Available online at www.sciencedirect.com

SciVerse ScienceDirect

South African Journal of Botany 83 (2012) 19–22

SOUTH AFRICAN JOURNAL OF BOTANY

www.elsevier.com/locate/sajb

Short communication

Unusual carpological characters in *Marlothiella gummifera* (Apiaceae)

M. Liu [a], B.-E. Van Wyk [b,*], P.M. Tilney [b]

[a] *Department of Biology, Harbin Normal University, 50 Hexing Road, Harbin 150080, PR China*
[b] *Department of Botany and Plant Biotechnology, University of Johannesburg, P.O. Box 524, Auckland Park 2006, Johannesburg, South Africa*

Received 29 March 2012; received in revised form 28 May 2012; accepted 22 June 2012
Available online 9 August 2012

Abstract

Flowers and fruits of the monotypic Namibian endemic *Marlothiella gummifera* were examined to explore anatomical variation and to highlight problems associated with the homology of certain character states. Some unusual new features observed in the fruits and ovaries raise questions regarding the homology of fruit heteromorphy, rib oil ducts, vittae and carpophores in subfamily Apioideae. These include the irregular occurrence of heterocarpic ovaries, oil ducts on both the internal and external sides of the vascular bundles (the inner dwarf ducts), short ducts in the commissural area, and carpophores (only rarely present). The fruits of *Marlothiella* share several unusual features with the genus *Lichtensteinia*, namely concentric rings of cells around the rib oil ducts, of which the innermost are irregular in size and shape, very small vascular bundles that are usually comprised of two separate strands, and the occurrence of heteromorphy in fruits and ovaries. These two genera are morphologically very different and it is encouraging to find anatomical data to support their presumptive relationship based on molecular studies.

Keywords: Apiaceae; Carpophore; Fruit anatomy; *Lichtensteinia*; *Marlothiella gummifera*; Oil duct; Vitta

1. Introduction

Marlothiella gummifera H. Wolff is a monotypic Namibian endemic. The plants are cushion-shaped shrublets with succulent, glabrous, pinnate to bipinnate leaves (Burtt, 1991; Dyer, 1975; Engler, 1921; Liu et al., 2007; Schreiber, 1967; Van Wyk, 2000; Wolff, 1912). The fruits were previously reported to be slightly heteromericarpic with very large rib ducts and crystals dispersed in the mesocarp (Liu, 2004; Liu et al., 2007). Recent molecular phylogenetic evidence places *Marlothiella* in the same clade as *Lichtensteinia* Cham. & Schltdl. (Magee et al., 2010) and sister to *Choritaenia* Benth. (the latter with secretory structures represented by globose oil vesicles). In this paper we present details of fruit and ovary structure based on a study of several fruits and flowers. Our aims were to study the remarkable variation in fruit and flower structure (previously overlooked) and to report on the discovery of unusual ducts in the fruits of *Marlothiella*.

2. Materials and methods

Fruits and flowers from six voucher specimens (Table 1) were rehydrated by slowly boiling in distilled water for 1 h, fixed in FAA for about 24 h and then treated according to the method of Feder and O'Brien (1968) for embedding in glycol methacrylate (GMA). Transverse sections, about 3–5 μm thick, were cut using a Porter-Blüm ultramicrotome. Sections were stained using the periodic acid-Schiff/toluidine blue method (Feder and O'Brien, 1968), and photographed. The three dimensional structure of the secretory structures was observed in additional material of rehydrated fruits, either by sectioning or by carefully peeling away the exocarp to expose the underlying structures. Sections of flowers and fruits of *Lichtensteinia* species were available from a previous study (Tilney et al., 2009).

3. Results

The ovary appears to be invariably heterocarpic, with a distinct median rib in one carpel and an indistinct median rib but with

* Corresponding author. Tel.: +27 115592412; fax: +27 115592411.
E-mail address: bevanwyk@uj.ac.za B.-E. Van Wyk).

0254-6299/$ -see front matter © 2012 SAAB. Published by Elsevier B.V. All rights reserved.
doi:10.1016/j.sajb.2012.06.006

Table 1
Summary of the variation in fruit and flower characters in 14 samples from six specimens of *Marlothiella gummifera*.

