

Taxonomy of *Exochaenium* and *Lagenias*: Two Resurrected Genera of Tribe Exaceae (Gentianaceae)

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Abstract—Morphological and molecular evidence has recently revealed the paraphyly of *Sebaea* (Gentianaceae: Exaceae), and support the establishment of three genera corresponding to highly supported clades. Consequently, the reinstatement of both *Exochaenium* and *Lagenias* as genera segregated from *Sebaea* is proposed here. *Exochaenium* consists of 22 species distributed in tropical continental Africa that are characterized by papillate stigmas and cubical seeds with star-shaped testa cells. *Lagenias* is a monotypic genus endemic to the Western Cape Province of South Africa, which differs from *Exochaenium* and *Sebaea* by its medifixed anthers, the insertion of the filaments at the base of the corolla tube, and cubical seeds with polygonal testa cells. The synapomorphies of *Sebaea* s. s. are the presence of secondary stigmas along the style and seeds with rectangular testa cells arranged in parallel rows. Differences with the other genera of tribe Exaceae (*Exacum*, *Gentianothamnus*, *Klackenbergia*, *Ornichia*, and *Tachiadenus*) are discussed. In addition, diagnostic characters as well as keys to the genera of the tribe and species of *Exochaenium* are provided. To account for the new circumscription of *Exochaenium*, 12 new combinations are also published here (*Exochaenium alatum*, *E. caudatum*, *E. clavatum*, *E. dimidiatum*, *E. fernandesianum*, *E. hockii*, *E. lineariforme*, *E. macropterum*, *E. oliganthum*, *E. perparvum*, *E. rotundifolium*, and *E. wildemanianum*).

Keywords—Africa, *Belmontia*, classification, floral morphology, *Parrasia*, *Sebaea*.

The tribe Exaceae in its current circumscription (Struwe et al. 2002; Klackenberg 2006; Kissling et al. 2009a) includes ca. 180 species in six genera: *Exacum* L. (including *Cotylanthera* Blume; Klackenberg 2006), *Gentianothamnus* Humbert, *Klackenbergia* Kissling, *Ornichia* Klack., *Sebaea* Sol. ex R. Br. and *Tachiadenus* Griseb. The Exaceae differ from other tribes in the gentian family by a main synapomorphy: the shape of petal epidermal cells that are rounded and convex as opposed to elongated and flat (Klackenberg 1985, 2002). Exaceae may also be distinguished by a bilocular ovary (although *Tachiadenus* presents a “pseudobilocular ovary”, the placenta stand together though not fused forming a “partition”, at least when young, Klackenberg 1985, 1987) and bilocular ovaries are also present in close relatives of Gentianaceae (e.g. Rubiaceae and Loganiaceae). Recently, a molecular phylogenetic study of Exaceae (Kissling et al. 2009c) revealed the paraphyly of the genus *Sebaea*, and supports its segregation into two clades and a monospecific lineage (Fig. 1).

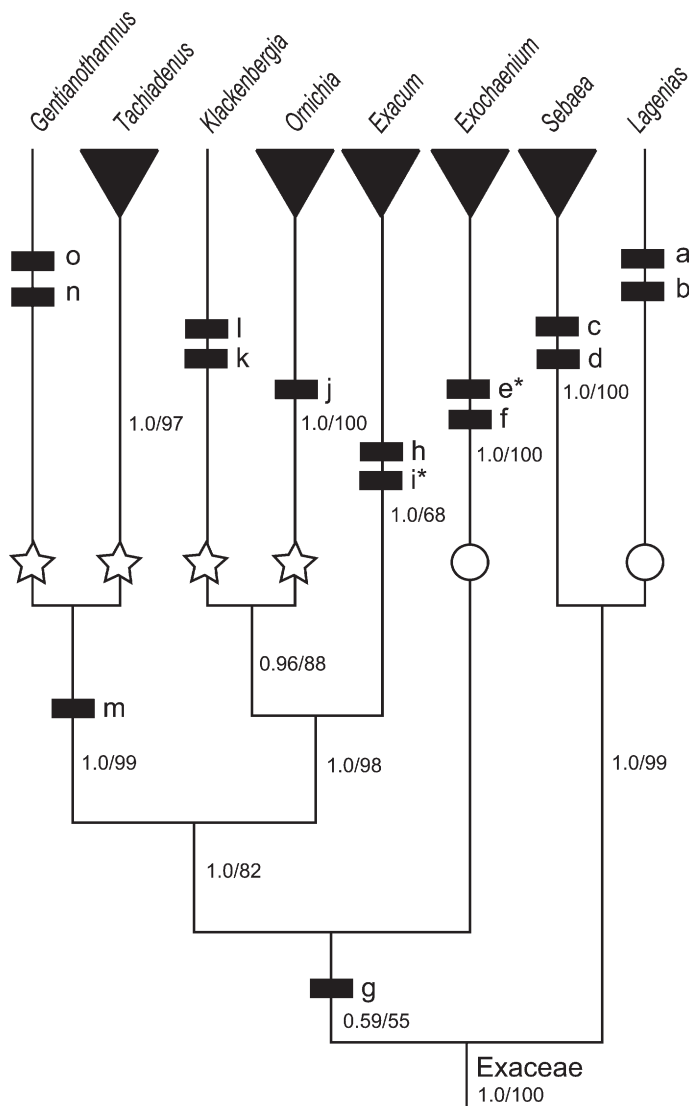
The first clade (*Sebaea* s. s.) is supported by two morphological synapomorphies: (i) the arrangement of seed testa cells in rows, and (ii) the presence of a secondary stigma along the style (i.e. diplostigmaty; Marloth 1909; Kissling et al. 2009b). *Sebaea* s. s. contains mainly South African species, some tropical African species, two Malagasy species, two Australian-New Zealand species and *S. microphylla* (Edgew.) Knobl., widespread in the Paleotropics. The second clade (*Exochaenium* Griesb.) comprises only tropical African species and is characterized by: (i) the papillate texture of the stigma and its linear to clavate shape, and (ii) in most of the species, the presence of a stylar polymorphism (short-styled vs. long-styled flowers). Finally, the third clade, a monospecific lineage, (*Lagenias* E. Mey.) is characterized by several morphological autapomorphies such as medifixed anthers, polygonal testa cells of the seeds, and a more or less crassulescent habit, and is endemic to the Western Cape.

The paraphyly of *Sebaea* was surprising for a group that has been regarded as a morphologically well-delimited assemblage by recent authors (e.g. Marais and Verdoorn 1963; Taylor 1963; Boutique 1972; Klackenberg 1990; Paiva and Nogueira 1990a, 1990b; Sileshi Nemomissa 2002). Nonetheless, in earlier works (Brown 1810; Rafinesque 1837; Meyer 1838; Grisebach 1845), some genera were described as segregates of *Sebaea* s. l. including *Belmontia* E. Mey., *Exochaenium*, *Lagenias*, and *Parrasia* Raf.

The first clade (*Sebaea* s. s.), in addition to containing the type species of *Sebaea* (*S. ovata* (Labill.) R. Br.), also contains the type species of *Belmontia* (*S. exacoides* (L.) Schinz). The second clade contains the type species of *Exochaenium* (*E. grande* (E. Mey.) Griseb.), while the type species of *Lagenias* (*L. pusillus* (Eckl. ex Cham.) E. Mey.) belongs to the monospecific lineage. Thus, the reinstatement of *Exochaenium* Griesb. and *Lagenias* E. Mey. is proposed in this article.

Taxonomic History of *Sebaea* s. l.—Solander described the genus *Sebaea* in a manuscript that was published by Brown (1810) and dedicated the genus to the Amsterdam-based pharmacist Albertus Seba (1665–1736). Solander transferred three yellow-flowered South African *Exacum* species, *Exacum albens*, *E. aureum*, and *E. cordatum* (= *S. exacoides*) and one Australian species, the type species, *E. ovatum*, to the new genus *Sebaea*. He based the new genus on the anther opening mechanism (longitudinal slits for *Sebaea* versus pores for *Exacum*), the form of the style (straight for *Sebaea* versus bent downward for *Exacum*), and the form of the stigma (“undivided” for *Exacum* versus bilobed for *Sebaea*).

Twenty-seven years later, Rafinesque (1837) described the genus *Parrasia* for the single species *S. cordata* (= *S. exacoides*), but *Parrasia* was not acknowledged by later authors. Only one year later, Meyer (1838) split *Sebaea* s. l. into three genera, namely *Belmontia*, *Sebaea* s. s. and *Lagenias*, transferring three species (*S. grandis*, *S. cordata* [= *S. exacoides*] and *S. spathulata*



Synapomorphies

- a. medifix anthers
- b. polygonal testa cells
- c. secondary stigma
- d. rectangular testa cells arranged in row
- e. stylar length polymorphism
- f. papillate stigma
- g. star-shaped testa cells
- h. anthers opening by pores
- i. enantiostyly
- j. hairy plants
- k. raceme-like inflorescence
- l. bracteoles much longer than the flower
- m. pseudo-bilocular ovary
- n. shrubby plants
- o. five-lobed disk below the ovary

Distribution

○: Endemic to continental Africa (*Exochaenium* and *Lagenias*)

☆: Endemic to Madagascar: (*Gentianothamnus*, *Klackenbergia*, *Ornichia* and *Tachiadenus*)

Exacum: Paleotropics and Australia

Sebaea: Paleotropics, Australia and Cape Floristic Region

FIG. 1. Simplified phylogenetic relationship within the tribe Exaceae (adapted from Kissling et al. 2009c), showing the synapomorphies supporting the different clades, as well as the distribution of the genera. Branch support values are posterior probabilities and bootstrap values (reported from Kissling et al. 2009c).

(E. Mey.) Steud.) to *Belmontia*, and *Sebaea pusilla* Eckl. ex Cham. to *Lagenias* (discussed below). *Sebaea* was distinguished from *Belmontia* by having: (i) exerted anthers becoming recurved, and (ii) capitate stigmas with a secondary division and eventually becoming bilobed ("stigmatum capitato-didymo"). It is interesting to note that *S. exacoides* (which was placed in *Belmontia*) clearly presents, when mature, a bilobed stigma. However, when the flower is at an early stage of development, the immature part (which will develop into a mature bilobed stigma) appears somewhat linear to clavate. The name *Belmontia* (1838) is conserved against its homotypic synonym *Parrasia* (1837; McNeill et al. 2006). On its side, *Lagenias* was characterized by having recurved anthers similar to *Sebaea* and filaments inserted in the corolla tube as in *Belmontia*.

Later, Grisebach (1845) erected a new genus, based on *B. grandis*, and named it *Exochaenium*. The main character that separated *Exochaenium* from *Belmontia* was connate anthers that form a tube around the style, in addition to being included

in the corolla tube. At that time, species of *Sebaea* s. l. were divided among four genera: *Belmontia*, *Exochaenium*, *Lagenias*, and *Sebaea* s. s. In *Genera Plantarum*, Bentham (1876) included *Lagenias* and *Exochaenium* in *Belmontia*, which was kept distinct from *Sebaea*. Schinz (1891) recognized both *Lagenias* and *Belmontia* as separate from *Sebaea*, but included most species of *Exochaenium* in *Belmontia*. Gilg (1898) followed Schinz's (1891) classification with minor modifications at the species level. Later, Schinz (1903) decided to merge *Belmontia* with *Sebaea*, and subdivided *Sebaea* into two sections: *Sebaea* ('Eusebaea') and *Belmontia*. These sections differed by anther insertion (inside the corolla tube for section *Belmontia*, and at the corolla sinus for section *Sebaea*). Only three years later, Schinz (1906) revised his own classification by accepting *Exochaenium*, to which he transferred most species of *Sebaea* sect. *Belmontia*, and merged *Lagenias* with *Sebaea*. *Exochaenium* was characterized by having anthers included in the corolla tube and "a disk of glands" (i.e. colleters) between the calyx and the corolla.

Hill (1908), when preparing *Flora Capensis*, followed Schinz's (1906) classification, adding one more character to *Exochaenium*, the style without "biglandular swelling" (i.e. secondary stigma), to separate it from *Sebaea*.

However, Marais (1961) argued that the characters used to uphold *Exochaenium* as distinct from *Sebaea* were unreliable, and synonymized *Exochaenium* with *Sebaea*. This was followed by Taylor (1963), Boutique (1972), Klackenberg (1990), Paiva and Nogueira (1990a) and Sileshi Nemomissa (2002).

In our effort to clarify the taxonomy of *Sebaea* s. l., two species endemic to Madagascar were recently placed in the

new genus *Klackenbergia*, based on morphological, karyological and molecular data (Kissling et al. 2008).

MATERIAL AND METHODS

Specimens were examined from the following herbaria: BM, BOL, BR, C, DSM, G, GRA, K, MO, MRSC, MPR, NBG, NEU, PRE, S, WAG, and Z, and personal collections of Dr L. Zeltner (CH-2400 Le Locle, Switzerland). Flowers and fruits were rehydrated with boiling water and preserved in a 70% ethanol solution. Fresh material was collected when possible in the field (Angola, Lesotho, South Africa, and Zambia), and preserved in a 70% ethanol solution. Authors of plant names follow Brummitt and Powell (1992).

