

A revision of the genus *Marlothiella* (Apiaceae)

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Abstract

Marlothiella gummifera is a small perennial shrublet endemic to the Skeleton Coast of Namibia. Surprisingly it was found that the general fruit morphology agrees with that typically found in Saniculoideae and other basally diverging taxa. It is remarkable in the combination of a compound umbellate inflorescence, slightly heteromorphic fruits and dispersed crystals (typical of basally divergent genera of the subfamily Apioideae) with several characters typical of the subfamily Saniculoideae: large rib ducts, no vittae, unicellular stellate trichomes (not yet observed in any other genus of the family), and ventral vascular bundles that are poorly developed or absent. New insights into the morphology and possible systematic affinities of this poorly known monotypic genus are presented, together with a detailed taxonomic revision.

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1. Introduction

During routine carpological studies of the African genera of Apiaceae, a surprising discovery was made that the monotypic Namibian endemic *Marlothiella* H. Wolff completely lacks vittae and rather has large rib oil ducts (the intrajugal oil ducts of Drude, 1898). The implication is that the genus does not belong to the subfamily Apioideae but that it is more likely related to the subfamily Saniculoideae. It became clear that a detailed analysis of this interesting and anomalous genus was an urgent priority, in view of numerous studies that are currently underway to devise a new familial and infrafamilial classification system for the Apiaceae (e.g., Plunkett et al., 1996, 1997; Downie and Katz-Downie, 1999; Downie et al., 2001; Plunkett, 2001; Valiejo-Roman et al., 2002; Chandler and Plunkett, 2004; Lowry et al., 2004; Plunkett et al., 2004). *Marlothiella* was not yet known at the time, but the system of Drude (1898), com-

prehensive and useful as it may have been, made no provision for the lesser known African genera such as *Lichtensteinia* and *Steganotaenia*. As a result, several of them would not be identified to the correct subfamily in Drude's key. Previous studies of the monotypic genus *Marlothiella* (Wolff, 1912; Engler, 1921; Schreiber, 1967; Dyer, 1975; Burt, 1991; Van Wyk, 2000) have been somewhat superficial, and rigorous morphological and anatomical observations were necessary for a revision of the genus and to assist in interpreting future molecular results.

The purpose of this paper is therefore to provide a detailed study of the morphology and especially the fruit structure of *Marlothiella* to determine if characters can be found to support the notion that the genus is misplaced not only in the tribe Apieae (Pimenov and Leonov, 1993) but indeed in the subfamily Apioideae.

2. Materials and methods

Leaves, bracts, bracteoles, flowers and mature fruits of *Marlothiella gummifera* were rehydrated prior to photographing and drawing. Voucher specimens (also listed in the figure captions) included *Dinter 6347* (PRE), *Marloth 5360* (PRE), *Merxmüller & Giess 2344* (WIND), *Merxmüller and Giess 28330* (PRE) and *Range 1742* (BOL). Portions of the leaf blades and petioles and

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Fig. 1. Herbarium specimen of *Marlothiella gummifera* showing the woody branches, thick, subsucculent leaves and short compound umbels.

some mature fruits were placed in FAA for a minimum of 24 h after rehydration and then treated according to the method of Feder and O'Brien (1968) for embedding in glycol methacrylate (GMA). A Porter-Blüm ultramicrotome was used to cut transverse sections, about 5 μm thick, and the periodic acid-Schiff/toluidine blue staining method (Feder and O'Brien, 1968) was used. Suitable sections were photographed and drawn. The terminology used is illustrated in the figures.

3. Results

3.1. Vegetative morphology and anatomy

The plants are cushion-shaped shrublets up to 0.4 m high and spreading to a width of 1 m when growing in sheltered places. They are gnarled, densely leafy and subsucculent (Fig. 1). The older stems are woody and have a smooth, pale brown surface.