Fruits and flower shown in Fig. 1	Voucher specimens	Fruit symmetry	Position of additional rib oil duct(s) (if present)	Number of additional rib oil duct(s)	Number of ducts in commissural area (in two mericarps)	Dwarf duct(s)	Presence of carpophore with vascular tissue	Presence of fully developed seeds
A	Merxmüller 4957 (PRE)	(Not sectioned)	–	–	–	2	–	–
B	Merxmüller 4957 (PRE)	Heteromorphic	–	–	2	–	–	–
C	Merxmüller 4957 (PRE)	Heteromorphic	marginal rib	1	3	2	–	–
D	Merxmüller 4957 (PRE)	Homomorphic	–	–	–	–	+	+
E	Merxmüller 4957 (PRE)	Heteromorphic	–	–	2	1	–	–
F	Merxmüller 2344 (WIND)	Heteromorphic	–		2	–	–	–
G	Merxmüller 2344 (WIND)	Homomorphic	median rib	1	4	1	–	+
H	Merxmüller 2344 (WIND)	Homomorphic	–	–	4	2	–	+
I	Range 1742 (BOL)	heteromorphic	–	–	2	2	–	–
J	Marloth 5360 (NBG)	Homomorphic	–	–	1	2	–	–
K	Marloth 5360 (NBG)	heteromorphic	–	–	2	2	–	–
L	Dinter 6347 (NBG)	Heteromorphic	–	–	4	2	–	–
M	Dinter 6347 (NBG)	Heteromorphic	–	–	3	–	–	–
N	Dinter 4028 (PRE)	Heteromorphic	–	–	–	–	–	–

prominent lateral ribs in the other (best seen in Fig. 1L1). The fruits are usually slightly heteromericarpic (e.g., Fig. 1B1, I) but sometimes homomericarpic (Fig. 1D1, H). Large rib oil ducts external to the vascular bundles were observed to lack septa (Fig. 1A1, 1B1, L2). Additional rib oil ducts may be present alongside the median or marginal ribs (Fig. 1C1, G). Dwarf ducts (vittae?) are often present internal to the vascular bundles, next to the endocarp (e.g., Fig. 1A2, L2, K). No septa were observed in these ducts. Large ducts in the commissural area (judged by their position to be homologous with commissural vittae), which are not associated with vascular bundles (e.g., Fig. 1G, L2) are easily overlooked in transverse sections because they are short (e.g., Fig. 1B1, D1). The typical large rib ducts have no septa and the lumen of each duct is surrounded by one inner layer of irregular cells and 3–5 concentric rings of cells (Fig. 1B2, see arrows), more or less uniform in shape and size. The vascular tissue in each rib usually occurs as two main separate strands but sometimes with additional bundles between (e.g., Fig. 1B2, see arrows). Amphiseminal druse crystals were observed in the mesocarp. The carpophore is usually not well developed even at fruit maturity and appears to be composed only of parenchyma cells (e.g., Fig. 1L3, see arrow). However, a carpophore composed of a single vascular strand was observed in one of the fruit samples (Fig. 1D1, D2). Very few of the mature fruits contained fully developed seeds (Fig. 1D1, G, H). A summary of character states is presented in Table 1.

