

APIACEAE SYSTEMATICS

A new generic classification for African peucedanoid species (Apiaceae)

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The African species currently residing in *Peucedanum* L. and associated platyspermous genera are not related to the Eurasian *Peucedanum* species. As the type of the genus is *P. officinale* L., which is part of the Eurasian group, a new generic classification is proposed for the African group. The affinities and circumscriptions of two previously enigmatic monotypic genera, *Afrologisticum* C. Norman and *Erythroselinum* Chiov., are clarified. The former is expanded, while the latter is subsumed into *Lefebvrea* A. Rich. along with six *Peucedanum* species. New combinations are formalized for 49 of the 58 species recognised, which are accommodated in six genera, as follows: *Afrologisticum* (13 spp.), *Afrosciadium* P.J.D. Winter gen. nov. (18 spp.), *Cynorhiza* Eckl. & Zeyh. (3 spp.), *Lefebvrea* (10 spp.), *Nanobubon* A.R. Magee gen. nov. (2 spp.), and *Notobubon* B.-E. van Wyk gen. nov. (12 spp.). Ten new synonyms are presented, in *Cynorhiza* (2), *Lefebvrea* (6) and *Notobubon* (2). Diagnostic characters include habit (woody shrubs, perennial herbs or monocarpic herbs), seasonality (evergreen or deciduous), leaf texture and arrangement, inflorescence structure, fruit morphology (size, shape and wing configuration) and fruit anatomy. The results of maximum parsimony analysis of 125 nuclear rDNA ITS sequences representing all tribes and major clades of the apioid superclade and closely related outgroups support the separation of the African group of genera from that of Eurasian *Peucedanum*.

KEYWORDS: Africa, Apiaceae, classification, ITS, new genera, *Peucedanum*

INTRODUCTION

The circumscription and subdivision of the polyphyletic genus *Peucedanum* L. into natural groups are among the most urgent challenges in the formal taxonomy of the Apiaceae (Burt, 1991; Pimenov & Leonov, 1993). This study results from a proposal made in Pretoria, South Africa, in 2003, at the fourth international Apiales symposium, to embark upon a collaborative project to solve the so-called *Peucedanum* problem.

Ostroumova & Pimenov (1997a) give an elegant literature review of various arguments for and against splitting *Peucedanum* into more natural segregates. Proponents of the broad concept argue that sensible splitting will only be possible once rigorous comparisons between all species on all continents become possible. Ostroumova & Pimenov (1997a) also proposed that some parts of the *Peucedanum* problem can best be addressed at a regional level. For example, they ascribed the carpological similarities between the Cape species of South Africa and species of the type section (*Peucedanum*) as convergent. The idea that *Peucedanum* s.l. is broadly polymorphic and polyphyletic has been expressed several times in the past (e.g., Ecklon & Zeyher, 1837; Sonder,

1862; Schur, 1866; Calestani, 1905; Burt & Davis, 1949; Kowal & Wojterska, 1973; Reduron, 1984; Pimenov, 1987; Frey, 1989; Hadaček, 1986; Burt, 1991; Pimenov & Leonov, 1993; Downie & al., 2000; Spalik & al., 2004). There seems to be general agreement that generic and subgeneric delimitations need improvement but there appears to be a lack of correlation between various classes of taxonomic evidence (Shneyer & al., 2003; Spalik & al., 2004). A limited sample of woody Cape *Peucedanum* was included in a large analysis of cpDNA *rps16* intron sequences by Calviño & al. (2006) but the absence of Eurasian species did not allow any conclusions about the monophyly of *Peucedanum*. A further analysis based on a broader sampling is presented here to investigate the phylogenetic relationship between the Eurasian and African species of *Peucedanum*.