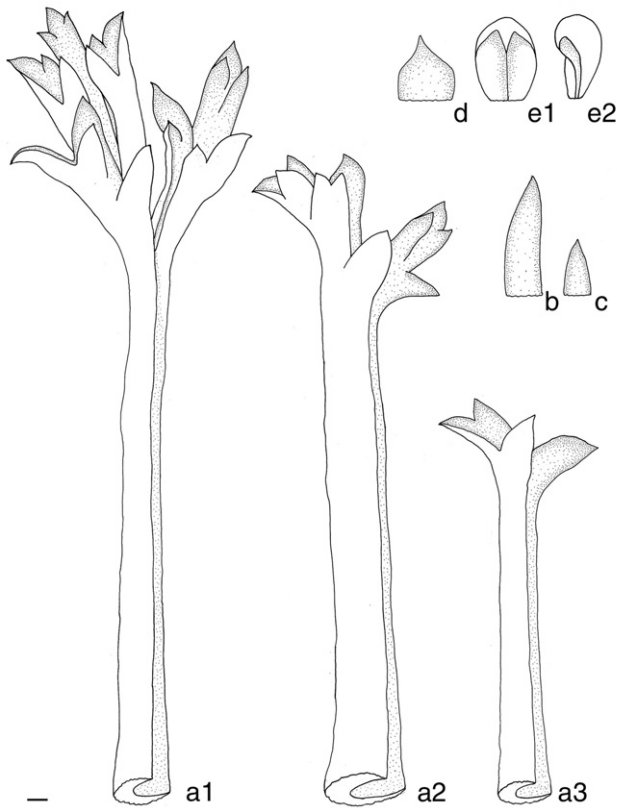


Fig. 2. The leaves (a1–3), bract (b), bracteole (c), calyx tooth (d) and petals (e1, e2) of *Marlothiella gummifera*. [leaves, bracts and bracteoles from *Merxmüller and Giess 28330* (PRE), calyx tooth and petals from *Marloth 5360* (PRE)]. Scale bar=1 mm in a–c and 0.18 mm in d and e.

Young stems are glabrous. The leaves (Fig. 2a1–3) are mostly clustered on short, lateral shoots. They are pinnate to bipinnate, completely glabrous, thick and fleshy. The petioles are very long and markedly grooved along their upper surfaces, with the bases somewhat sheathing. The lamina is much reduced, relatively small and conduplicate, with short, thick and acute ultimate segments. The epidermal cells of the leaf blade and petiole are anticlinally elongated (Fig. 3a1, a2, b) and the stomata occur on

both surfaces where they are deeply sunken (Fig. 3a1, a2). Slightly lignified cells occur between the epidermis and the larger oil ducts especially of the petiole. The vascular bundles are dispersed in the mesophyll. Oil ducts of varying sizes are present immediately inside the palisade parenchyma.

3.2. Reproductive morphology and anatomy

Inflorescences are very short, the umbels compound with short peduncles and a few (ca. six or seven) short rays. Bracts (Fig. 2b) and bracteoles resemble the leaf segments. They are oblong to ovate, thick and fleshy, with acute apices (Fig. 2c). The flower number varies from about three to seven per umbel. The flowers are completely sessile, resulting in the secondary umbels being capitate. Calyx teeth are somewhat fleshy, broadly ovate-triangular in shape, with a thickened midrib (containing a large, unbranched, median oil duct) and an acute, slightly inflexed tip (Figs. 2d and 4a). The greenish white or pinkish petals (Fig. 2e1, e2) are ovate, inflexed at the apex, with the inflexed portion not free but continuous with a distinct keel along the inner face (Fig. 2e1, e2).

The fruits are broadly ovoid, 4–5 mm long and 3–4 mm wide (Fig. 4b). A very unusual feature is the stellate trichomes covering the mericarp surface. Surprisingly, these hairs appear to be unicellular (Fig. 4c) with branches having exceptionally thick cell walls. Another unexpected character is the symmetry of the fruits. The two mericarps are slightly heteromorphic (Fig. 4d, e) — the one mericarp has one large median rib and two large marginal ribs, while the other has two large lateral ribs. The most interesting and significant observation is the presence of large rib oil ducts (surrounded by several concentric layers of cells) and the absence of vittae. Each mericarp usually has five large rib ducts, but sometimes there may be an additional rib duct in one or both of the marginal ribs. The lignified xylem cells of each vascular bundle are dispersed rather than forming a single group of cells as is usual for almost all other Apiaceae. The commissure (the area where the two mericarps are joined) is about half of the mericarp width. A ventral vascular bundle may be absent but, if present, is small (Fig. 4d–f) and does not