4. Discussion

Fruit structure in *M. gummifera* is far more variable in symmetry and in the presence of oil ducts than has been reported, even in the same plant. Existing descriptions should be updated. Fruits that vary from homomericarpic to heteromericarpic within the same species are very rare in the Apiaceae but have been found in *Dasispermum suffruticosum* (Berg.) B.L. Burtt (Tilney and Van Wyk, 1995), *Annesorhiza laticostata* Magee (Magee et al., 2011) and some *Lichtensteinia* species (Tilney et al., 2009). The fact that the ovary is apparently always heterocarpic in *Marlothiella* suggests that homomorphy is a secondary development during fruit ontogeny, as was found in *Steganotaenia araliacea* Hochst. (Liu et al., 2004). The cells of the inner cell layer bordering on the lumen of the rib ducts are markedly irregular in size and shape. Such irregularity has only been observed elsewhere in *Lichtensteinia* (Tilney et al., 2009) and not in any of the very large number of other taxa we have studied to date (e.g., Liu et al., 2003, 2004; Liu, 2004; Tilney et al., 2009). As reported before (Magee et al., 2010; Tilney et al., 2009), the concentric rings of cells around the rib ducts appear to be a unique synapomorphy for *Marlothiella* and *Lichtensteinia*. Large rib ducts without septa are also typical of *Lichtensteinia* and many genera of tribe Saniculeae of the protoapioids (e.g., *Hacquetia* Neck. ex DC. and *Alepidea* La Roche) but rib ducts with septa were observed in *Bupleurum* L. (Liu, pers. obs.) and *Lefebvrea* (Magee et al., 2009). The ducts observed in the commissural region of the fruits of *Marlothiella* are completely absent in *Lichtensteinia* (Liu, 2004; Tilney et al., 2009).

These interesting differences show that a rigorous comparative ontogenetic study, representing all major lineages of protoapioids and euapioids is necessary to determine the homology of rib oil ducts and vittae. In *Marlothiella* it is unclear whether the dwarf ducts interior to the vascular bundles and those ducts observed in the commissural area are homologous to vittae. The only other genus in which we have observed additional ducts interior to the vascular bundles is *Notobubon* (Magee et al., 2009). These were interpreted by Magee et al. (2009) as additional rib vittae because they were anatomically similar to the regular vallecular vittae and not continuous with the vascular system. However, these authors also listed three other species where similar ducts may possibly be present: *Peucedanum oreoselinum* (L.) Moench, *Elaeoselinum asclepium* Bertol. and *Lefebvrea atropurpurea* (Hochst. ex A.Rich.) P.J.D.Winter.

The occurrence of two main vascular strands in each rib in *Marlothiella* and also in *Lichtensteinia* (Tilney et al., 2009) is rare in the family, and has only been observed in a few other protoapioids such as *Actinolema macrolema* Boiss, *Alepidea amatymbica* Eckl. & Zeyh., and *Phlyctidocarpa flava* Cannon & Theobald (Liu, pers. obs.), as well as *Choritaenia*, *Heteromorpha* and *Anginon* (Magee et al., 2010). In *Marlothiella*, as in