Drude (1897–98) treated 20 sub-Saharan African species in three of four subgenera of *Peucedanum*: *Peucedanum*, *Lefebvrea* (A. Rich.) Drude, and *Bubon* sensu Drude, non L. The latter two were strictly African, and he further presented *Cynorhiza* and *Sciothamni* as unranked groups to accommodate the African component of subgenus *Peucedanum*. Koso-Poljansky reinstated *Cynorhiza* Eckl. & Zeyh. as a genus in 1917, but subsequent authors

ignored this, presumably because it was based solely on carpological characters (Burt, 1991).

Engler (1921) provided the only comprehensive treatment of all the African *Peucedanum* species, which he classified in nine of fourteen groups, these again unranked following Drude (1897–98). Of these groups, “*Agasyllis*” (non Spreng.) and “*Sciothamnus*” represented an alternate arrangement of the shrubby Cape *Peucedanum* species, with the exception of a single non-shrubby species in “*Sciothamnus*”. His *Crenato-serrata* group combined several tropical Afrotropical perennial species based on leaf features. Despite treating *Peucedanum* in a broad sense, including *Cynorhiza*, *Afroligusticum* C. Norman, *Physotrichia* Hiern and *Steganotaenia* Hochst., he considered *Erythroselinum* Chiov. and *Lefebvrea* worthy of recognition as distinct genera.

Norman (1934) treated 31 *Peucedanum* species of tropical Africa in eight sections. Five of these sections included species in our present study group. Besides three monotypic sections, *P. sect. Cervaria* Drude (sensu Norman) represented an earlier informal grouping of Wolff (1927) that consolidated some species that did not conform to *P. sect. Crenato-serrata* Engl. ex C. Norman. The latter section, however, lost the neat definition Engler (1921) had given it, particularly through Norman’s inclusion of several monocarpic species that Engler would undoubtedly have excluded from *Peucedanum* and allocated to *Erythroselinum* or *Lefebvrea*. Townsend (1987, 1989) studied African *Peucedanum*, *Erythroselinum*, and *Lefebvrea* and suggested that though distinct, the affinities amongst them appeared to be stronger than any possible Eurasian links. Burt (1991) concentrated on the southern African region and particularly on typification and nomenclature, in preparation of subsequent taxonomic work. He mentions that “Even within southern Africa, *Peucedanum* is very diverse and the possibility that it will eventually need to be subdivided is a real one.” As a first contribution towards a revision and rational subdivision of African *Peucedanum*, Ostroumova & Pimenov (1997a, b) analysed the fruit structure of 43 southern African and 27 tropical African species of *Peucedanum* and divided the fruits into several carpological (not taxonomic) groups. Their data are a useful foundation for future morphological analyses.

The main objective of this paper is to propose a new generic classification system to accommodate the considerable diversity amongst the African peucedanoid species (*Peucedanum* and allied genera) on the basis of morphological and anatomical evidence. We also present molecular evidence (maximum parsimony analysis of nrDNA ITS sequences) that the African species hitherto accommodated in *Peucedanum* are not closely related to the Eurasian species (which include the type species of *Peucedanum*).

MATERIALS AND METHODS

General morphology. — Populations were studied and sampled in situ in Malawi, South Africa and Zimbabwe over a period of several years. This was supplemented by a study of all the African *Peucedanum* specimens in the following herbaria: BM, BOL, J, JRAU, K, NBG, P, PRE, PRU, S, SAM, SRGH, W, WIND. All the species studied are listed in Table 1, together with their correct author citations (these are not repeated elsewhere in the text). Major groupings within African *Peucedanum* and associated genera, based on a combination of habit, leaf, inflorescence and fruit characters, are presented in Table 1.

Fruit anatomy. — Fruits from herbarium specimens and material preserved in formalin-acetic acid-alcohol (FAA) were used in the anatomical studies. Three fruits per taxon were sampled for the Cape taxa and one fruit per taxon for the remaining African species. This material was rehydrated (if necessary) and placed in FAA for a minimum of 24 h and then treated according to a modification of the method of Feder & O’Brien (1968) for embedding in glycol methacrylate (GMA). This modification involves a final infiltration of five days in GMA. The embedded material was mounted in the desired orientation and sections of 3–5 μm thick were cut. Staining was done according to the periodic acid Schiff/toluidine blue (PAS/TB) staining method.