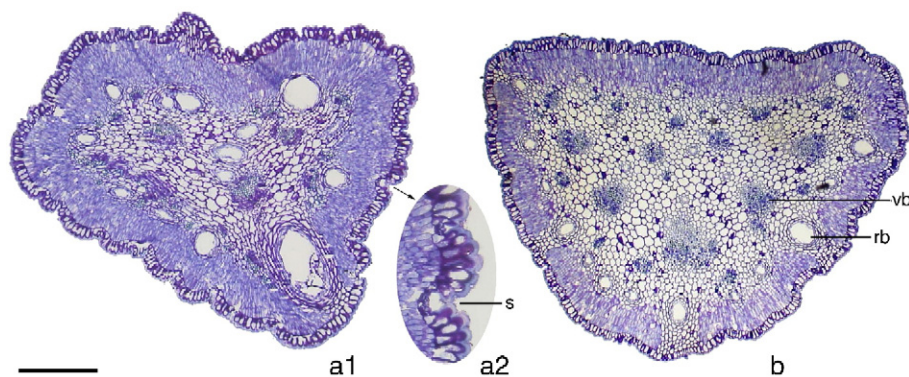


Fig. 3. Transverse sections of the leaf blade (a1, a2) and petiole (b) of *Marlothiella gummifera* [voucher specimen: *Marloth 5360* (PRE)], showing the anticlinally elongated epidermal cells, sunken stomata (s), dispersed vascular bundles (vb) and oil ducts (rb). Scale bar=0.5 mm in a1 and b, and 0.2 mm in a2.

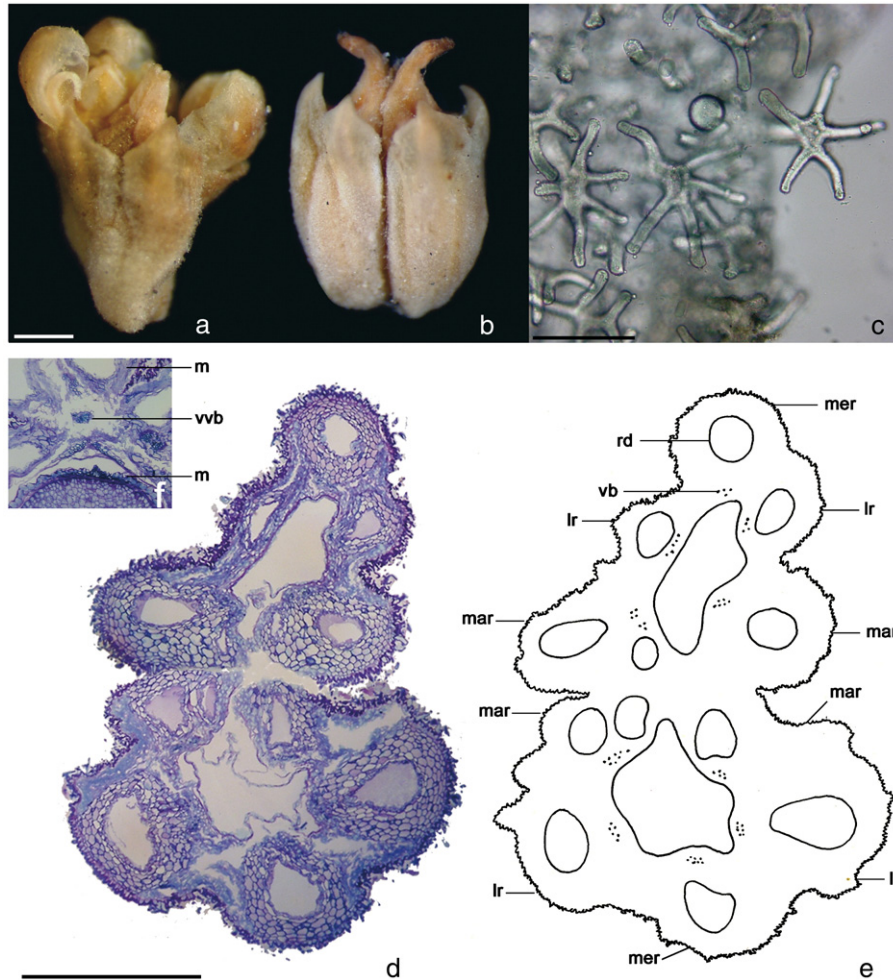


Fig. 4. A flower (a) [voucher specimen: *Marloth 5360* (PRE)] and fruit (b–e) [voucher specimen: *Merxmüller and Giess 2344* (WIND)] of *Marlothiella gummifera*. Stellate trichomes (c) are visible on the mericarp surfaces. Transverse section of fruit (d, e) showing the slightly heteromorphic mericarps (mer=median rib; lr=lateral rib; mar=marginal rib), large rib ducts (rd) and small vascular bundles (vb). Small portion of commissural area of mericarps (m) with ventral vascular bundles (vvb). Scale bar=1 mm.

form a carpophore. Many druse crystals are present and they are dispersed in the mesocarp.