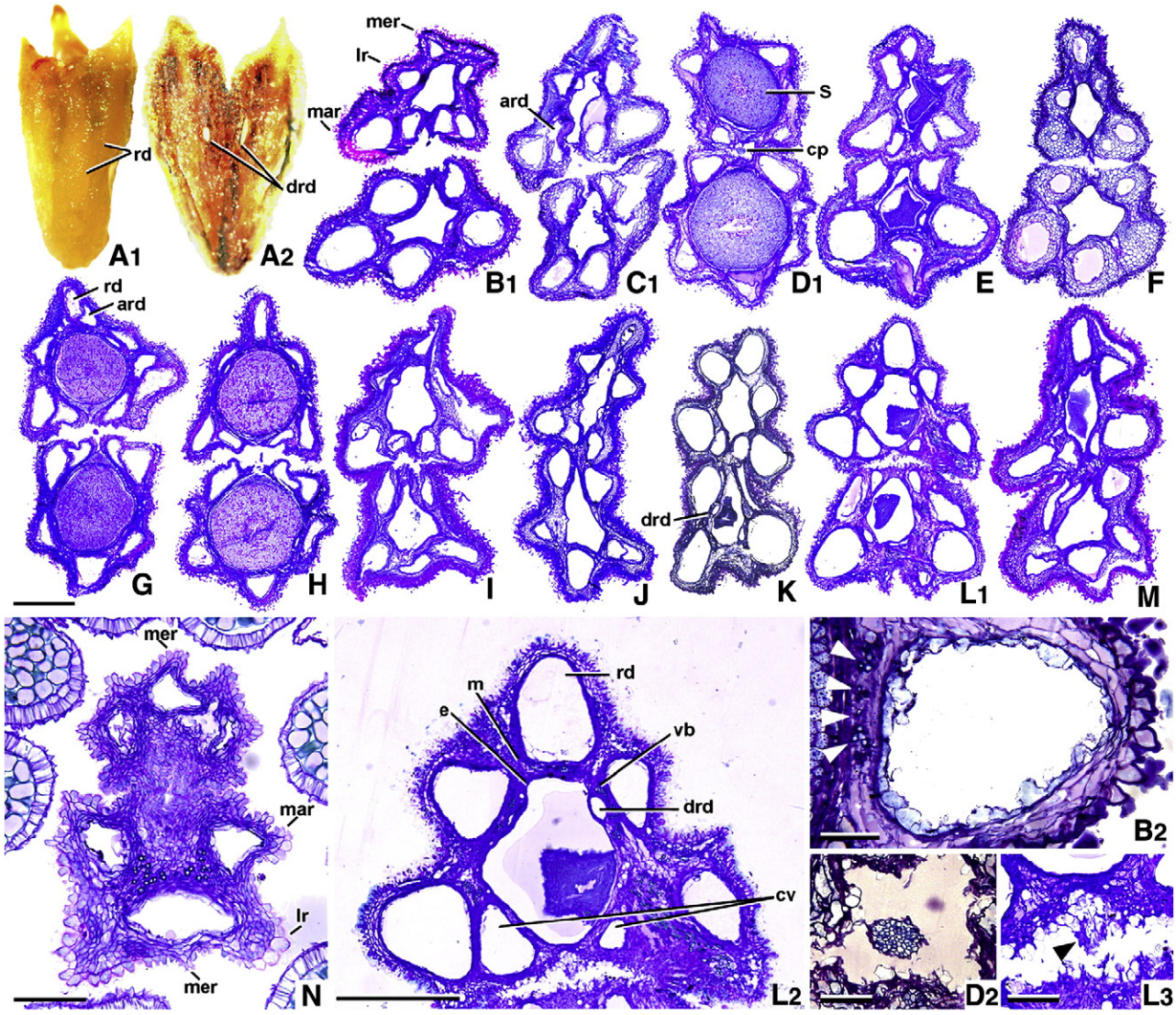

Fig. 1. Fruits of *Marlothiella gummifera*, illustrating some of the structural variation. Dorsal view to show the position of rib oil ducts (A1) and lateral view to show dwarf rib ducts (A2). Transverse sections of the fruits and flowers or portions thereof (B1–N) to compare the symmetry of the two mericarps, the number, position and size of the rib oil ducts, the ducts in the commissural area and the structure of the carpophore; ard = additional rib duct (next to duct in commissural area); cp = carpophore; cv = duct in commissural area; drd = dwarf rib duct; e = endocarp; m = mesocarp; lr = lateral rib; mar = marginal rib; mer = median rib; rd = rib oil duct; s = seed; vb = vascular bundle. Voucher specimens are listed in Table 1. Scale bars: (A–M, L2) 0.5 mm. (N, B2) 0.1 mm; (D2, L3) 0.05 mm.

Lichtensteinia (Tilney et al., 2009), relatively few ovules seem to develop into viable seeds. Amphiseminal druse crystals, present in both genera, are diagnostic for the protoapioids (Liu, 2004; Liu et al., 2003, 2004, 2007; Magee et al., 2010; Tilney et al., 2009). An interesting observation in *Marlothiella* is the extreme variability of the carpophore. Among Apiaceae it is usual that the carpophore, if present, is visible even in a young fruit and it is therefore exceptional to have carpophores either present or totally absent in mature fruits.

5. Conclusions

The fruits of *M. gummifera* are unusually variable in structure and both states of some fundamental characters can be found among fruits and flowers from different specimens or even a single umbel. This variability was previously undocumented. The fruits of *Marlothiella* and *Lichtenisteinia* share many common features (some very rare in the family) in contrast to the large differences in the shape of the leaves and several other morphological features. The fruit anatomy of *Marlothiella* provides additional evidence for a relationship to *Lichtensteinia* as indicated by molecular studies. Likely synapomorphies for the two genera include the irregular size and shape of the cells lining the rib oil ducts, the concentric rings of cells around the rib oil ducts, the very small vascular bundles that are usually comprised of about two separate strands, as well as the occurrence of heteromorphy in fruits and ovaries.