DNA sequencing. — Nuclear rDNA internal transcribed spacer (ITS) sequences were obtained for 45 accessions primarily from Africa. It is important to note that the sampling was simply aimed at investigating the monophyly of the genus *Peucedanum* and not to explore relationships amongst the African taxa. The sources of this newly sequenced material, voucher specimen information, and GenBank reference numbers are listed in Appendix 1. Because the molecular investigations were carried out independently in two laboratories, our strategies differed slightly. Total genomic DNA was extracted from 0.5–1.0 g of fresh leaf material or approximately 20 mg of herbarium material using the 2X CTAB method of Doyle & Doyle (1987) or the DNeasy Plant Mini Kit (Qiagen, Valencia, California, U.S.A.), respectively. For the former, the extracts were cleaned and concentrated in QIAquick silica columns (Qiagen) according to the manufacturer’s protocol. The entire ITS region was PCR-amplified using pairs of primers described in Sun & al. (1994) or Downie & Katz-Downie (1996). For template purification, the QIAquick PCR Purification or the QIAquick Gel Extraction Kits (Qiagen) were used following the manufacturer’s instructions. Sequencing reactions were carried out using the BigDye Terminator version 3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, California, U.S.A.) and sequenced using either an ABI (Applied Biosystems) 3130 XL or 3730 XL sequencer. Complimentary strands were assembled and edited using

Table 1. Major groupings in African *Peucedanum* that were assessed in this study and their related genera, arranged according to our proposed new genera.