4. Discussion

Our previous studies (Liu, 2004; Liu et al., 2003a,b) showed that fruits with heteromorphic mericarps are present in the basally diverging genera *Annesorhiza* Cham. and Schltldl, *Heteromorpha* Cham. and Schltldl, *Molopospermum* W.D.J. Koch, *Polemanniopsis* B.L. Burt and *Steganothaenia* Hochst (only in the young flower stage). These are all endemic African genera except *Molopospermum* (widely distributed in Europe). They have prominent lateral ribs or wings in one mericarp as in *M. gummifera*. *Polemanniopsis* and *Steganothaenia* were placed close to the subfamily Saniculoideae (Downie and Katz-Downie, 1999; Plunkett, 2001). Both genera share the common character of large rib ducts (or cavities) and an absence of regular vittae (Liu et al., 2003b). The unicellular hairs in *Marlothiella* are different from the clearly multicellular stellate hairs which are present in some

genera of Azorelloideae (*Bolax* Commerson ex Jussieu, *Bowlesia* Ruiz and Pav., *Drusa* DC. and *Homalocarpus* Hook. and Arn.). Secretory structures and crystals in the fruits are important in the classification of Apiaceae (e.g. Drude, 1898). In *M. gummifera* the secretory structures differ from those of other genera included in the Apioideae. In the latter, vittae are regular (of even size, shape and distribution) and occur between the ribs and in the commissure [e.g. *Apium nodiflorum* (L.) Lag.], or are cyclic around the endocarp (e.g. *Smyrniolum olusatrum* L.). Fruits with rib ducts (but no vittae), crystals dispersed in the mesocarp and lacking carpophores, as in *Marlothiella*, were also found in some species of another endemic African genus, viz. *Lichtensteinia* Cham. and Schltldl. (Liu, 2004; Liu et al., 2003a). In both genera, the rib ducts are surrounded by several concentric layers of cells, a very uncommon feature in the family that may indicate that these two taxonomically isolated genera are related. Crystals are usually absent in the Apioideae but, if present, they occur in the commissure only (e.g. *Caucalis leptophylla* L.). The same combination of fruit features (rib ducts, dispersed

crystals and an absence of regular vittae and carpophores) found in *Marlothiella* and *Lichtensteinia* are also found in the Saniculoideae (in which branching or anastomosing vittae may be present). Fruit anatomy thus provides support for the placement of *Marlothiella* and *Lichtensteinia* close to the Saniculoideae rather than in the Apioideae. Molecular studies are necessary to confirm their phylogenetic position.

5. Taxonomy

5.1. *Marlothiella* H. Wolff

Marlothiella H. Wolff, Bot. Jahrb. 48: 263 (1912); Engler, Pflanzenwelt Afrikas 3(2): 807, fig 331 (1921); Schreiber, Prod. Fl. Südwestafr. 103: 7 (1967); Dyer, Gen. S. Afr. Flow. Plants 1: 421 (1975); Burt, Edinb. J. Bot. 48: 225 (1991); Pimenov and Leonov, Gen. Umbel.: 73 (1993). Type species: *M. gummiferum* H. Wolff.

Woody, cushion-shaped shrublets of up to 0.4 m high and 1 m wide, often with persistent dry umbels remaining on the stems. **Leaves** subsucculent, sparsely pinnate to bipinnate, (12-) 25–30 (–45) mm long, 5–15 mm wide, mostly clustered on short, lateral shoots; base slightly sheathing, ultimate segments subterete, acute, with sunken stomata. **Inflorescence** a short compound umbel, 25–45 mm long, with 1–3 small umbels of 15–30 mm in diameter; the rays, bracts and fruits covered in a layer of minute, unicellular, stellate hairs. **Flowers** greenish white. **Bracts** conspicuous, ovate and boatshaped, 2.5–4.5 mm long, 1.0–1.5 mm wide, bracteoles similar to the bracts. **Calyx** with small ovate-triangular teeth. **Petals** greenish white, with brownish or purplish apex. **Fruit** broadly ovoid, ± 2.5 mm long, ± 2.0 mm wide, covered with stellate hairs; mericarps halfmoon-shaped. **Ventral vascular bundle** undivided or sometimes absent (if present, not forming a carpophore). **Ribs** inconspicuous. **Vittae** absent. **Rib oil ducts** large, 5 (–7), 1 in each rib or with an additional oil duct in one or both of the marginal ribs.