TAXONOMIC TREATMENT

KEY TO THE GENERA OF THE TRIBE EXACEAE

1. Anthers dehiscing by terminal pores *Exacum*
1. Anthers dehiscing by a slit along each theca 2
2. Corolla tube longer than 1.5 cm, Madagascar 3
3. Flowers blue or white; filaments less than 2 mm long *Tachiaadenus*
3. Flowers yellow; filaments longer than 5 mm *Gentianothamnus*
2. Corolla tube shorter than 1.5 cm, or, if longer from continental Africa (i.e. *Exochaenium teucszii* (Schinz) Schinz and *Sebaea thomasi* (S. Moore) Schinz 4
4. Flowers blue to purple, rarely white; leaves \pm hairy, at least with unicellular trichomes on the leaves nerve (abaxial face) *Ornichia*
4. Flowers salmon, yellow or white; leaves glabrous 5
5. Flowers white, subsessile, axillary, solitary or in fascicles; bracts much longer (1–1.5 times) than the flowers; *Klackenbergia*
5. Flowers white, yellow or salmon, clearly pedicellate, in a dense or lax dichasium, solitary or rarely in a panicle; bracts shorter than or rarely as long as the flowers; 6
6. Plants more or less crassulescent; anthers medifixed, inserted at the base of the corolla tube *Lagenias*
6. Plants usually herbaceous; anthers basifixed, inserted at mid-length of the corolla tube or above 7
7. Stigma papillate, entire, usually slightly clavate (exceptionally bifid in *Exochaenium pygmaeum* Milne-Redhead); stamens and apical glands always included in the corolla tube; style without secondary stigma *Exochaenium*
7. Stigma smooth, bilobed; stamens often exerted; style usually with a secondary stigma *Sebaea*

TAXONOMIC TREATMENT OF EXOCHAENIUM GRISEB.

EXOCHAENIUM Griseb., DC. Prod. 9: 55. 1845.—TYPE: *Exochaenium grande* (E. Mey.) Griseb.

Annual, erect, sometimes dwarf herbs, rarely achlorophyllous (*Exochaenium oliganthum* (Gilg) Kissling). Stems simple or branched, usually tetragonal, sometimes 4-ridged or winged. Leaves sessile, opposite, linear-lanceolate to suborbicular, rarely reduced and scale-like. Flowers 5-merous, pedicellate, terminal, solitary, corolla usually white, sometimes yellow (*E. caudatum* (Paiva and Nogueira) Kissling, *E. clavatum* (Paiva and Nogueira) Kissling, *E. dimidiatum* (Sileshi) Kissling, *E. lineariforme* (Sileshi) Kissling, *E. rotundifolium* (Peter) Kissling, *E. wildemanianum* (Boutique) Kissling) or salmon (*E. grande*), often pendant or inclined, generally with a stylar polymorphism (short- and long-styled flowers), sometimes with a reciprocal position of the anthers (e.g. *E. grande*, *E. lineariforme*, *E. oliganthum*). Calyx lobes almost free or forming a short tube; lobes linear-lanceolate to ovate or obovate, dorsally keeled or winged. Corolla tube cylindrical or infundibuliform, the lower portion enlarged in fruit; lobes oblong-obovate, obtuse at the apex or acuminate; when the flower is white, then the inner part of the corolla tube is usually yellowish and striate; while in yellow or salmon flowers the inner part of the corolla is homogeneously colored. Filaments filiform, inserted at mid-length of the corolla tube. Anthers oblong, basifixed, included in the corolla tube, with a conspicuous apical stipitate gland, with or without 2 basal minute glands. Ovary ovoid or obovoid or almost globose, bilocular, placentas axile, ovules numerous.

Style filiform, included in the corolla tube, never with secondary stigmas (in contrast to *Sebaea* s. s.). Stigma straight or clavate, entire or slightly bilobed (*E. grande*), rarely bifid (*E. pygmaeum*), papillate. Capsule ovoid or obovoid, membranous or coriaceous, septicidally bivalved. Seeds minute (150–250 μ m), numerous, cubical, black; testa cells star-shaped. Figure 2.

Distribution—Twenty-two species, all endemic to sub-Saharan Africa, are recognized. Most species occur on the Katanga plateau (Angola, Democratic Republic of the Congo, and Zambia), many extending their distribution to the Sudano-Zambesian region and the Sudano-Zambesian/Guineo-Congolian transition zone sensu White (1986; Fig. 3), except *E. oliganthum*, which occurs in the Guineo-Congolian region and the Sudano-Zambesian/Guineo-Congolian transition zone sensu White (1986).

Differences with the Other Genera of the Exaceae—*Exochaenium* differs from *Sebaea* by several morphological features. The seeds of *Exochaenium* have star-shaped testa cells (Fig. 2), while *Sebaea* has seeds with testa cells \pm rectangular aligned in rows (see Fig. 4B in Kissling et al. 2009c). The stigma of *Exochaenium* is papillate and entire (exception: *E. pygmaeum* with a bifid stigma) while the stigma of *Sebaea* is smooth and clearly bilobed (exceptions: *S. thomasi*, *S. spathulata*). Most species of *Sebaea* have a secondary stigma on the style (Hill 1913; Marais and Verdoorn 1963), except *S. thomasi* (where the secondary stigma is confluent with the apical one) and *S. minutiflora* Schinz (where the secondary stigma appears as traces along the style, it is not clear yet if it further develops), while *Exochaenium* never has such

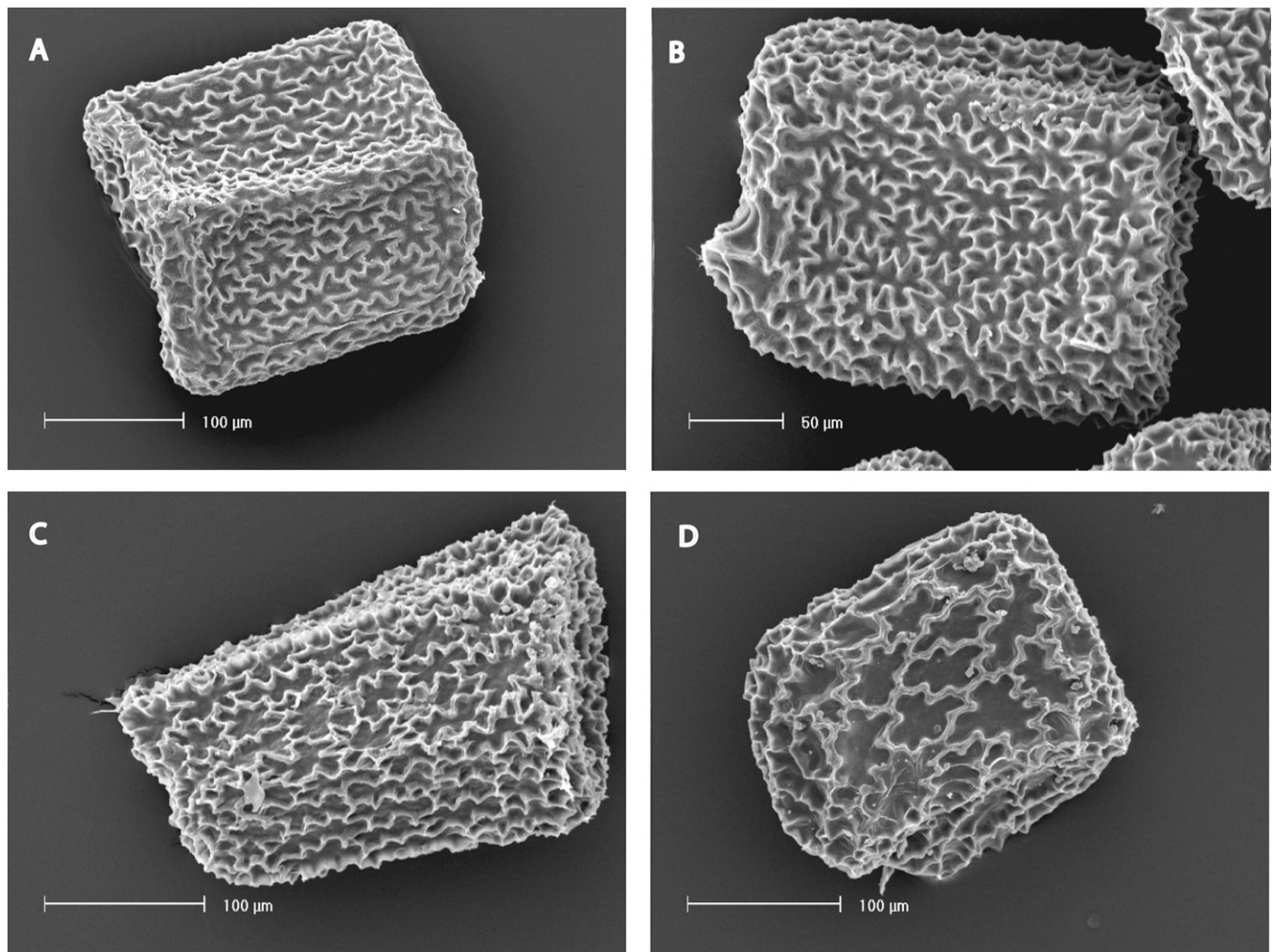


FIG. 2. Seeds of *Exochaenium* (SEM micrographs) showing polyhedric seeds with distinctly star-shaped testa cells. A. *Exochaenium macropterum* (Bidgood et al. 4012). B. *E. teucszii* (Dessein et al. 701). C. *E. clavatum* (Dessein et al. 543). D. *E. oliganthum* (Dessein et al. 499).

features. The stamens of *Exochaenium* are always inserted at mid-length of the corolla tube, while the stamens of *Sebaea* are usually inserted near or in the corolla lobe sinuses (exceptions: *S. exacoides*, *S. membranacea* Hill, *S. thomasii*).

Exochaenium differs from *Lagenias* by its seed morphology (star-shaped testa cells versus polygonal testa cells; see Fig. 4A in Kissling et al. 2009c), by its anther fixation (basifixed versus medifixed), and also by its habit (*Lagenias* has a crassulescent habit).

Exochaenium can be easily distinguished from *Tachiadenus* by its ovary structure (bilocular for *Exochaenium* versus “pseudobilocular” for *Tachiadenus*), and its distribution (tropical Africa for *Exochaenium* versus Madagascar for *Tachiadenus*). The long corolla tube and the blue-purple color of the flowers of *Tachiadenus* are also useful to distinguish the two genera. Nevertheless, some species of *Exochaenium* (*E. teucszii*) also have rather long corolla tubes (up to 3.5 cm).

The remaining genera of tribe Exaceae (*Exacum*, *Gentianothamnus*, *Klackenbergia*, and *Ornichia*) are easily distinguished from *Exochaenium*. *Exacum* has poricidal anthers, and usually has blue-purple flowers, while *Exochaenium* has anthers dehiscing by slits, and generally white or yellow flowers. *Gentianothamnus* is a subshrub up to two m in height, endemic to Madagascar, while species of *Exochaenium* are all

herbs. *Gentianothamnus* is also characterized by the presence of a shallowly 5-lobed disk supporting the ovary (Klackenberg 2002), a feature that is absent in *Exochaenium*. Species of *Klackenbergia* are endemic to Madagascar and with their axillary flowers and particularly long bracteoles are distinguishable at first glance. *Ornichia*, also endemic to Madagascar, has hairs on the leaves, while *Exochaenium* species are glabrous.

Remark—The current species number might be underestimated, due to few collections from countries of tropical Africa. Likewise, several species have been described based on a single collection. Even though most of the taxa in *Exochaenium* are recognizable at first glance, species delimitation is difficult within a complex of morphologically similar and poorly collected species (i.e. *E. alatum* (Paiva and Nogueira) Kissling, *E. debile* Welw., *E. exiguum* A. W. Hill, *E. fernandesianum* (Paiva and Nogueira) Kissling, *E. gracile* (Welw.) Schinz, *E. rotundifolium* and *E. wildemanianum*). Indeed, most of the characters used to uphold specimens (usually a single collection) to the rank of species are known to be plastic in annual Gentianeae (e.g. height of the plants, length of the pedicels). However, when in doubt, I choose here to maintain most of the described species and try to use more stable morphological characters (i.e. shape of the

leaves and presence/absence of basal glands on the stamens). Nevertheless, increased sampling and the help of molecular work, cross-fertilization and/or control growth of those morphologically related species is needed to better understand the taxonomy and evolution of that species complex.

This taxonomic treatment does not modify the species circumscription of recent authors. Therefore accurate species descriptions and illustrations can be found in African

floras (i.e., Taylor 1963; Boutique 1972; Paiva and Nogueira 1990a and Sileshi Nemomissa 2002). Nevertheless, in the present treatment, I synonymize three species (*Sebaea africana* under *Exochaenium debile*, *Sebaea brevicaulis* under *Exochaenium rotundifolium*, and *Sebaea gentili* under *Exochaenium teucszi*) for which the description in African floras is still accurate. without affecting their current species circumscriptions.