Groups / genera	New combination	Groups / genera	New combination
Genus 1. <i>Notobubon</i>		Genus 5. <i>Afroscidium</i>	
<i>P. galbanum</i> group (shrubs)		<i>P. magalismontanum</i> group (perennial herbs)	
<i>P. camdeboense</i> B.L. Burtt	<i>N. laevigatum</i>	<i>P. abyssinicum</i> Vatke	<i>A. abyssinicum</i>
<i>P. capense</i> (Thunb.) Sond.*	<i>N. laevigatum</i>	<i>P. articulatum</i> C.C. Towns.	<i>A. articulatum</i>
<i>P. dregeanum</i> D. Dietr.	<i>N. montanum</i>	<i>P. caffrum</i> (Meisn.) E. Phillips	<i>A. caffrum</i>
<i>P. ferulaceum</i> (Thunb.) Eckl. & Zeyh.*	<i>N. ferulaceum</i>	<i>P. dispersum</i> C.C. Towns.	<i>A. dispersum</i>
<i>P. galbaniopse</i> H. Wolff*	<i>N. galbaniopse</i>	<i>P. englerianum</i> H. Wolff	<i>A. englerianum</i>
<i>P. galbanum</i> (L.) Drude*	<i>N. galbanum</i>	<i>P. eylesii</i> C. Norman	<i>A. eylesii</i>
<i>P. gummiferum</i> (L.) D.O. Wijnands*	<i>N. gummiferum</i>	<i>P. friesiorum</i> H. Wolff	<i>A. friesiorum</i>
<i>P. kamiesbergense</i> B.L. Burtt*	<i>N. capense</i>	<i>P. gossweileri</i> C. Norman	<i>A. gossweileri</i>
<i>P. pearsonii</i> Adamson*	<i>N. pearsonii</i>	<i>P. harmsianum</i> H. Wolff	<i>A. harmsianum</i>
<i>P. polyactinum</i> B.L. Burtt*	<i>N. capense</i>	<i>P. kerstenii</i> Engl.	<i>A. kerstenii</i>
<i>P. pungens</i> E. Mey. ex Sond.*	<i>N. pungens</i>	<i>P. lundense</i> Cannon	<i>A. lundense</i>
<i>P. sonderi</i> (M. Hiroe) B.L. Burtt	<i>N. sonderi</i>	<i>P. lynesii</i> C. Norman	<i>A. lynesii</i>
<i>P. striatum</i> (Thunb.) Sond.*	<i>N. striatum</i>	<i>P. magalismontanum</i> Sond.*	<i>A. magalismontanum</i>
<i>P. tenuifolium</i> Thunb.*	<i>N. tenuifolium</i>	<i>P. natalense</i> (Sond.) Engl.	<i>A. natalense</i>
Genus 2. <i>Nanobubon</i>		<i>P. nyassicum</i> H. Wolff	<i>A. nyassicum</i>
<i>P. strictum</i> group (pyrophytic suffrutices)		<i>P. platycarpum</i> E. Mey. ex Sond.	<i>A. platycarpum</i>
<i>P. capillaceum</i> Thunb.*	<i>N. capillaceum</i>	<i>P. rhodesicum</i> Cannon	<i>A. rhodesicum</i>
<i>P. strictum</i> (Spreng.) B.L. Burtt*	<i>N. strictum</i>	<i>P. trisectum</i> C.C. Towns.	<i>A. trisectum</i>
Genus 3. <i>Cynorhiza</i>		Genus 6. <i>Lefebvrea</i>	
<i>Cynorhiza</i> group (perennial herbs)		<i>Lefebvrea</i> A. Rich. (s.str.)	
<i>P. millefolium</i> Sond.	<i>C. meifolia</i>	<i>L. abyssinica</i> A. Rich.*	
<i>P. olifantianum</i> (Koso-Pol.) M. Hiroe	<i>C. typica</i>	<i>L. brachystyla</i> Hiern	
<i>P. sulcatum</i> Eckl. & Zeyh. ex Sond.*	<i>C. typica</i>	<i>L. droopii</i> C.C. Towns.	
<i>P. typicum</i> (Eckl. & Zeyh.) B.L. Burtt*	<i>C. typica</i>	<i>L. grantii</i> (Hiern) S. Droop*	
Genus 4. <i>Afroligusticum</i>		<i>L. longipedicellata</i> Engl.*	
<i>Afroligusticum</i> C. Norman		<i>Erythrosetinum</i> Chiov.	
<i>Afroligusticum elliotii</i> (Engl.) C. Norman*		<i>E. atropurpureum</i> (A. Rich.) Chiov.	
<i>Crenato-serrata</i> group (perennial herbs)		<i>L. atropurpurea</i>	
<i>P. aculeolatum</i> Engl.	<i>A. aculeolatum</i>	Monocarpic group (monocarpic herbs)	
<i>P. claessensii</i> C. Norman	<i>A. claessensii</i>	<i>P. angustisectum</i> (Engl.) C. Norman	<i>L. angustisecta</i>
<i>P. elgonense</i> H. Wolff	<i>A. elgonense</i>	<i>P. camerunense</i> Jacq.-Fél.	<i>L. angustisecta</i>
<i>P. linderi</i> C. Norman	<i>A. linderi</i>	<i>P. kupense</i> I. Darbyshire & Cheek.	<i>L. angustisecta</i>
<i>P. mattirolii</i> Chiov.	<i>A. mattirolii</i>	<i>P. madense</i> C. Norman	<i>L. grantii</i>
<i>P. petitianum</i> A. Rich.*	<i>A. petitianum</i>	<i>P. oblongisectum</i> C.C. Towns.	<i>L. oblongisecta</i>
<i>P. runssoricum</i> Engl.	<i>A. runssoricum</i>	<i>P. stenospermum</i> C.C. Towns.	<i>L. stenosperma</i>
<i>P. scottianum</i> Engl.	<i>A. scottianum</i>	<i>P. tenue</i> C.C. Towns.	<i>L. tenuis</i>
<i>P. thodei</i> T.H. Arnold	<i>A. thodei</i>	<i>P. upingtoniae</i> (Schinz) Drude	<i>L. grantii</i>
<i>P. townsendii</i> Charpin & Fern. Casas	<i>A. townsendii</i>	<i>P. wildemanianum</i> C. Norman	<i>L. grantii</i>
<i>P. volkensii</i> Engl.	<i>A. volkensii</i>		
<i>P. wilmsianum</i> H. Wolff	<i>A. wilmsianum</i>		

* denotes species included in the ITS analysis.