Acknowledgments

We gratefully acknowledge support from the Chinese National Science Foundation and the Science and Technique Innovation Foundation of Heilongjiang Province and Harbin

Normal University (30870148, 31070169 and KJTD2011-2) to ML, and financial assistance from the University of Johannesburg. The National Herbarium of South Africa (PRE), the National Herbarium of Namibia (WIND), Bolus Herbarium (BOL) and Compton Herbarium (NBG) are thanked for making specimens available for study.

References

Burtt, B.L., 1991. Umbelliferae of southern Africa: an introduction and annotated checklist. Edinburgh Journal of Botany 48, 135–275.

Dyer, R.A., 1975. The genera of South African flowering plants. Dicotyledons, vol. 1. Department of Agricultural Technical Services, Pretoria, p. 421.

Engler, A., 1921. Die Pflanzenwelt Afrikas insbesondere seiner tropischen Gebiete. Charakterpflanzen Afrikas. 2: Die dikotyledonen Angiospermen Euphorbiaceae. Sapindales bis Umbelliflorae (Schluss), vol. 3 (2). Wilhelm Engelmann, Leipzig, pp. 807–808.

Feder, N., O'Brien, T.P., 1968. Plant microtechnique: some principles and new methods. American Journal of Botany 55, 123–142.

Liu, M., 2004. A taxonomic evaluation of fruit structure in the family Apiaceae. PhD Thesis, University of Johannesburg.

Liu, M., Van Wyk, B.-E., Tilney, P.M., 2003. The taxonomic value of fruit structure in the subfamily Saniculoideae and related African genera (Apiaceae). Taxon 52, 261–270.

Liu, M., Van Wyk, B.-E., Tilney, P.M., 2004. Ontogeny of the fruits of two anomalous African woody genera *Polemanniopsis* and *Steganotaenia* (Apiaceae) and their phylogenetic relationship. Edinburgh Journal of Botany 60, 249–257.

Liu, M., Van Wyk, B.-E., Tilney, P.M., 2007. A revision of the genus *Marlothiella* (Apiaceae). South African Journal of Botany 73, 208–213.

Magee, A.R., Tilney, P.M., Van Wyk, B.-E., 2009. A revision of the woody Cape genus *Notobubon* (Apiaceae). Systematic Botany 34, 220–242.

Magee, A.R., Calviño, C.I., Liu, M., Downie, S.R., Tilney, P.M., Van Wyk, B.-E., 2010. New tribal delimitations for the early diverging lineages of Apiaceae subfamily Apioideae. Taxon 59, 567–580.

Magee, A.R., Van Wyk, B.-E., Tilney, P.M., Vessio, N., 2011. A taxonomic revision of the *Annesorhiza triternata* group (Apiaceae, Apioideae): the transfer of *Peucedanum triternatum* and *P. filicaule* and the description of five new species. Systematic Botany 36, 508–519.

Schreiber, A., 1967. Apiaceae. Prodromus einer Flora von Südwestafrika 103, 1–9.

Tilney, P.M., Van Wyk, B.-E., 1995. Unusual structural variation in the fruit of *Dasispermum suffruticosum* (Apiaceae): a new record of heteromorphic fruits in the family. South African Journal of Botany 61, 1–4.

Tilney, P.M., Van Wyk, B.-E., Downie, S.R., Calviño, C.I., 2009. Phylogenetic relationships in the genus *Lichtensteinia* (Apiaceae) based on morphological, anatomical and DNA sequence data. South Africa Journal of Botany 75, 64–82.

Van Wyk, B.-E., 2000. Apiaceae. In: Leistner, O.A. (Ed.), Seed Plants of Southern Africa: Families and Genera. Strelitzia, vol. 10. National Botanical Institute, Pretoria, pp. 62–71.

Wolff, H., 1912. Umbelliferae africanae. Botanische Jahrbücher für Systematik 48, 261–283.

Edited by JC Manning