M. gummifera H. Wolff, Bot. Jahrb. 48: 263 (1912); Engler, Pflanzenwelt Afrikas 3(2): 807, fig 331 (1921); Schreiber, Prod. Fl. Südwestafr. 103: 7 (1967); Burt, Edinb. J. Bot. 48: 225 (1991). Type: Namibia, Great Namaqualand, Angra Pequena [now Luderitz], *Marloth 4805* (B?; K?, not located). [Note: No duplicates of *Marloth 4805* have so far been located, despite a careful search and the fact that *Burt (1991)* cited a specimen in K. The type folder in K contains *Dinter 6347* and not *Marloth 48905*. We refrain from designating a neotype until a wider search can be made. In any case, the species is morphologically and geographically so distinctive that there is no possibility of a misidentification].

The single species, *M. gummifera*, has a localised distribution in the restricted diamond area on the coast of southern Namibia, from Luderitz (previously known by the Portuguese name *Angra Pequena*) southwards in the remote region around Bogenfels, Pomona and Baker's Bay (Fig. 5). The ecology and phenology of this unusual plant is poorly known but the limited herbarium record indicates that flowers and fruits are formed during late summer, from February to March.

The genus is phylogenetically very isolated but is likely to have some relation to the subfamily Saniculoideae and to *Lichtensteinia* but not to any genera of the subfamily Apioideae, where it was hitherto placed.

5.2. Specimens examined

–**2615** (Luderitz): Angra Pequena [now Luderitz] (–CA), November 1908, *Marloth 4620* (PRE); Buntfeldschuh, (–CA), 24 March 1958, *Merxmüller 2344* (BM, K, PRE); Buntfeldschuh, at foot of mountain (–CA), 5 September 1958, *De Winter* and *Giess 6206* (K, PRE, WIND); Luderitzbucht [Luderitz Bay], Diamond Area 1, Kolmanskoppe (–CA), February 1914, *Marloth 5360* (BM, K, PRE, 2x).

–**2715** (Bogenfels): Pomona (–AB), September 1925, *Beetz s.n.* sub *PRE 48214* (PRE), August 1922, *Dinter 4023a* (PRE), 10 May 1929, *Dinter 6347* (BM 2x, K, PRE); Pomona area (–AB), 13 September 2000, *Mannheimer Loots, Dauth and Roberts 885* (WIND); Towards coast from Pomona house (–AB), 14 September 2000, *Mannheimer 946* (PRE); Bogenfels (–AD), 1 December 1948, *Koch and Van Son s.n.* sub *PRE 48213* (PRE), 9 September 1972, *Merxmüller and Giess 28330* (PRE, WIND); District Chameis, hills to the east of Baker's Bay (–DC), 23 July 1993, *Williamson 5121* (WIND).

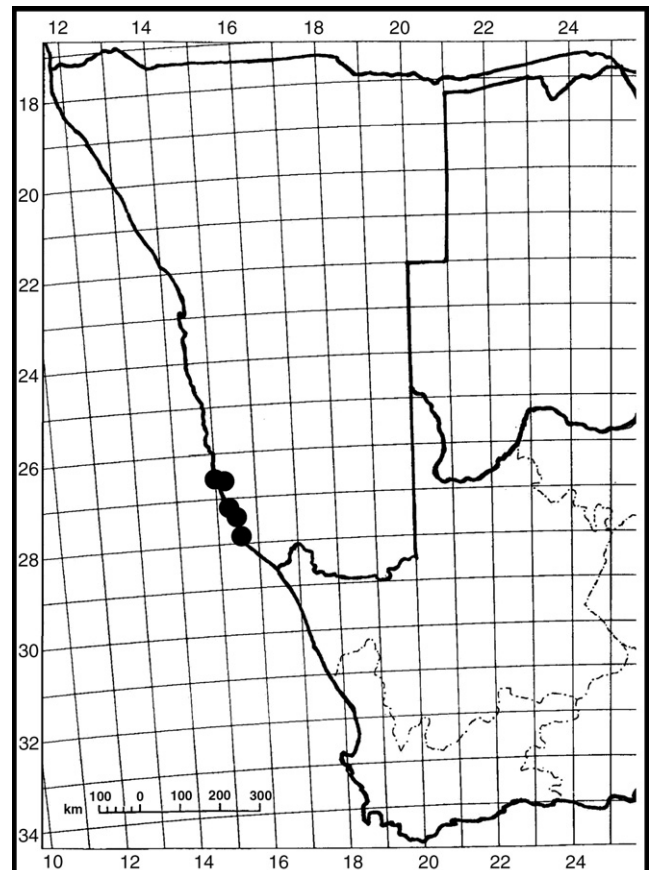


Fig. 5. The known geographical distribution of *Marlothiella gummifera* (●).

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