Sequencher 3.1.2 (Gene Codes Corporation). Simultaneous consideration of both DNA strands across the entire ITS region permitted unambiguous base determination in all taxa. No evidence of ITS sequence additivity at any nucleotide site was found which would have been suggestive of divergent rDNA copies in the genome.

Phylogenetic analysis. — To ascertain the phylogenetic position of the African species currently residing in *Peucedanum* and their associated platyspermous genera, the 45 ITS sequences obtained in this study were analysed with 73 additional ITS sequences representing all tribes and major clades of the apioid superclade (Downie & al., 2001). Included here were representatives of Eurasian *Peucedanum* and its segregates, including the type of *Peucedanum*, *P. officinale*. These taxa are listed in Appendix 2 with their corresponding GenBank numbers. They were obtained from previously published studies (Downie & al., 2000; Spalik & al., 2004; Spalik & Downie, 2007), from unpublished studies but where DNA sequences are available in GenBank, or from Ajani & al. (2008). Seven species from tribes Smyrnieae and Oenantheae were used as outgroups, with those of Oenantheae used to root the trees, as previous studies have established a close relationship between these tribes and the apioid superclade (e.g., Downie & al., 2001). For 37 previously published ITS sequences, data for the 5.8S gene were unavailable. The DNA sequences were aligned initially using ClustalX (Jeanmougin & al., 1998), with default parameters for gap penalty and extension, and realigned manually as necessary. Alignment of these 125 ITS sequences resulted in a matrix of 689 positions, of which 56 were eliminated from subsequent analysis because of alignment ambiguities. Of the remaining positions, 253 were not variable, 67 were variable but uninformative, and 313 were parsimony informative. Gaps were positioned to minimize nucleotide mismatches but were not considered as additional, binary-scored characters in the phylogenetic analysis. These sequence data were analyzed using maximum parsimony, as implemented by PAUP* version 4.0b10 (Swofford, 2002), and because of the large number of maximally parsimonious trees obtained during preliminary searches (> 60,000), the tree searching strategies described by Downie & al. (1998) were employed. Using these strategies, a strict consensus tree of 10,000 minimal-length trees is presented. While this tree adequately summarizes the available evidence, the exact number of minimal length trees is unknown. Bootstrap values (Felsenstein, 1985) were calculated from 500,000 replicate analyses using “fast” stepwise addition of taxa and only those values compatible with a 50% majority-rule consensus tree were recorded. The following scale was applied for support percentages: 50%–74%, weak; 75%–84%, moderate; and 85%–100%, strong. The number of additional steps required to force particular taxa into monophyly was calculated using the constraint option of PAUP*.

RESULTS AND DISCUSSION

Habit. — The extreme diversity of habit (Fig. 1) could be divided into discrete character states that proved to be very useful for the delimitation of taxa. Species of the *P. galbanum* group (Table 1) are shrubs or shrublets with permanent, distinctly woody branches (Fig. 1A), both rare features in the Apiaceae, while the *P. strictum* group (Table 1) comprises two pyrophytic suffrutices with woody subterranean stems (Fig. 1D). The shrubby habit is for the first time explicitly interpreted as distinct from woodiness of other taxa that are not true phanerophytes. The remaining species are all non-woody herbs (Fig. 1B–C). Drude (1897–98), Engler (1921) and subsequent authors unfortunately placed the emphasis on woodiness rather than life form, and the somewhat woody main stems of robust monocarpic herbs appear to have been considered homologous with the permanent branches of these phanerophytes. *Lefebvrea*, *Erythroselinum* and several tropical African *Peucedanum* species in our Monocarpic group (Table 1) are distinguished from all other African species by their monocarpic rather than perennial habit. Jacques-Félix (1970) drew attention to the monocarpic habit of most West African *Peucedanum* and *Lefebvrea* species in contrast to the perennial *Peucedanum townsendii*. Perhaps due to the floristic nature of his work, the taxonomic value of this character was never realized until now.