KEY TO THE SPECIES OF *EXOCHAENIUM* GRISEB

1. Achlorophyllous, mycotrophic or rarely parasitic plant 14. *E. oliganthum*
1. Chlorophyllous plant 2
2. Plant small (< 0.8 cm) 15. *E. perparvum*
2. Plant taller 1 cm or taller 3
3. Basal rosette present from which several long pedicellate (ca. 50 mm) flowers develop 4
4. Pedicel and calyx hyaline when dry; calyx narrowly winged (wings < 0.3 mm wide) 11. *E. hockii*
4. Pedicel and calyx green when dry; calyx conspicuously winged (wings 1.9–2.5 mm wide) 13. *E. macropterum*
3. Basal rosette absent 5
5. Corolla tube cylindrical, not exceeding 3 mm in diameter, 15–35 mm long; white 21. *E. teucszi*
5. Corolla tube infundibuliform, at least 3 mm in diameter, 3–15 mm long; if longer, corolla yellow or salmon (if not, white) 7
7. Plant with the basal leaves oriented downwards, and adhering to the stem when dried 8
8. Anthers tailed at the base, without basal glands 3. *E. caudatum*
8. Anthers not tailed at the base, with two basal glands 4. *E. clavatum*
7. Plant with basal leaves normally oriented upwards or horizontally, not adhering to the stem when dried 9
9. Pedicels long (> 50 mm) or much longer than the internode below 10
10. Calyx wing 1–1.5 mm wide; anthers ca. 1.3 mm long 20. *E. rotundifolium*
10. Calyx wing 0.3–0.8 mm wide; anthers 0.7–1 mm long 8. *E. fernandesianum*
9. Pedicels short (< 50 mm), equal to or shorter than the internode below 11
11. Stigma bifid 19. *E. pygmaeum*
11. Stigma entire 12
12. Corolla 15–30 mm in diameter 13
13. Calyx wing narrow, ca. 0.5 mm broad; cauline leaves linear to lanceolate 12. *E. lineariforme*
13. Calyx wing cordate, 1–2 mm broad; cauline leaves ovate, elliptic to lanceolate 14
14. Corolla bright yellow 6. *E. dimidiatum*
14. Corolla salmon, rarely white 15
15. Plant slender; corolla white; calyx segment dorsally winged (up to 1 mm); style absent (stigma emerging directly from the ovary); stamens inserted near the base of the corolla lobes 1. *E. alatum*
15. Plant robust; corolla salmon, rarely white (South Africa); calyx segment dorsally broadly winged (wings 1–2 mm); style present; stamens inserted near the middle of the corolla tube 16
16. Plant tall (> 15 cm); stem not branching at the base 10. *E. grande*
16. Plant short (< 15 cm); stem branching at the base 17. *E. primulaeflorum*
12. Corolla < 10 mm in diameter 17
17. Plant filiform, taller than 20 cm; stem usually unbranched, bearing a single small flower; leaves linear, usually as broad as the stem 2. *E. baumianum*
17. Plant slender, shorter than 20 cm; stem usually branched, with few flowers (1–)3–(–)5; leaves linear to elliptic or ovate, broader than the stem 18
18. Anthers without basal glands; calyx wing width 0.7–1.2 mm; flowers always inclined to pendulous 16. *E. platypterum*
18. Anthers with or without basal glands; calyx wing width 0.25–0.5 mm; flowers usually erect, or slightly pendent 19
19. Plant 5–15(–20) cm high; cauline leaves (middle of the stem) linear to lanceolate 20
20. Corolla tube as long as to slightly longer than the calyx; anthers without basal glands 9. *E. gracile*
20. Corolla tube longer than the calyx; anthers with two minute, globose basal glands 7. *E. exiguum*
19. Plant 1.5–8(–17) cm high; cauline leaves (middle of the stem) ovate to elliptic 21
21. Leaves markedly 3-nerved, petiolate; corolla yellow 22. *E. wildemanianum*
21. Leaves 1 nerved, sessile; corolla white 22
22. Corolla lobes ca. 1/5 of the corolla tube in length 18. *E. pumilum*
22. Corolla lobes longer than half the length of the corolla tube in length 5. *E. debilis*

1. ***Exochaenium alatum*** (Paiva and Nogueira) Kissling, comb. nov. *Sebaea alata* Paiva and Nogueira, Anal. Jard. Bot. Madrid 47: 96, Fig. 5. 1990.—TYPE: ZAMBIA. Chishinga Ranch, near Luwanga, 27 Apr 1961, *Astle* 545 (holotype: K!).

Iconography—Paiva and Nogueira, Anal. Jard. Bot. Madrid 47: 96, Fig. 5. 1990.

Distribution and Ecology—The species is found in Zambia, in dambo (i.e. seasonally waterlogged, predominantly

grass-covered, depressions bordering headwater drainage lines; Mackel 1985), flowering from March to April.

Remarks—This species is morphologically similar to *E. exiguum*, from which it differs by the size of the whole plant (ca. 10–17 cm for *E. alatum* versus ca. 3.5–10(–17) cm for *E. exiguum*), the flowers (ca. 1.5 cm long for *E. alatum* versus ca. 1 cm long for *E. exiguum*), and the style seems to be absent (stigma emerging directly from the ovary) for *E. alatum*.

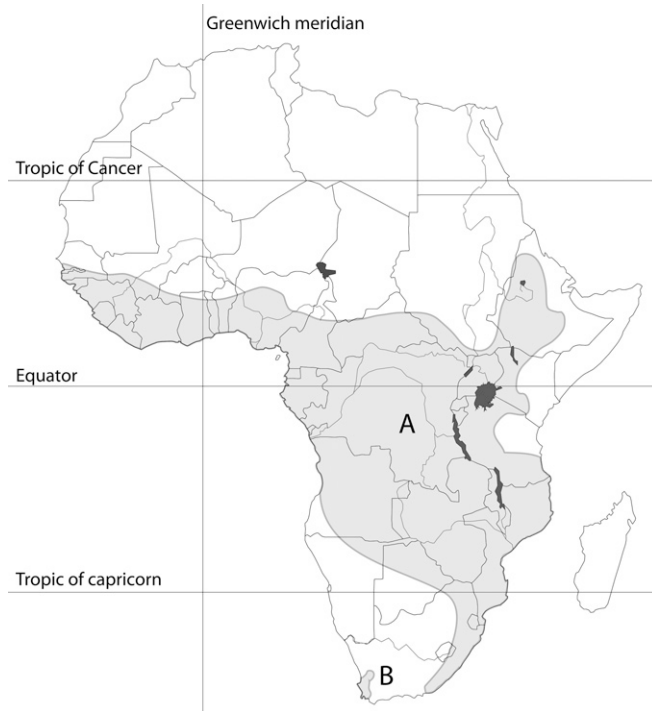


FIG. 3. A. Distribution of *Exochaenium*. B. Distribution of *Lagenias*.

Due to the common records of hybridization within Gentianaceae (Pringle 1965; Zeltner 1978; Ubsdell 1979; Guggisberg et al. 2006; Riesman et al. 2006), introgression might explain the overlapping of some of the characters (e.g. plant robustness, size of the calyx wing, and leaf shape) between these two species.

2. *EXOCHAENIUM BAUMIANUM* (Gilg) Schinz, Bull. Herb. Boiss. Ser. 2, 6: 716. 1906. *Belmontia baumiana* Gilg, in Baum, Kunene-Samb.-Exped. 331. 1903. *Sebaea baumiana* (Gilg) Boutique, Fl. Afr. Centr., Gentianaceae: 46. 1972.—TYPE: ANGOLA. am Longa oberhalb des Quirri, an Sumpfrändern, 1,250 m, *Baum* 692 (holotype: K!; isotype: E!, Z!).

Distribution and Ecology—The species is known from Angola, southern Democratic Republic of the Congo, and Zambia. It grows in damp soil, among grasses, flowering in (December)-February-March-(April).

Remarks—This species is morphologically similar to *E. teusczii*, from which it differs by the length of the flowers (< 1 cm for *E. baumianum*, > 1.5 cm for *E. teusczii*) and the size of the petal lobes (< 0.5 cm for *E. baumianum*, > 1 cm for *E. teusczii*).

This species has rarely been collected; maybe because of its extremely slender, filiform habit, making it difficult to spot among grasses. Nevertheless, it was present in most of the dambos I visited.

Representative Specimens Examined—DEMOCRATIC REPUBLIC OF THE CONGO. Kingama Kuni, vallée en auge (nkengu), 10 Mar 1959, *L. Pauwels* 2119 (BR).

ZAMBIA. Mwinilunga district, Oct 1937–Feb 1938, *E. Milne-Redhead* 3578 (K); North-Western province, Miwinilunga district, 37 Km of Mwinilunga on Matonchi road, 11°42'S, 24°08'E, 1,390 m, 24 Jan 1975, *R. K. Brummitt et al.* 14090 (K); Luwinda, 29 Mar 1962, *E. A. Robinson* 5066 (K); Dambo along Luongo River, 28 Mar 2004, 10°11'29.6"S, 29°42'20.2"E, 1,451 m, *S. Dessein et al.* 809 (BR, NEU); Chintunta dambo along the

Mwinilunga-Ikelenge road, 14 Apr 2004, 24°22'47.5"S, 11°30'19.0"E, 1,389 m, *S. Dessein et al.* 970 (BR, NEU).

3. *Exochaenium caudatum* (Paiva and Nogueira) Kissling, comb. nov. *Sebaea caudata* Paiva and Nogueira, Anal. Jard. Bot. Madrid 47: 89–92, Fig. 2. 1990.—TYPE: ZAMBIA. Mapanza, *E. Robinson* 1251 (holotype: K!).

Iconography—Paiva and Nogueira, Anal. Jard. Bot. Madrid 47: 91, Fig. 2. 1990.

Distribution and Ecology—This species is only known from the type in Zambia, Mapanza, Simansunda Dambo, flowering in April.

Remarks—Despite recent joint efforts to find this species it has only been collected once. This species is morphologically similar to *E. clavatum*, from which it differs only by its caudate anthers.

4. *Exochaenium clavatum* (Paiva and Nogueira) Kissling, comb. nov. *Sebaea clavata* Paiva and Nogueira, Anal. Jard. Bot. Madrid 47: 97, Fig. 6. 1990.—TYPE: ZAMBIA. Mbala, the Dambo, 15 miles along the road from Senga Hill to Mporokoso, 08 Jun 1956, *E. Robinson* 1736 (holotype: K!, isotype: S!).

Iconography—Paiva and Nogueira, Anal. Jard. Bot. Madrid 47: 98, Fig. 6. 1990.

Distribution and Ecology—This species is endemic to Zambia where it is usually growing in shallow water, in dambos or along inundated lakeshores. It is only known from four localities. Flowering from March to April.

Remarks—This species together with *E. caudatum* forms a morphologically distinct group. Both are easily recognizable by their comparatively large size (ca. 50 cm tall), and their bright yellow flowers. In herbarium collections, the basal leaves are massed together with the stem, and the roots are reddish. *Exochaenium clavatum* is the only known species of the genus that grows partly submerged in water, but more information about the ecological niche of *E. caudatum* is needed. Some species, like *E. teusczii*, sometimes grow in up to ca. 20 cm deep water, but it is apparently not the ecological preference of this species. The red roots of *E. clavatum* and *E. caudatum* are likely not related to their inundated habitats, as they are also found in *E. platypterum* (Baker) Schinz.

Representative Specimens Examined—ZAMBIA. Abercorn district, near Mporokosa, 5,000 ft, 8 Jun 1936, *B. D. Burt* 6116 (BM); Mporokoso district, Lumangwe Falls, 29°23'E, 09°34'S, in stream near Rest House, 14 Apr 1989, *R. Smith et al.* 5686 (K); Swamp area near Kalaso Mukuso village, 11°49'18.5"S, 29°36'32.7"E, 1,170 m, 14 Mar 2004, *S. Dessein et al.* 543 (BR, NEU).

5. *EXOCHAENIUM DEBILE* Welw., Trans. Linn. Soc. 27: 48. 1869. *Belmontia debilis* (Welw.) Benth. and Hook, Viertelj. Nat. Gesellsch. Zürich 36: 332. 1891. *Parrasia debilis* (Welw.) Hiern, Cat. Welw. Afr. Pl. 1, 3: 708. 1898. *Sebaea debilis* (Welw.) Schinz, Bull. Herb. Boiss., Sér. 2, 6: 734. 1906.—TYPE: ANGOLA. Pungo Andongo, *Welwitsch* 1511 (holotype: K!).

Sebaea africana Paiva and Nogueira, Anal. Jard. Bot. Madrid 47: 94–95, Fig. 4. 1990. syn. nov.—TYPE: ZAMBIA. Kwambwa-Mbereshi Rd., 19 Apr 1957, *M. A. Richards* 9337 (holotype: K!).

Iconography—Boutique, Flore d'Afrique centrale, Gentianaceae 49, pl. 7. 1972; Th. and H. Dur., Syll. 374, pl. 7. 1909; Paiva and Nogueira, Anal. Jard. Bot. Madrid 47: 95, Fig. 4. 1990; drawing on the holotype (K).

