnaas and Komaggas [3017AA], 15 May 2014, *Powell, Klak and Magee 41* (holotype: NBG!; isotype: BOL!).

Small erect to spreading dome-shaped shrublet to 150 mm tall. Branches to 4 mm thick; upper branches brown; leaves crowded towards tips of branches, old leaves not remaining on the branches. Leaves triquetrous, globose to subglobose in outline, 2.0–4.0 × 1.5–2.0 mm, leaf pairs fused for ¾ of the length; mucro obscure; slightly velvety; yellow-green. Flowers in compound cymose inflorescences; central primary axis to 4 mm long, equal proportionally to capsule length, bracteoles caducous; spines present, arranged in compound cyme, secondary axes with spines arranged in simple cyme; spines derived from aborted axillary buds and less frequently from old pedicels; spines branching at ± 45°, sharp, elevated above terminal leaf pair; filamentous staminodes many, forming a complete series around the stamens. Fruit 7- to 8-locular; top convex, base funnel-shaped, ± 3.9 × 4.7 mm; closing rodlet conspicuous; valve wings absent. Figure 6.

Etymology—The species epithet refers to the small nature of the shrub and its leaves.

Diagnostic Characters—*Schlechteranthus parvus* is the smallest among the spiny species in subgenus *Microphyllus* and only reaches 150 mm in height. It is most similar to *S. stylosus* as they share small leaves with a high degree of fusion (Fig. 1H, I) and the same spine arrangement, with spines derived from aborted axillary buds (Fig. 3B). However, *S. stylosus* is a much larger shrub and reaches 400 mm in height.

The new species is distinguished by its many filamentous staminodes, which form a complete series around the stamens (Fig. 6A) (filamentous staminodes in *S. stylosus* are few or absent, forming an incomplete series around the stamens). The leaf shape can also be used to distinguish the species, with *S. parvus* possessing leaves subglobose in outline without a prominent mucro (leaves ovoid with a very prominent mucro in *S. stylosus*). *Schlechteranthus parvus* shares a globose leaf shape with *S. subglobosus* (Fig. 1D, I) but can be distinguished by the highly fused leaves, the obscure mucro (leaf pairs fused for a third of the length and mucro very prominent in *S. subglobosus*), and also by the flowers arranged in a compound, spiny, cymose inflorescence (flowers solitary in *S. subglobosus*).

Distribution and Ecology—*Schlechteranthus parvus* occurs along the western coast of Namaqualand (Fig. 8I), associated with quartz patches. Although the species has not been collected in flower, the species flowered in September in the greenhouse at Kirstenbosch.

Additional Specimens Examined—South Africa. NORTHERN CAPE: 2917 (Springbok): 19 km south of Port Nolloth on road to Grootmis, Kwaggakop River, east of road on low hillocks (–AC), *Klak 2387* (BOL); west of Wolfberg mine, along road from Kleinsee to Springbok (–CB), *Klak 2400* (BOL). **3017 (Hondeklipbaai):** Komaggas, alongside road between Koingnaas and Komaggas (–AA), *Klak 2362* (BOL).

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APPENDIX 1. Morphological characters and character states coded in the morphological cladistics analysis for species of subgenus *Microphyllus.* 1) Locule number: 10–12 locules = 0; 7–9 locules = 1. 2) Closing bodies: large, blocking three quarters of the locule = 0; small, blocking a third of the locule = 1. 3) Inflorescence: flowers solitary = 0; cymose=1. 4) Bracteole: persistent = 0; caducous = 1. 5) Pedicels becoming spinescent: absent = 0; present = 1. 6) Spines derived from aborted buds: absent = 0; present = 1. 7) Habit: caespitose = 0; shrubby = 1. 8) Flower color: yellow = 0; magenta = 1.