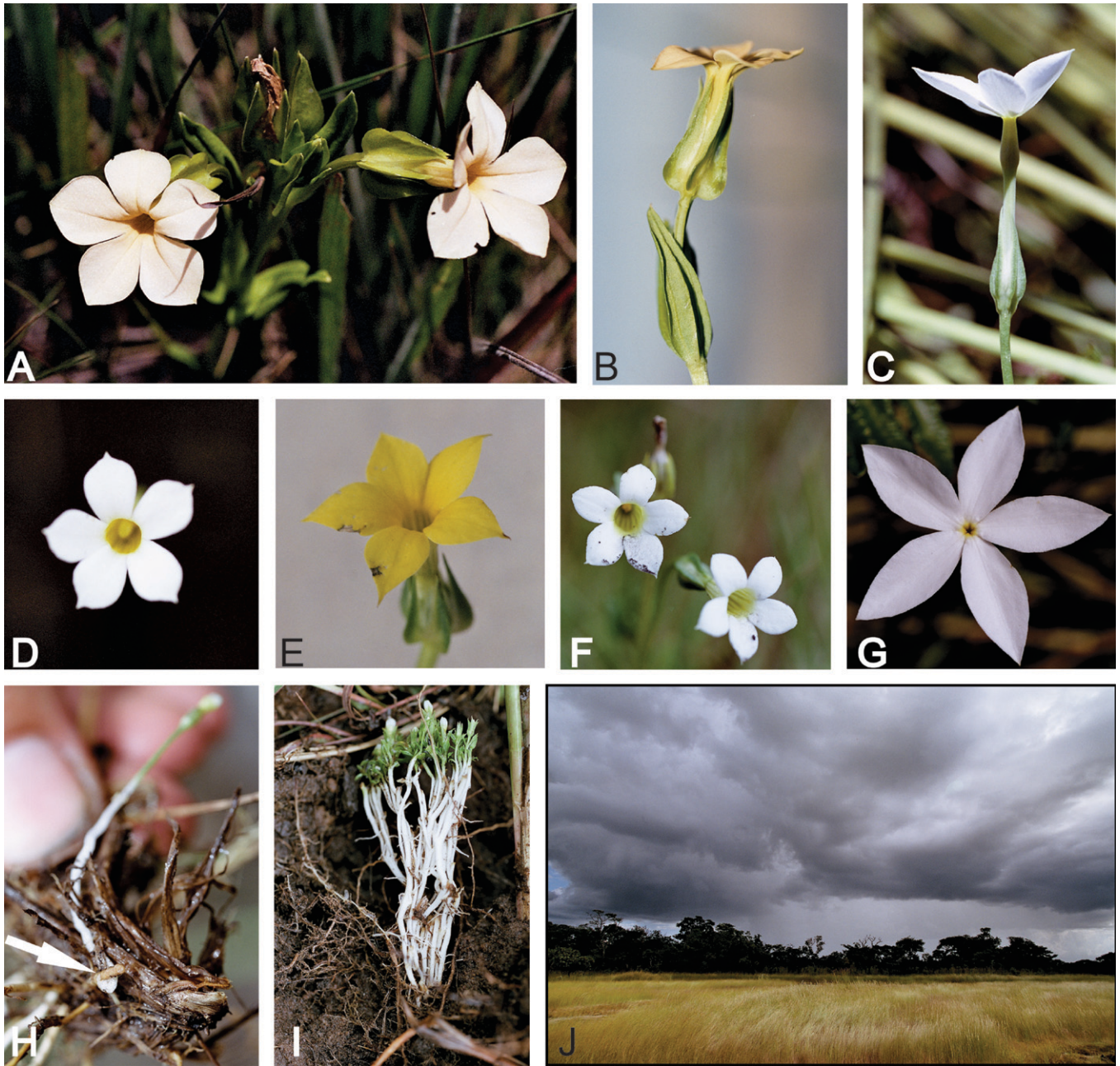


FIG. 4. Selected species of *Exochaenium*. A-B. *E. grande*. C and G. *E. teuczii*. D. *E. exiguum*. E. *E. clavatum*. F. *E. fernandesianum*. H. haustorium of *E. oliganthum* (indicated by an arrow). The brown root to which the white stem of *E. oliganthum* is attached belongs to an unidentified Poaceae. I. Root system of the minute *E. perparvum*. J. A typical dambo area where *Exochaenium* species are to be found. This plate shows a locality where *E. fernandesianum* and *E. baumianum* are found in sympatry (Zambia, Zambezi rapids near Kalene Hill) (photographs by J. Kissling).

Distribution and Ecology—This species is known from Angola, Namibia (Caprivi strip) and Zambia, growing in savannah, on sandy soil, flowering from March to April.

Remarks—This minute species is similar to *Exochaenium pygmaeum*, from which it only differs by its stigma (entire for *E. debile* versus bifid for *E. pygmaeum*). *Exochaenium debile* also resembles *E. pumilum* (Baker) Hill, but can be distinguished from the latter by its longer corolla lobes (ca. 1/5 of the corolla tube for *E. pumilum* versus ca. 1/3 for *E. debile*) and the size of the apical gland (as long as or longer than the anther in *E. debilis*, much shorter in *E. pumilum*).

Paiva and Nogueira (1990b), when describing *S. africana*, only compared it to *E. pumilum*, and not with *E. debile*. *Sebaea*

africana does not differ from *E. debile* and the description of *S. africana* overlap the one of *E. debile*. It is thus synonymized here.

Representative Specimens Examined—DEMOCRATIC REPUBLIC OF THE CONGO. Entre Kakani et Kalanga, sur le sentier, 1,200 m, 23 Apr 1926, W. Robyns 2090 (BR); Env. 3 km à l'W du village Katema, 1,490 m, 21 Jan 1969, St. Lisowski et al. 408 (BR); Dembo Kandale, à 1.5 km à l'E de Kabiashia, Katanga, 23 May 1969, F. Malaisse 6430 (BR); Tête vallée Kantala, Plateau de la Manika, mare dans le dilungu, 25 Mar 1975, F. Malaisse 8555 (BR); Abords de rivière Kapanga, Nov 1933, Overlaet 1088 (BR); Kanonga, Parc National de l'Upemba, 18 Feb 1949, G. F. de Witte 05543 (BR). NAMIBIA. E Caprivi Zipfel, Kakumba Island, 17 Jan 1959, D. J. B. Killick & O. A. Leistner 3421 (K, PRE). ZAMBIA. Area around the Ntumbachushi waterfalls, 09°51'11.7"S, 28°56'42.1"E, 1,050 m, 17 Mar 2004, S. Dessein et al. 603 (BR, NEU); Dambo along Mbereshi-Kawambwa

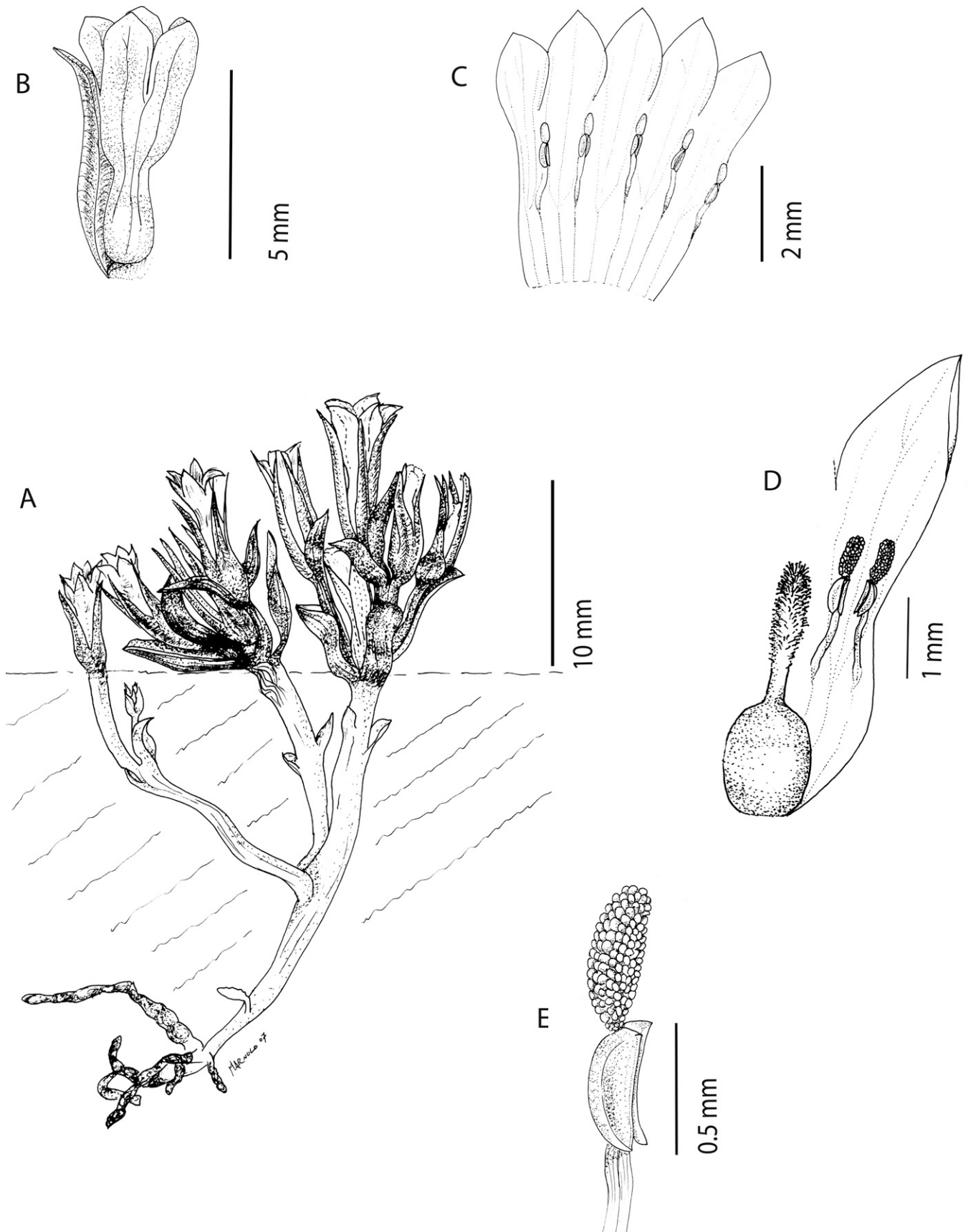


FIG. 5. *Exochaenium perparvum*. A. Habit. B. Flower with one sepal. C. Opened corolla. D. Opened flower with corolla lobe, two stamens and gynoecium. E. Anther. From *Dessein et al.* 728 (NEU, BR). Illustrated by Maeva Arnold.

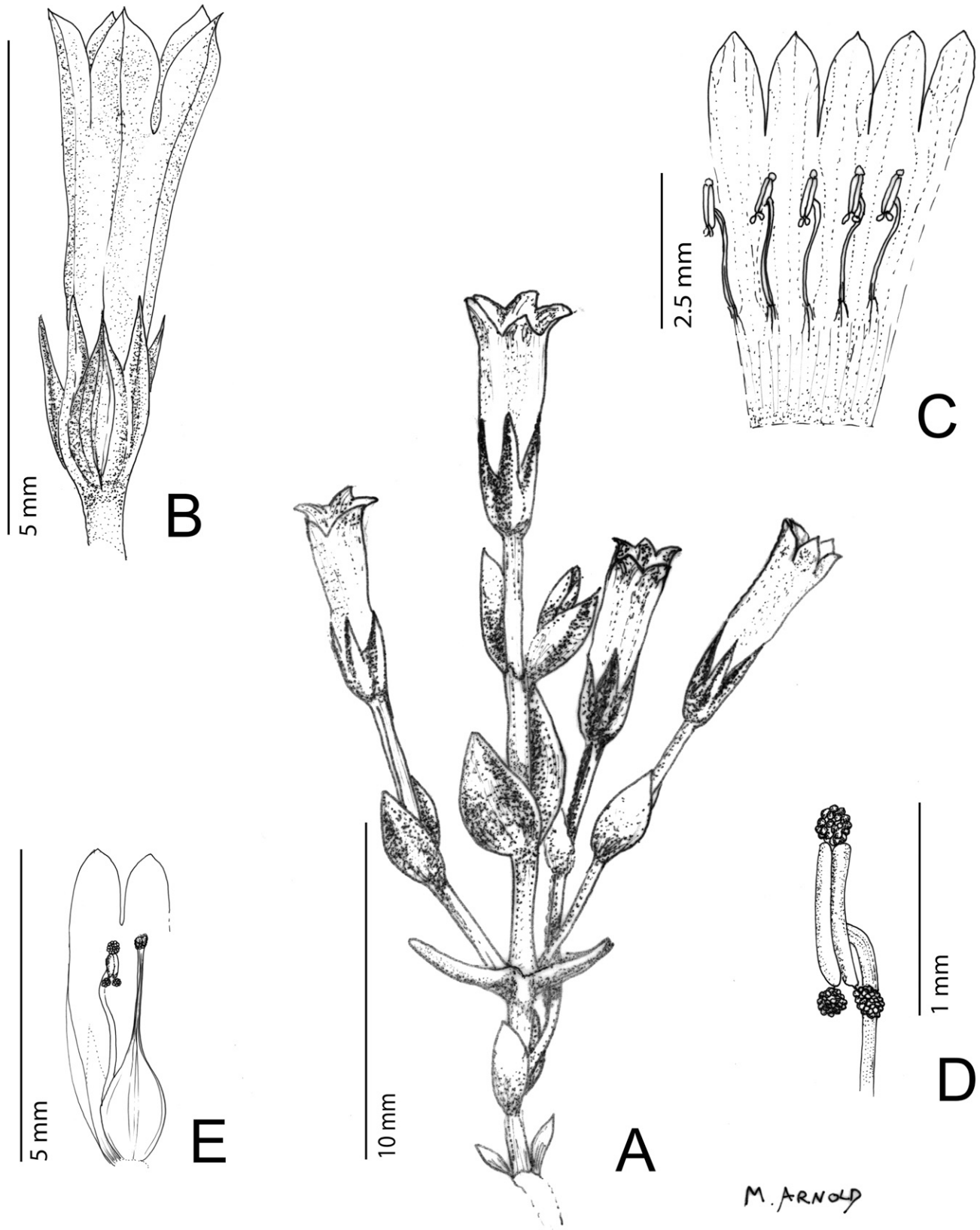


FIG. 6. *Lagenias pusillus*. A. Habit. B. Flower. C. Opened corolla. D. Opened flower with two corolla lobes, anthers and gynoecium. E. Anther with three glands. From Kissling and Zeltner 64 (NEU, BOL). Illustrated by Maeva Arnold.

route, 09°50'12.6"S, 28°57'13.9"E, 1,298 m, 18 Mar 2004, *S. Dessein et al.* 604 (BR, NEU); Dambo near Ntenke village, 09°43'09.8"S, 29°04'44.2"E, 1,336 m, 18 Mar 2004, *S. Dessein et al.* 617 (BR, NEU); Shallow dambo along the Kawambwa-Lake Mweru road, 09°32'06.6"S, 28°56'54.1"E, 1,255 m, 19 Mar 2004, *S. Dessein et al.* 623 (BR, NEU).

6. *Exochaenium dimidiatum* (Sileshi) Kissling, comb. nov.
Sebaea dimidiata Sileshi, Kew Bull. 55: 214–217, Fig. 2. 2000.—TYPE: TANZANIA. Manyoni district, Kazi Kazi, near Lambo ya Mulengali, 17 May 1932, *Burt* 3632 (holotype: K!).

Iconography—Sileshi *Nemomissa*, Kew Bull. 55: 216, Fig. 2. 2000.

Distribution and Ecology—This species is endemic to Tanzania where it grows in marshy sites in grassland, flowering from June to September.

Additional Specimens Examined—TANZANIA. T4, Near Tabora, 4,000 ft, 26 Apr 1962, *A. C. Tallantire* T.179 (K); Kapapa, on track through forest, 9 miles from Kapapa, 17 Sep 1970, *Richards & Arasululu* 25392 (K); Shinyanga district, Shinyanga, *Bax* 224 (K); Kaliua, 16 Jun 1980, *Hooper et al.* 2001 (K).

7. EXOCHAENIUM EXIGUUM A. W. Hill, Bull. Misc. Inform. Kew 1909: 50. 1909. *Sebaea minuta* Paiva and Nogueira, Anal. Jard. Bot. Madrid 47: 99. 1990.—TYPE: ZIMBABWE. Bulawayo, *F. Eyles and W. Johnson* 1032 (holotype: GRA!; drawing from the type: K!).

Note—Paiva and Nogueira while transferring *Exochaenium exiguum* to *Sebaea* had to choose a new epithet because *Sebaea exigua* (Oliv.) Schinz, Geogr. Ges. Lübeck 17: 26. 1903. already exists.

Distribution and Ecology—This species is widespread in the Zambesian region where it is found in dambo, damp open grassland, and stream banks on sandy soil, flowering from March to April, usually ca. one month after the end of the rain season.

Representative Specimens Examined—ZAMBIA. Chinsali, Lake Young, Shiwa Ngandu, 17 Jan 1959, *Richards* 10712 (K); 13 km N of Choma, 17 Apr 1958, *E. Robinson* 2835 (K); Kasanshi, 55 km SE of Mporokoso, 13 May 1962, *E. Robinson* 5170 (K); 7 km of Chizera, 27 Mar 1961, *R. Drummond & R. Rutheford-Smith* 7420 (K; PRE). Area around Lupupa waterfalls, 10°24'22.2"S, 31°04'32.2"E, 1,415 m, 21 Mar 2004, *S. Dessein et al.* 656 (BR, NEU); Kaniki dambo along the Mporokoso-Kasama road, bordering the Kasanshi river, 09°29'24.5"S, 30°34'37.8"E, 1,411 m, 21 Mar 2004, *S. Dessein et al.* 692 (BR, NEU).

ZIMBABWE. Gokwe, Sergwa Reserve Station, 16 Apr 1968, *N. Jacobsen* 618 (K); Farm Chasterfield, Mar 1958, *O. Miller* 5129 (K).

8. *Exochaenium fernandesianum* (Paiva and Nogueira) Kissling, comb. nov. *Sebaea fernandesiana* Paiva and Nogueira, Anal. Jard. Bot. Madrid 47: 92–93, Fig. 3. 1990.—TYPE: ZAMBIA. Mwinilunga, Zambesi Rapids, ca. 6 km N of Kalene Hill, *Hooper and Townsend* 256 (holotype: K!).

Iconography—Paiva and Nogueira, Anal. Jard. Bot. Madrid 47: 93, Fig. 3. 1990.

Distribution and Ecology—This species is from Tanzania and Zambia, found in damp soil over rocky outcrops, and flowering from February to May.

Remarks—This species is similar to *E. rotundifolium* and *E. macropterum* (Sileshi) Kissling. Due to the few available specimens, a firm decision on merging *E. fernandesianum* with *E. rotundifolium* or/and with *E. macropterum* cannot be made at this time. Thus, those three species are tentatively maintained. Based on current data: *E. fernandesianum* differs from *E. rotundifolium* in the size of the calyx wing (0.3–0.8 mm wide for *E. fernandesianum* versus 1–1.5 mm wide for *E. rotundifolium*) and the size of the anthers (0.7–1 mm

for *E. fernandesianum* versus ca. 1.3 mm for *E. rotundifolium*). *Exochaenium macropterum* differ from both *E. fernandesianum* and *E. rotundifolium* by the presence of a basal rosette of leaves.

Additional Specimens Examined—TANZANIA. T4. Mpanda district, Uvinza road, Uzondo Plateau, 05°29' S, 30°32' E, 1675 m, 29 May 2000, *S. Bidgood et al.* 4507 (K).

ZAMBIA. Zambezi rapids near Kalene Hill, 11°07'38.8"S, 24°11'21.3"E, 1,223 m, 15 Apr 2004, *S. Dessein et al.* 1011 (BR, NEU).

9. EXOCHAENIUM GRACILE (Welw.) Schinz, Bull. Herb. Boiss., sér. 2, 6: 716. 1906. *Belmontia gracilis* Welw., Trans. Linn. Soc. 27: 47. 1869. *Parrasia gracilis* (Welw.) Hiern, Cat. Pl. Welw. 1: 708. 1898. *Sebaea gracilis* (Welw.) Paiva and Nogueira nom. illeg., Anal. Jard. Bot. Madrid 47: 100. 1990.—TYPE: ANGOLA, Huila, river Monino, Apr 1860, *F. Welwitsch* 1524 (holotype (selected here): BM! isotype: K!, BM!, P!). non *Sebaea gracilis* (Mart.) Spreng., Syst. Veg. (ed. 16): 338. 1827. = *Schultesia gracilis* Mart. Nov. Gen. Sp. Pl. (Martius) 2: 105. t.181. 1827.—TYPE: BRAZIL. Prov. Minas Gerais, Habitat in campis Contenda (lectotype: M). non *Sebaea gracilis* A. Cunn. Ann. Nat. Hist. 2, 7: 45. 1838.—TYPE: NEW ZEALAND. Northern island, in bogs at Mangamuka, Hokianga, *R. Cunningham* 1834, which according to the description of *R. Cunningham* correspond likely to *Sebaea ovata* (Allan 1961).

Belmontia luteo-alba A. Chev., J. Bot. (Morot). 22. 119. 1909. *Sebaea luteo-alba* (A. Chev.) P. Taylor, Taxon 12:294. 1963.—TYPE: REPUBLIC OF GUINEA. Fouta Djallon, Dalaba, 05 Oct 1907, *Chevalier* 20206 (lectotype (chosen here): P!).

Note—Chevalier in his publication only mentions the origin of his collection i.e. Kouria, Kala, Dalaba, Diaguissa and Bouroukountou (without a collecting number). However on one of them (Dalaba) he wrote "type." This sample is chosen here as holotype. The collecting number on the type might have been added only after he published his new species.

Iconography—drawing on sheet *P. Jaeger* 574 (K).

Distribution and Ecology—Angola, Zambia, and West Africa. In dambo, marsh soil and shallow soil over rocks. Flowering time: March–April, usually ca. one month after the end of the rainy season.

Remarks—There are no differing morphological characters to support *E. luteo-album* as a distinct species from *E. gracile*. *Exochaenium gracile* is similar to *E. exiguum*, but differs by the absence of basal glands on the anthers as well as the size of the calyx.

Additional Specimens Examined—SIERRA LEONE. Mnt Loma, Nov 1944, *P. Jaeger* 574 (K).

ZAMBIA. Kitwe, 20 Apr 1957, *D. B. Fanshawe* 3197 (K); Dambo just E of Mumbuluma falls, 10°55'46.4"S, 28°44'05.5"E, 1,189 m, 16 Mar 2004, *S. Dessein et al.* 584 (BR, NEU).

10. EXOCHAENIUM GRANDE (E. Mey.) Griseb., DC., Prodr. 9: 55. 1845. *Belmontia grandis* E. Mey., Comm. 183. 1837. *Sebaea grandis* (E. Mey.) Steud., Nom. Bot., ed. 2, 4: 550. 1841. *Parrasia grandis* (E. Mey.) Hiern, Cat. Welw. Afr. Pl. 1: 707. 1898.—TYPE: SOUTH AFRICA. Cape, between Umtentu R. and Umzimkulu R., *Drege s. n.* (lectotype: K!, typified by Sileshi *Nemomissa* 2002).

Exochaenium grande var. *major* (S. Moore) Schinz, Bull. Herb. Boiss. Sér. 2, 6: 802. 1906. *Parrasia grandis* var. *major* S. Moore, J. Bot. 40: 384. 1902.—TYPE: SOUTH

AFRICA. Transvaal, Pienaarsport, *Pateshall Thomas s. n.* (holotype: BM!).

Exochaenium macranthum Hill., Bull. Misc. Inform. 1908: 339. 1908.—TYPE: ANGOLA. Longa river, 4,000 ft, *Baum 640* (lectotype: K!) A lectotype is chosen here among the paratypes *Doggett s. n.*, *Brown 139*, *Johnson 260*, *McClounie 98* and *McClounie 126*.

Belmontia natalensis Schinz, Bull. Herb. Boiss. Sér. 2, 2: 220. 1894. *Sebaea natalensis* (Schinz) Schinz nom. illeg., Bull. Herb. Boiss. Sér. 2, 6: 732. 1906. *Exochaenium grande* var. *homostylum* Hill, Kew Bull 1908: 338. 1908.—TYPE: SOUTH AFRICA. Natal, Clairmont, *Schlechter 3060*. (holotype: Z!, isotype: K). non *Sebaea natalensis* Schinz, Bull. Herb. Boiss. Sér. 2, 4: 442. 1896.—TYPE: SOUTH AFRICA. Natal, in saxos. Pr. Mount West, 5,400 ft *Schlechter 6819* (holotype: Z!).

Belmontia zambesiaca Baker., Bull. Misc. Inform. 1894: 25. 1894. *Sebaea zambesiaca* (Baker) Schinz, Bull. Herb. Boiss. Sér. 2, 6: 744. 1906. *Exochaenium zambesiacum* A. W. Hill, Bull. Misc. Inform. Kew. 1908: 336. 1908.—TYPE: BOTSWANA. in the valley of the Leshumo, *Holub s. n.* (holotype: K!).

Iconography—Hill, Bull. Misc. Inform. Kew. 1908: 317. 1908; Paiva and Nogueira, Flora Zambesiaca, vol. 7 part 4: 21, Table 8A. 1990; Sileshi Nemomissa, Flora of Tropical East Africa, Gentianaceae: 14, Fig. 3. 2002.

Distribution and Ecology—This species is widespread throughout tropical Africa, from Ethiopia to eastern South Africa, and from West Africa (Republic of Guinea) to Kenya. It grows in a wide range of habitats, usually in open grassland, among rocks and clay or sandy soil. Flowering usually ca. one to two months after the end of the rainy season (e.g. March–April for Zambia or September–October for the Republic of Guinea).

Remarks—This well-defined species is of particular interest because its corolla color can vary geographically, from pure white or bright yellow (only known from South Africa) to salmon (the most common color). The variations in flower morphology, particularly the styler polymorphism, were studied by various authors (e.g. Schinz 1906; Hill 1908; Wolfe et al. 2009).

Representative Specimens Examined—BOTSWANA. Molapo ya Koshimile to Xade near G.S camp, 22°7'30"S, 24°7'30"E, 900 m, 01 Mar 1989, I. J. Barnard 366 (PRE); Kweneng district, Kutse Game reserve. Btw. Kutse pan 1 and Kutse pan 2, 32°22'S, 22°40'E, 1,000 m, 28 Mar 1978, O. J. Hansen 3392 (C). BURUNDI. Territoire: Muramvya, localité: Mwaro, 3, Feb 1973, M. Reekmans 2396 (MO); Territoire: Matana, Kiryama, 1,900 m, J. Lewalle 744 (BR); Territoire: Muramvya, près Ijenda (route vers Muramvya), 2000 m, 09 Mar 1969, J. Lewalle 3319 (BR); Territoire: Ruyigi, Musongati, 1700 m, 10 May 1974, M. Reekmans 3366 (BR); Territoire: Muramvya, Mwaro, 2,000 m, 02 Mar 1973, M. Reekmans 2396 (BR).

DEMOCRATIC REPUBLIC OF THE CONGO. Nyamutanga, Plaine de la Ruzizi, 09 Mar 1950, R. Germain 6487 (BR); Kisantu, entre Nto Mbombo et Kinfwoto, 09 Jan 1959, L. Pauwels 1230 (BR).

ETHIOPIA. Wellega region, ca. 20 km S of Asosa, 9°55'N, 34°40'E, 1500 m, 23 Oct 1996, I. Friis et al. 7902 (C); Gamu-Gofa region, Eastern slopes of Gughe highlands above Arba Minch, 6°03'N, 37°35'E, 1,800 m, 03 Nov 1975, M. G. Gilbert et al. 403 (UPS, WAG); Sidamo province, 40 km NW of Kebre Mengist, along the road to Agere Selams, 06°06'N, 39°52'E, 2,300 m, 19 Mar 1970, J. J. F. E. de Wilde 6695 (WAG).

GABON. Nyanga, Gamba, 37.5 km from Gamba airport, road to Mayonamie on the Nyanga river, 02°58'S, 10°18'E, 03 Dec 1994, J. J. F. E. de Wilde & R. W. de Wilde-Bakhuizen 11291 (WAG).

MALAWI. Zomba, 990 m, 06 Apr 1991, P. Bamps & F. Malaisse 8977 (BR).

MOZAMBIQUE. Lourenço marques, Libombos, near Namaacha, Mt Mpondium, 800 m, 22 Feb 1955, A. W. Exell et al. 501 (BM).

NIGERIA. 12 miles S of Gusau, NW of Zaria, 03 Jul 1967, P. N. de Leeuw 1940 (WAG).

RWANDA. Bugesera, entre le camp de Gako et Nyamasa, 1,500 m, 13 Mar 1972, P. Auquier 2897 (BR); Prefecture de Kibungo, Parc National de l'Akagera, region des lacs, plateau de Rwisirabo, 1,600 m, 26 Apr 1969, G. Bouxin & M. Radoux 315 (BR); Commune Runda, colline Sheri, 09 Apr 1970, G. Bouxin & M. Radoux 1656 (BR); Territ. Kibuye, Rusenyi, 1,600 m, 17 Jun 1954, A. R. Christiaensen 477 (BR).

SOMALIA. 3.5 km W of Haghadera 4°40'N, 47°51'E, 240 m, 10 Jun 1979, J. B. Gillett et al. 22499 (PRE).

SOUTH AFRICA. Eastern Cape, Mkambati Game reserve, at horseshoe waterfalls, 31°16'04"S, 30°0'33"E, 175 m, 16 Jan 1997, G. Germishuizen 9128 (PRE); Orange Free state, Farm Driekoppe, 42 km south east of Vrede on road to Verkykerskop, foot of Aasvoelkop, at back of old farm house, 2,000 m, E. Retief 2041 (PRE); Transvaal, 30 km West of Panbult on road to Amersfoot, 07 Mar 1986, G. Germishuizen 3939 (PRE); Transvaal, Brits district, S of Hartbeespoort Dam; Farm Haddedah Boerdery; SE slopes of hills above homestead, 22 Feb 1994, M. Heymann et al. 99 (PRE); Transvaal, Mountains near Trichardsdal, The Downs, 1,800 m, 06 Mar 1973, J. Vahmeijer 2371 (PRE); Natal, Bergville district, Umlambonja Valley, Cathedral Peak area, 4,700 ft, 26 Jan 1965, E. A. Schelpe 7247 (BOL).

SWAZILAND. Mbabane, 07 Feb 1959, E. Werdermann & H.-D. Oberdieck 2226 (BR).

TANZANIA. Arusha district, Mt. Meru, E slope, 5,300 ft, 27 Apr 1969, P. J. Greenway & D. V. Fitzgerald 13612 (PRE); Iringa district, Great North Road, between Matanana and Malangali, 84 ml S of Iringa 5,800 ft, 27 Mar 1962, R. Polhill & S. Paulo 1892 (PRE); T8 Nahomba Valley, 8°38'S, 38°07'E, ca. 400 m, 07 Feb 1978, K. Vollesen MRC-4898 (C).

UGANDA. Mont Namutamba, 27°15'30"E, 10°46'S, 1,180 m, 15 Feb 1987, F. Malaisse 14121 (BR); E Ankole (U2), Kashari, Nyakatoky-Buyenje, 00°22'S, 30°31'E, 1700 m, 15 Nov 1992, P. K. Rwaburindore 3499 (MO, PRE); Western province, Toro district, Ruwenzori, kilembe, 4,500 ft, 19 Dec. 1934, G. Taylor 2535 (BM).

ZAMBIA. Dambo area along Kasama-Luwingu road, 114 km W of Kasama, 10°11'50.0"S, 30°20'35.2"E, 1384 m, 27 Mar 2004, S. Dessein et al. 802 (BR, NEU); Area around Lupupa waterfalls, 11°24'22.2"S, 32°04'32.2"E, 1,416 m, 22 Mar 2004, S. Dessein et al. 657 (BR, NEU); Dambo complex, Chishinga ranch, 10°06'05.6"S, 29°43'26.2"E, 1,562 m, 28 Mar 2004, S. Dessein et al. 815 (BR, NEU); Lusaka province, Kapuka farm, Lusaka SE 22km 15°28'S, 28°29'E, 1,280 m, M. G. Bingham 8888 (BR, K); Southern province, Namwera escarpment, Jalasi, 1,120 m, 15 Mar 1955, A. W. Exell et al. 902 (BM).

ZIMBABWE. Melsester district, Chimanimani Mts at NE base of second range, 3,500–4,000 ft, 12 Feb 1958, A. V. Hall 441 (BOL); Great Dyke, Sutton mine (North), 17°22'45"S, 30°36'00"E, 1,340 m, 16 Feb 2000, Th. Baudesson et al. 81 (BR); Mappinga km 73, Muneni, 17°29'45"S, 30°34'30"E, 1,530 m, 04 Mar 2000, Th. Baudesson et al. 336 (BR).

11. *Exochaenium hockii* (De Wild.) Kissling, comb. nov. *Belmontia hockii* De Wild., Bull. Jard. Bot. Etat, Brux., 3: 266. 1911. *Sebaea hockii* (De Wild) Boutique, Fl. Afr. Centr., Gentianaceae: 48. 1972.—TYPE: [DEMOCRATIC REPUBLIC OF THE] CONGO. Katanga, Monts Kundelungu, Jun 1910, *Hock s. n.* (holotype: BR!).

Distribution and Ecology—This species is endemic to the Democratic Republic of the Congo (Katanga Province) and is found in open grassland, on quartzic soil, flowering in both March and September.

Remarks—This remarkable species is easily recognizable. It has basal leaves in a rosette surmounted by many long-pedicellate flowers, like *E. macropterum*. However, in herbarium specimens, the calyx and pedicels are hyaline, conversely to *E. macropterum*. See also *E. macropterum*.

Additional Specimens Examined—DEMOCRATIC REPUBLIC OF THE CONGO. Parc National de l'Upemba, Bnuyi-Bala, 1,750 m, 30 Mar 1948, G. F. de Witte 03599 (BR, K); Parc National de l'Upemba, près du marais Bukama, 1,810 m, 21 Aug 1949, G. F. de Witte 07037 (BR); A env. 1 km au NW de la source occidentale de la Lutshipuka (Plateau des Kundelungu, Katanga), 28 Apr 1969, St. Lisowski et al. 5672 (BR).

12. *Exochaenium lineariforme* (Sileshi) Kissling, comb. nov. *Sebaea lineariformis* Sileshi Nemomissa, Kew Bull. 54: 193,

Fig. 2. 1999.—TYPE: TANZANIA. Nkansi district: 5 km N of Namanyere, 2 May 1997, *Bidgood, Sitoni, Vollesen and Whitehouse* 3630 (holotype: K!).

Iconography—Sileshi Nemomissa, *Kew Bull.* 54: 194, Fig. 2. 1999.

Distribution and Ecology—This species is endemic to western Tanzania where it is found in seepage areas in grassland or woodland, flowering from May to August.

Remarks—This species resembles *E. alatum*, but the leaves are larger. The flowers are yellow (versus white for *E. alatum*), and the calyx is broadly winged and wider at the base (versus narrowly winged for *E. alatum*).

Additional Specimens Examined—TANZANIA. 6 miles S of Tabora, 4,000 ft, Sep 1937, *H.v.A. Lindeman* 299 (BM); T4. Kaliua, rice cultivation at junction of railway lines near station, 16 Jun 1980, *S. S. Hooper et al.* 2001 (K); Mpanda district, 19 km on Mpanda-Uvinza road, 14 May 1997, *S. Bidgood et al.* 3922 (K); Kigoma district, Mwanga, Aug 1932, *Rounce* 204 (K).

13. **Exochaenium macropterum** (Sileshi) Kissling, comb. nov., *Sebaea macroptera* Sileshi Nemomissa, *Kew Bull.* 54: 191, Fig. 1. 1999.—TYPE: TANZANIA. Mpanda district: 48 km on Mpanda-Uvinza road, 18 May 1997, *Bidgood, Sitoni, Vollesen and Whitehouse* 4012 (holotype: K!).

Iconography—Sileshi Nemomissa, *Kew Bull.* 54: 191, Fig. 1. 1999.

Distribution and Ecology—This species is endemic to western Tanzania, Mpanda district and only known from the type which grows on shallow soil over rocks in *Barchystegia* woodland, flowering in May.

Remarks—*Exochaenium macropterum* shares a basal rosette with *E. hockii*, but in herbarium specimens has a green peduncle and calyx (versus hyaline for *E. hockii*), see also *E. fernandesianum*.

14. **Exochaenium oliganthum** (Gilg) Kissling, comb. nov., *Belmontia oligantha* Gilg, in *Bot. Jahrb.* 26: 102. 1898. *Sebaea oligantha* (Gilg) Schinz, *Bull. Herb. Boiss.*, sér. 2, 6: 736. 1906.—TYPE: GABON. Sibange-Farm, auf einem steinhart getretenen Fusspfade unter Ölpalmen wachsend [growing on a footpath hard like rock, under oil palm trees]; im Januar 1880 blühend, *H. Soyaux s. n.* (holotype: B, delet.).—NEOTYPE: CAMEROON. im Urwalde bei Moliwe, Aug 1905, *R. Schlechter* 15721 (neotype: P!; isoneotype: K!, WAG!, typified by A. Raynal, 1967).

Sebaea mildbraedii Gilg, *Wiss. Ergebn.* 2. Deutsch. Zentr.-Afr. Exped. 1910–11. 2: 98. 1922.—TYPE: *Mildbraed* 6048 (holotype: B, delet.).

Exochaenium evrardii A. Rob., *Bull. Jard. Bot. Etat Bruxelles* 32: 472. 1962.—TYPE: *Evrard* 6265 (holotype: BR!).

Exochaenium bugandense A. Rob., *Bull. Jard. Bot. Etat Bruxelles* 32: 473. 1962.—TYPE: *Dawkins* 695 (holotype: K!).

Note—No isotype of *H. Soyaux s. n.* was found by A. Raynal (1967) at BM, C, Fl, G, K, HBG, W or Z. The following herbaria were searched without success by the author: BOL, BR, MO, NEU, PRE and S.

Iconography—Raynal, *Adansonia sér.* 2, 7: 212, Pl. 1 and 216, Pl. 2. 1967.

Distribution and Ecology—The distribution is mainly in the Guineo-Congolian region. It is found in forests among dead leaves, or in moist habitats in grasses. It has also been collected in the Sudano-Zambesian region, and is found in moist sites among grasses, flowering throughout the year.

Remarks—The ecology and particular morphology of this species were described by Raynal (1967). It was said by most authors (e.g. Raynal 1967; Boutique 1972; Sileshi Nemomissa 2002) to be a “saprophyte” (i.e. mycoheterotroph, Leak 1994; Franke et al. 2006), but was often found to “parasitize” (i.e. attached to) roots of other plant species (mainly Cyperaceae or Poaceae). The species is achlorophyllous. However, I found a population with some green individuals (*Dessein et al.* 499, NEU). No studies focusing on the transition between mycoheterotrophism to parasitism in *E. oliganthum* have yet been performed. Sileshi Nemomissa (2002) reported a tendency for alternate phyllotaxy in this species that I also observed. The species described as *Belmontia* sp. by Andrews in *Fl. Pl. Sudan* 3: 64. 1956. is certainly *Exochaenium oliganthum* as suggested by Raynal (1967).

Representative Specimens Examined—ANGOLA. Lunda, near Vila Henrique de Carvalho, ca. 1,100 m, 22 Apr 1937, *A. W. Exell & F. A. Mendonça* 982 (BM);

BURUNDI. Base Ruzizi, Paysannat Bulamata, Mar 1950, *R. Germain* 6583 (BR).

CAMEROON. 13 km SW of Eséka, right bank Nyong R., near ferry in road to Lolodorf, 200 m, 13 Mar 1965, *A. J. M. Leeuwenberg* 5160 (WAG).

DEMOCRATIC REPUBLIC OF THE CONGO. Ubangui-Chari-A. E. F. Haute-Kotto, 12 Oct 1921, *G. Le Testu* 3346 (BR); Yangambi, camp de la botanique, ± 470 m, 21 Dec 1939, *R. Germain* 46 (BR); Weko Jan 1949, *R. Germain* 4669 (BR); Weko, à 28 Km au Nord de Yangambi, ± 470 m, 10 Aug 1939, *J. Louis* 15734 (BR); Parc National Upembza Kanonga, ± 675 m, 21 Feb 1949, *G. F. De Witt* 5592 bis (BR).

ETHIOPIA. Wollega Region: E slope of Didessa R. valley ca. 09°03'N, 36°11'E, 1,300 m, 12 Sep 1975, *M. G. Gilbert & M. Thulin* 709 (UPS, WAG).

GUINEA-BISSAU. Canamine, 11°08' N, 15°05'W, 15 m, 8 Nov 1995. *F. Malaisse & V. Craes* 14837 (BR).

IVORY COAST. Forêt de Yapo, Sep 1965, *G. Mangenot & L. Aké Assi* (K); Yapo-forest, ca. 15 km SSE of Agkoowille, 1961, *J. J. F. E. De Wild* 3147 (WAG).

NIGERIA. Ondo, Erin Odo-ridge above waterfalls, 3 Nov 1968, *J. B. Hall* 854 (K).

TANZANIA. T4. Kigoma district, Kasye Forest, 05°41'S, 29°55'E, 900 m, 19 Mar 1994, *S. Bidgood et al.* 2816 (K, WAG).

ZAMBIA. 14 km W of Lusaka, 15°25'12.9"S, 28°10'37.7"E, 1,259 m, 12 Mar 2004, *S. Dessein et al.* 499 (BR, MPR, NEU).

15. **Exochaenium perparvum** (Sileshi) Kissling, comb. nov. *Sebaea perparva* Sileshi, *Fl. Trop. E. Afr.*, Gentianaceae: 19. 2002.—TYPE: TANZANIA. Sumbawanga district, Mbizi Mts, 07°56'S, 31°39'E, 2,050 m, 29 Apr 1997, *Bidgood S., Sitoni D., Vollesen K. and Whitehouse C.* 3586 (holotype: K!).

Distribution and Ecology—This species is known from the Democratic Republic of the Congo, Tanzania, and Zambia. This species probably has a wide Zambesian distribution like most *Exochaenium* species. However, due to its small size (< 8 mm), it has probably not been collected often. It grows on black clay in damp, or temporarily inundated grassland. It has been found once on lateritic soil (*Dessein et al.* 851, NEU). It flowers from March to April–(June).

Remarks—This dwarf species forms small mats (up to 0.8 mm high) with a few flowers (from 1–10 or more). Its impressive underground root system (Fig. 4, 5) is unique within the genus; in this way, it can be easily distinguished from the two other dwarf species. It has an entire stigma (versus bifid stigma in *E. pygmaeum*) and is chlorophyllous (versus achlorophyllous for *E. oliganthum*).

Additional Specimens Examined—DEMOCRATIC REPUBLIC OF THE CONGO. Kipopo, 20 Km NO d'Elisabethville, 28 Jan 1958, *A. Schmitz* 5866 (BR); Lubumbashi-Likasi Km 70, 1,200 m, 11 Feb 1987, *F. Malaisse* 14024 (BR).

ZAMBIA. Dambo 15 km W of Luwingu, 10°13'16.3"S, 29°44'57.7"E, 1,548 m, 28 Mar 2004, S. Dessein et al. 827 (BR, NEU); Dambo near Twatasha village, W of Mbala, 08°56'49.8"S, 31°11'25.7"E, 1,524 m, 23 Mar 2004, S. Dessein et al. 728 (BR, NEU).

16. *EXOCHAENIUM PLATYPTERUM* (Baker) Schinz, Bull. Herb. Boiss., sér. 2, 6: 716. 1906. *Belmontia platyptera* Baker, Bull. Misc. Inform. 1894: 25. 1894. *Parrasia platyptera* (Baker) Hiern, Cat. Pl. Afr. Welw. 1, 3: 706. 1898. *Sebaea platyptera* (Baker) Boutique, Fl. Afr. Centr., Gentianaceae: 48. 1972.—TYPE: ANGOLA. province Huila, *Welwitsch 1524 (1512)* (holotype: K!, isotype BM! —but see note).

Note—Hiern (1898) stated that the no. 1524 on the sheet from Kew is a mistake, it should read 1512. I agree with him. The current *Welwitsch 1524* is the type of *E. gracile*.

Iconography—Sileshi Nemomissa, Flora of Tropical East Africa, Gentianaceae: 17, Fig. 4. 2002.

Distribution and Ecology—This species is known from the Zambesian region and the Guineo-Congolia/Zambesia transition zone (sensu White 1986) where it grows on damp soil, usually in open forest, flowering from March to April–(June).

Remarks—This taxon is easily recognizable from the rest of *Exochaenium*, by its pendant, small flowers and a conspicuously winged calyx.

Representative Specimens Examined—BURUNDI. Territoire Bururi, Nyanza lac, route de Makamba, 900 m, 19 Mar 1967, J. Lewalle 1700 (BR, WAG).

DEMOCRATIC REPUBLIC OF THE CONGO. Haut-Katanga, source de la Kasombo, Jun 1934, *Quarré 4047* (BR); Mumiama, 9 Apr 1957, *E. Detilleux 786* (BR); Route Lubumbashi-Kasenga km 42, env. 1,200 m, 23 Apr 1974, *F. Malaisse 7756* (BR); Environ d'Elisabethville, vallée de la Lubumbashi, ± 1,280 m, 19 Mar 1926, *W. Robyns 1690* (BR).

TANZANIA. Mbeya district, Muvwa, 08°50'S, 33°20'E, 1,250 m, J. C. Lovett & C. J. Kayombo 4508 (MO); T4. Nkansi district, 18 km on Namanyere-Kipili road, 07°27'S, 30°54'E, 1,150 m, 6 May 1997, S. Bidgood et al. 3730 (K); T4. Mpanda district, 31 km on Mpanda-Inyonga road, 06°24'S, 31°19'E, 1,050 m, 17 May 1997, S. Bidgood et al. 3996 (K).

ZAMBIA. Southern province, Ncheu district, Lower Kirk Range, Chipusiri, 1,460 m, 17 Mar 1955, A. W. Exell et al. 935 (BM); Victoria, Rhodesia, C. F. H. Monroe, 1775 (BM); Lusaka province, Jellis' farm; Lusaka SE 20 km 1528A4, 1,300 m, 28 Mar 1993, M. G. Bingham 8950 (K); Northern province, Mporokoso district, Lumangwe Falls on the Kalungwishi R., 45 km NE of Kawamba. 32°10'E, 10°00'S, 1,100 m, D. J. Goyder et al. 3030 (K); Lusaka East Protected Forest Reserve, 028°25.22'S, 015°28.51'E, 1,325 m, 18 Apr 2004, J. Kissling 75 (NEU).

ZIMBABWE. Miami, Apr 1926, R. F. Rand 67 (BM).

17. *EXOCHAENIUM PRIMULAEFLORUM* Welw., Trans. Linn. Soc. London 27: 47. 1869. *Parrasia primuliflora* (Welw.) Hiern. Cat. Afr. Pl. 1: 707. 1896. *Belmontia primulaeflora* (Welw.) Engl., Abh. Königl. Wiss. Berlin 2: 336. 1892. *Sebaea primulaeflora* (Welw) Sileshi, Kew Bull. 55: 217. 2000.—TYPE: ANGOLA. Huilla, towards Humpata, Apr 1860, *Welwitsch 1513* (lectotype: K!, typified by Sileshi Nemomissa 2000, isotype: M!, C!).

Exochaenium primulaeflorum var. *nanum* Welw., Trans. Linn. Soc. London 27: 48. 1869. *Parrasia primuliflora* var. *nana* (Welw.) Hiern, Cat. Afr. Pl. 1: 708. 1896.—TYPE: ANGOLA. Huilla, towards Gambos, Apr 1860, *Welwitsch 1514* (holotype: K!).

Distribution and Ecology—This species is endemic to Angola, flowering from April to June.

Remarks—his species resembles *E. grande* but differs by its general habit. The plant is branched from the base, and the inflorescence is formed of many flowers (5–10), while *E. grande* has a typical erect habit and few flowers (2–3(–5)).

Additional Specimens Examined—ANGOLA. Huila, Humpata district, upper Zootechnica, 54.617°S, 17.264°E, 2,185 m, 16 Jan 2009, *DUB 1190a* (PRE, LUBA); Huila district, Apr 1860, *Welwitsch 1514* (BM); Huila, between Sada Bandeira and Humpata, near Humpata, ca. 2,000 m, 05 Jun 1937, A. W. Exell & F. A. Mendonça 2611 (BM); Huila, between Sa da Bandeira and Humpata, ca. 2,000 m, 15 May 1937, A. W. Exell & F. A. Mendonça 1953 (BM).

18. *EXOCHAENIUM PUMILUM* (Baker) Hill, Bull. Misc. Inform. 1908: 336. 1908. *Belmontia pumila* Baker, Bull. Misc. Inform. 1894: 25. 1894. *Sebaea pumila* (Baker) Schinz, Bull. Herb. Boiss., Sér. 2, 6: 731. 1906.—TYPE: NIGERIA. swamp at Nupe, near mouth of Niger, *Barter 1680* (holotype: K! —but see note).

Note—In the protologue, Baker defined the type, as “Swamps at Bupe, near the mouth of Niger, *Barter*.” It seems clear that Baker referred to herbarium sheet *Barter 1680*.

Iconography—Sileshi Nemomissa, Flora of Tropical East Africa, Gentianaceae: 17, Fig. 4. 2002; drawing on sheet *Hehandeles 1289* (K) and on the holotype (K).

Distribution and Ecology—This species is known from Angola, Democratic Republic of the Congo, Kenya, Mozambique, Nigeria, Republic of South Sudan, Tanzania, Uganda, and Zambia. It is widespread in the Sudano-Zambesian region, flowering mainly from March to May, but it has been collected throughout the year.

Remarks—see *E. debile*.

Representative Specimens Examined—DEMOCRATIC REPUBLIC OF THE CONGO. Nsanda (près du Fleuve), territoire Kasengulu, 17 Mar 1976, L. Pauwels 5324 (BR); Parc National de la Garamba, piste centrale vers km 30, Vallée? de la Garamba, 03 Sep 1952, *Troupin 1358* (BR).

TANZANIA. Songea district, about 1.5 km E of Songea in damp soil at margin of boggy grassland and *Brachystegia* woodland, 1,050 m, 04 Feb 1956, *Milne-Redhead & Taylor 8483* (BR); Songea district, Kwamponjore Valley about 9.5 km SW of Songea in boggy grassland overlying laterite, 1,000 m, 26 Apr 1956, *Milne-Redhead & Taylor 9835* (BR).

UGANDA. Masche district, near lake Nabugato, 3,750–3,800 ft, Aug 1985, *Hehandles 1289* (K); Katera-Kiebbe road, 1 mile from Katera, 1,150 m, 01 Oct 1953, *Drummond & Hemsley 4521* (K, BR).

19. *EXOCHAENIUM PYGMAEUM* Milne-Redhead, Kew Bull. 4: 377. 1951. *Sebaea perpusilla* Paiva and Nogueira, Anal. Jard. Bot. Madrid 47: 99. 1990.—TYPE: [ZAMBIA], Mwinilunga, Sinkabalo Dambo, 9 Dec 1937, *E. Milne-Redhead 3579* (holotype: K!).

Note—Paiva and Nogueira when transferring *Exochaenium pygmaeum* to *Sebaea* had to choose a new epithet because *Sebaea pygmaea* Schinz, Bull. Herb. Boiss., sér. 2, 6: 740. 1906. already exists.

Iconography—drawing on sheet: *E. Milne-Redhead 3579* (K).

Distribution and Ecology—This species has been collected in Zambia, Mwinilunga, Sinkabalo Dambo and in Mongu, flowering from December to January.

Remarks—see *E. debile*. This minute species is similar in all points to *E. debile*, from which it only differs by its stigma (entire for *E. debile* versus bifid for *E. pygmaeum*). The bifid stigma of *E. pygmaeum* might only be a local aberration of *E. debile*. In doubt I decided to maintain *E. pygmaeum* as distinct from *E. debilis*. In the collection *Robinson 6829* (K), some flowers even exhibit two distinct style and carpels (the two carpels in *Exochaenium* are usually postgenitally fused. For the role of postgenital and congenital fusion, see Endress 2006).

Additional Specimens Examined—ZAMBIA. Mongu, 29 Jan 1966, *Robinson 6829* (K).

20. *Exochaenium rotundifolium* (Peter) Kissling, comb. nov. *Belmontia rotundifolia* Peter, Abh. Ges. Wiss. Gottingen n.

f. 13, 2: 89., Fig. 19. 1928.—TYPE: TANZANIA. Uvinza, bei km 1140.8 westlich von der Bahnstation Uvinza, 990m, 06 Feb 1926, *Peter* 36357 (holotype: B!). non *Sebaea rotundifolia* A.W. Hill, Bull. Misc. Inform. Kew 1908: 326. 1908.—TYPE: SOUTH AFRICA. Natal, Drakensberg, *Buchanan* 31.

Sebaea brevicaulis Sileshi, Kew Bull. 55: 213–214, Fig. 1. 2000. syn. nov.—TYPE: TANZANIA. Mapanda district, 56 km on Uvinza-Mpanda road, 27 May 1997, *Bidgood*, *Sitoni*, *Vollesen* and *Whitehouse* 4121 (holotype: K!).

Iconography—Peter, Abh. Ges. Wiss. Göttingen n. f. xiii. II: 90. 1928 and Sileshi Nemomissa, Kew Bull. 55: 215, Fig. 1. 2000.

Distribution and Ecology—This species is endemic to Tanzania and only known from the type localities, flowering in February and May.

Remark—see *E. fernandesianum*. Unfortunately Sileshi Nemomissa (2000) while working on the *Flora of East Tropical Africa* did not notice that his new species *Sebaea brevicaulis* had already been described by Peter (1928), also from a specimen from Tanzania. Thus *S. brevicaulis* Sileshi is synonymized with *E. rotundifolium* here.

21. EXOCHAENIUM TEUCSZII (Schinz) Schinz, Bull. Herb. Boiss. Sér 2, 6: 716. 1906. *Belmontia teuszii* Schinz, Viertlj. Nat. Gesellsch. Zürich. 36: 335. 1891. *Sebaea teuszii* (Schinz) Taylor, Taxon 12: 294. 1963.—TYPE: ANGOLA. Malange, *Teusz* 387 (holotype: Z!; isotype: K!, MO).

Belmontia teuszii var. *angustifolia* De Wild., Bull. Jard. Bot. Etat. Brux. 3: 279. 1911.—TYPE: [DEMOCRATIC REPUBLIC OF THE CONGO]. Kundelungu, 13 Mar 1908, *Th. Kassner* 2584 (holotype: K!).

Tachadenus continentalis Baker in Bull. Misc. Inform. 1895: 70. 1895.—TYPE: ZAMBIA. Fwambo?, 1894, *A. Carson* 33 (holotype: K!).

Belmontia mechowiana Schinz, Viertlj. Nat. Gesellsch. Zürich. 36: 333. 1891. *Exochaenium mechowianum* (Schinz) Schinz, Bull. Herb. Boiss. Sér 2, 6: 716. 1906. *Tachadenus mechowianus* (Schinz) Hill, Bull. Misc. Inform. 1908: 337. 1908.—TYPE: ANGOLA. Benguella, bank of Hamba, near Gambo, Jul 1880, *Mechow* 503 (holotype: Z!).

Belmontia chevalieri Des Abbayes and Schnell, Bull. Soc. Bot. Fr. 96: 204. 1950.—TYPE: REPUBLIC OF GUINEA. Fouta-Djalón, Plateaux du Benna, Nov 1944, *Schnell* 2135 (holotype: P!; isotype P!).

Exochaenium gentilii De Wild., Ann. Mus. Congo, Bot., Sér. 5, 2: 336. 1908. *Sebaea gentilii* (De Wild) Boutique, Fl. Afr. Centr., Gentianaceae: 48. 1972. *Belmontia gentilii* De Wild, Th. and H. Dur., Syll.: 373. 1909. syn. nov.—TYPE: [DEMOCRATIC REPUBLIC OF THE CONGO]. Kanda Kanda, *Gentil* s. n. (holotype: BR!).

Belmontia chionantha Gilg, in Baum, Kunene.-Samb.-Exped.: 332. 1903. *Exochaenium chionanthum* (Gilg) Schinz, Bull. Herb. Boiss. Sér 2, 6: 716. 1906.—TYPE: ANGOLA. am Lazingna, auf Moorboden zwischen Gras, ziemlich selten, 1,300 m, 19 Apr 1900, *Baum* 838 (lectotype: Z!, isolectotype: E, M, S!, W!). A lectotype is chosen here among the three paratypes *Baum* 316, *Baum* 702, and *Baum* 838.

Note—The protologue and all subsequent treatments use the epithet *teuszii*, and mentioned the collector as *Teusz*.

Sileshi Nemomissa (2002) postulated that the correct spelling of his name is *Teusz*, and corrected the specific epithet to *teuszii* (Article 60 of the Code).

Iconography—Sileshi Nemomissa, Flora of Tropical East Africa, Gentianaceae: 17, Fig. 4. 2002.

Distribution and Ecology—This species is distributed in the Sudano-Zambesian region. In swamps, inundated savannah, along lakeshores, and usually growing in wet places. Flowering is from (January)-February-April-(June), (May), (September) in the Zambesian region. However, this species was found to flower throughout the year. Its flowering time depends on water availability.

Remarks—This species could be divided in two groups that only vary in diameter of corolla. With a short-size group corresponding to *E. chionanthum*, and a large-size group corresponding to *E. teuszii* s. s. Here I follow recent authors (e.g. Boutique 1972; Paiva and Nogueira 1990a; Sileshi Nemomissa 2002) who have treated these two groups as a single species. I was not able to find any morphological difference between those two groups except the general size of the flowers (i.e. corolla of 20–45 mm in diameter for the large-size group versus 5–10 mm in diameter for the small-size group). In addition, the ecology of this species is strongly related to water availability; this kind of variation in corolla diameter may be explained by different germination and floral resource allocation strategies depending on the local environment.

Exochaenium teuszii was once placed within the genus *Tachadenus* because of its long corolla tube (up to 3.5 cm). This character is a convergence between the two genera. *Tachadenus* is endemic to Madagascar, while *Exochaenium* is endemic to tropical Africa. *Exochaenium gentilii* De Wild. is synonymized here. I did not find morphological support to treat *E. gentilii* as distinct from *E. teuszii*. However, Boutique (1972) stated that the corolla of *E. gentilii* is yellow. Corolla color variation within a species is not rare in the Gentianaceae (e.g. white and pink *Centaurium pulchellum*, several white and blue *Gentiana* and *Gentianella* or white, salmon and yellow *Exochaenium grande*) and I thus did not consider this character as distinctive for the two species.

Representative Specimens Examined—ANGOLA. Lunda, between Vila Henrique de Carvalho and Muriege, 100–1,100 m, 20 Apr 1937, *A. W. Exell* & *F. A. Mendonça* 783 (BM).

DEMOCRATIC REPUBLIC OF THE CONGO. Region de Tchoma et de Mwero Wantipa (Katanga), 25 Aug 1939, *H. J. Bredo* 3435 (BR); Province: Katanga, territoire: Mitwaba, location: Kaziba-Parc National Upemba, 1,500 m, 16 Feb 1948, *G. F. de Witte* 3386 (BR, C); Plateau des Kundelungu (près de la source de la Lutshipuka), 1,670 m, 5 May 1986, *F. Malaisse* 13851 (BR); Plateau des Kundelungu, 5.8 km au N du poste de Katshupa, 1,680 m, 4 Aug 1966, *F. Malaisse* 4519 (BR); Kundelungu, 1908, *L. C. Kassner* 2584 (BM); District de Mbomo, Région de la cuvette, “ésobé” à 2 km à l’Est du camp Mboko, dans la savane entre les rivières Lékéné et Lango (grande depression en savane), 00°35’N, 14°55’E, 400 m, 17 Dec 1994, *D. Champluvier* 5133 (BR); Entre Ngoma et Kikuransa, territoire: Popokabaka, 5 May 1959, *L. Pauwels* 2794 (BR); Nganga, Kwango, Vallée de la Njari, 24 Feb 1956, *R. Devred* 2799 (BR); Entre les chutes François-Joseph et Tanzi (Kivango), env. 700 m, Jan 1930, *J. Lebrun* 128 (BR); Lovanium, Kinshasa, 23 Feb 1971, *J. Bouharmont* 6981 (BR).

REPUBLIC OF GUINEA. Dalaba, plateau de Diaguissa, vers 1,300 m, 12 Feb 1951, *H. des Abbayes* 310 (de 1951) (BM).

SIERRA-LEONE. Top of hills opposite Bumban School, Gbenge Hills, 28 Nov 1966, *J. K. Morton* SL2887 (WAG).

TANZANIA. T4 Mpanda district, 56 km on Uvinza-Mpanda road, 05°29’S, 30°32’E, 1,600 m, 21 May 1997, *S. Bidgood et al.* 4124 (C, K); T4. Sumbawanga district, 6 km on Tatanda-Mbala road, 08°32’S, 31°30’E, 1,700 m, 24 Apr 1997, *S. Bidgood et al.* 3410 (C, K).

ZAMBIA. Northern province, 72 km south of Abercorn on Kasama road, 30 Mar 1955, *A. W. Exell et al.* 1339 (BM); Abercorn, Mbuga of Lake

Chile, 24 Sep 1949, A. A. Bullock 1061 (BR); A 3 km de Samfya, "Dambo" humide de la Kasamba (versant NW), 17–18 Apr 1963, J. J. Symoens 10311 (BR); N Katete by irrigation terraces, 3 Jan 1937, C. K. Ricardo 522 (BM); Abercorn, Mketé woodland, near Ndundu, 5,800 ft, 12 Mar 1967, H. M. Richards 22157 (MO); Between Serenje–M'pika, 16 Sep 1930, I. B. Pote Evans 2910 (PRE); Northern province, Mpika district, 32 km S of Mpika, third dambo from great north road on road down Luangwa escarpment, 30 Mar 1984, R. K. Brummitt et al. 16999 (K, MO); Mporokoso district, along Mporokoso–Kasama road, 95 km ESE of intersection of Mporokoso–Nsama–Kasama roads N of Mporokoso. At bridge over Nchelenje River, 09°43'31"S, 30°43'58"E, 1,410 m, 9 Dec 1993, D. K. Harder et al. 2284 (MO); Between Kasenga and Kazembe, just W of Pembe lagoon, 09°51'06.2"S, 28°45'28.6"E, 930 m, 17 Mar 2004, S. Dessein et al. 599 (BR, NEU); Chikoti dambo, 10°15'08.5"S, 30°03'39.3"E, 1,348 m, 29 Mar 2004, S. Dessein et al. 833 (BR, NEU); Uningi dambo, S of Mbala, 08°56'09.5"S, 31°21'36.7"E, 1,674 m, 26 Mar 2004, S. Dessein et al. 771 (BR, NEU).

22. *Exochaenium wildemanianum* (Boutique) Kissling, comb. nov. *Sebaea wildemaniana* Boutique, Bull. Jard. Bot. Nat. Belg., 41: 262. 1971. *Exochaenium wildemanianum* Gilg ex De Wild., Ann. Mus. Congo. Bot., ser 5, 2: 336. 1908; nomen nudum.—TYPE: DEMOCRATIC REPUBLIC OF THE CONGO. Kasai, rive du Kasai, Luja 222 (holotype: BR!).

Distribution and Ecology—This species is known from the southern Democratic Republic of the Congo, growing in marsh grassland, riverbanks, flowering in March.

Remarks—This species has marked 3-nerved leaves, like sometimes is found in *E. grande*, but differs by its size (up to 5 cm versus 10–20 (30) cm for *E. grande*). The flowers of *E. wildemanianum* are pure white, while *E. grande* usually has salmon flowers.

Additional Specimen Examined—DEMOCRATIC REPUBLIC OF THE CONGO. Environ de Bokala, sur bac de sable, 31 Mar 1908, M. Laurent 607 (BR).

Uncertain Sedes—*Sebaea species* A sensu Sileshi Nemomissa, in FTEA, Gentianaceae: 21. 2002.—Kenya, Northern frontier district: Moyale, 3 Jul 1952, Gillett 13475 (K!). This species has not been formally described and, according to the description, has to be placed in *Exochaenium*. It is an annual herb about 4 cm high. The stem is simple, leaves are sessile, the flower is 5-merous, yellow, the filaments are short and stamens are inserted into the corolla tube, the stigma is clavate, papillate. The material is insufficient to be described as a new species.

Distribution and Ecology—This species is only known from the above collection, flowering in July.

TAXONOMIC TREATMENT OF *LAGENIAS* E. MEY

LAGENIAS E. Mey., Comm. Pl. Afr. Austr. 186. 1837.—TYPE: *Lagenias pusillus* (Eckl. ex Cham.) E. Mey., Comm. Pl. Afr. Austr. 186. 1837. *Sebaea pusilla* Eckl. ex Cham., Linnaea 6: 346. 1831.

Annual, erect herbs (1–12 cm). Stems simple or branched, slightly 4-ridged or terete. Leaves well developed, sessile, opposite, ovate-lanceolate or elliptic, acute, somewhat fleshy. Inflorescences (1)–3–5-flowered, with relatively conspicuous bracts. Flowers pedicellate, 5-merous, terminal, solitary, yellow. Calyx free, linear-lanceolate. Corolla tube cylindrical, 5–10 mm long; lobes orbicular or elliptic-obovate, rounded or usually subacute at the apex. Filaments filiform, with a particular S-shape (Fig. 6), inserted in the corolla tube, at the level of the upper part of the ovary. Anthers oblong, medifixed, included in the corolla tube, with an apical gland and with 2 basal glands. Ovary ovoid or obovoid or almost globose, bilocular, placentas axile, ovules numerous. Style long (ca. 2 mm), filiform, included, never with secondary stigma. Stigma capitate, slightly bilobed. Capsule ovoid or obovoid, membranous or coriaceous, septicidally bivalved.

Seeds minute, very numerous, cubical with polygonal testa cell.

Differences with the Other Genera of the Exaceae—*Lagenias* can easily be distinguished from other genera of Exaceae by both its medifixed anthers, and its seeds (cubical with polygonal testa cells). *Lagenias* differs from *Sebaea* by its included stamens (versus usually exerted in *Sebaea*), and the absence of a secondary stigma on the style, which is a synapomorphy for *Sebaea*. *Lagenias* differs from *Exochaenium* by its stigma shape (bilobed versus entire for *Exochaenium*), and from *Exacum*, *Gentianothamnus*, *Klackenbergia*, *Ornichia*, and *Tachiadenus* by its yellow flowers (versus white or blue-purple).

LAGENIAS PUSILLUS (Eckl. ex Cham.) E. Mey., Comm. Pl. Afr. Austr. 186. 1837. *Sebaea pusilla* Eckl. ex Cham., Linnaea 6: 346. 1831.—TYPE: SOUTH AFRICA. Cape, Table Mountain, Ecklon s. n. (holotype: HAL, not seen; isotype: K!, C!).

Sebaea pusilla var. *major* Hill, Bull. Misc. Inform. Kew 1909: 49–50. 1909.—TYPE: SOUTH AFRICA. Cape, Clanwilliam, Leipoldt 654 (holotype: GRA!, isotype: K!).

Distribution and Ecology—*Lagenias* is endemic to southwestern South Africa (Fig. 3); it has been found from Table Mountain up to Nieuwoudtville and Calvinia and mostly grows in moist sandy soils, flowering from September to November–(December).

Representative Specimens Examined—SOUTH AFRICA. Clanwilliam district, Boontjieskloof, NE of Pakhuis, 24 Oct 1970, Esterhuysen 32514 (S); Piketberg district, Piketberg Mt, 15 Dec 1979, Esterhuysen 25219 (S); Theewaterskloof, along a path going down from the road R44, 22 Nov 2010, Kissling 29/2010 (NEU, BOL); Devils Peak, along path to the top, 33°57.505'S, 018°25.710'E, 23 Nov 2010, Kissling 31/2010 (NEU, BOL); Nieuwoudville, 8 km avant Nieuwoudville, en venant depuis la N7, 31°23.346'S, 019°02.640'E, 773 m, 26 Nov 2005, Kissling & Zeltner 64 (NEU, BOL); Houw Hoek, 24 Nov 1896, Schlechter 9376 (BM); Cape peninsula, 22 Nov 1932, Salter 2872 (BM).

NOTES ON *BELMONTIA* E. MEY. AS SYNONYMS OF *SEBAEA* R. BR. EX SOL.

In my work on the African Exaceae, I conclude that that *Belmontia* is inseparable from *Sebaea* and should be treated as a synonym of the latter. Synapomorphies delimitating *Sebaea* are: (i) seed shape and seed testa cell patterning (Kissling et al. 2009c) and (ii) the presence of a secondary stigma (Hill 1908; Kissling et al. 2009c). *Sebaea exacoides* (the type species of *Belmontia*) shares with all the remaining *Sebaea* the presence of secondary stigma. Furthermore, recent molecular phylogenies (Kissling et al. 2009b, 2009c) show that *S. exacoides* is nested deeply within *Sebaea*. Therefore, the genus *Belmontia* has to be treated as synonymous with *Sebaea*.

SEBAEA R. Br. Ex Sol., Prod. 451. 1810.—TYPE: *Sebaea ovata* (Labill.) R. Br., Prodr. 451. 1810. *Exacum ovatum* Labill., Novae Hollandiae plantarum 1. Paris 38. 1805.

Belmontia E. Mey, nom. cons. Comm. Pl. Afr. Austr. 183. 1837. *Parrasia* Raf., nom. rejic. Fl. Tellur. 3: 78. 1836.—TYPE: *Sebaea exacoides* (L.) Schinz, Bull. Herb. Boiss., Sér. 2, 6: 728. 1906. *Gentiana exacoides* L., Sp. Pl. Ed. 2: 332. 1762. *Exacum cordatum* L. f., Suppl. 124. 1781. *Sebaea cordata* (L. f.) Roem et Schult., Syst. Veg. 3: 161. 1818. *Parrasia cordata* (L. f.) Rafin., Fl. Tellur. 3: 78. 1836. *Belmontia cordata* (L. f.) E. Mey., Comm. 183. 1837.

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