Leaves. — Both the woody Cape groups (viz. *P. galbanum* group, *P. strictum* group) are evergreen with sclerophyllous leaves borne on permanent woody branches (Fig. 1A, D–E). The remaining species have their leaves either in a basal rosette (Fig. 1B) or if slightly cauline, then borne on deciduous branches that die back in the dry season (summer or more often winter). The *Cynorhiza* group (Table 1) is distinguished from other deciduous species in that their leaves are senescent at the time of fruiting (Fig. 1C), so that fruiting plants are usually totally leafless. They are also the only summer-deciduous group (albeit somewhat variable in the case of *P. typicum*). *Erythroselinum* and *Lefebvrea* have leaves with the same texture and prominent abaxial veins as those of species in Engler’s (1921) *Crenato-serrata* group (Table 1), and although broadly-segmented forms are common, they show a tendency for longer, narrower leaf segments. Vein prominence is shared among these three groups, but the pattern of venation has proved useful to distinguish *Lefebvrea* and *Erythroselinum* from *Peucedanum* (Townsend, 1987). Species of the *P. magalismontanum* group (Table 1) have narrower leaf segments than those of the *P. petitianum* group, typically less than 5 mm wide, and if wider, the texture is more coriaceous, resulting in less conspicuous venation.

Inflorescence structure. — Many of the species in the *P. galbanum* group have relatively large, multiradiate

and often orbicular compound umbels borne on very short peduncles (Fig. 1E). The *Cynorhiza* group shares with the woody Cape species the presence of a single, dominant terminal umbel (that is often very large) surrounded by reduced (or even absent) secondary umbels (Fig. 1C). Several members of the Monocarpic group (Table 1) have inflorescences with a sympodial arrangement of branches, and numerous umbels with fewer and mostly shorter rays than in the other genera studied here. The relatively high ratio of umbels to vegetative biomass in this group seems to indicate a higher investment of resources into fruits than into roots or leaves, a strategy suited to a short life cycle. The *P. magalimontanum* group likewise has few rays, though these are longer in most species, umbels are less numerous, and secondary or further branching of the inflorescence is not as prevalent as in the Monocarpic group.

Fruit morphology. — Mericarps of all the major groups of African species are represented in Figures 2 and 3. They vary considerably in size, shape and wing width (Fig. 2). The mericarps of all the African peucedanoid species are dorsally compressed with a broad commissure extending from wing margin to wing margin (Fig. 3). In almost all the species the marginal ribs are prominently

winged, except in *P. pearsonii* and *Afrologisticum elliotii* (Fig. 2K). In both these species, however, the commissure extends for the full width of the mericarp (i.e., to the very edge of both marginal ribs). The marginal wings are typically broad and thin in most of the tropical African species (Fig. 3B–E). The *P. galbanum* group can be distinguished by the combination of very small fruits (less than 8 mm long—Fig. 2A–E) with thick, narrow marginal wings (Fig. 3G–H) and the *P. strictum* group by the large fruits (Fig. 2R–S) with thick, very broad marginal wings (Fig. 3I). *Lefebvrea* has fruit wing tips that extend beyond the base of the stylopodium on either side of the mericarp, so that the fruit appears to be apically notched (Fig. 2H, J), while those of *Erythroselinum* and the Monocarpic group do not extend above the level of the calyx (Fig. 2F). Variation in the extent of wing lobes in the fruits of the Monocarpic group is continuous, however, with *P. madense* and *P. upingtoniae* showing some individuals with lobes extending beyond the stylopodium, and others where these merely reach half of the stylopodium height.

The *Cynorhiza* group shares the apically notched mericarp wings with *Lefebvrea*. However, their fruits are usually much larger, particularly the fertile part (Fig. 2T–V).

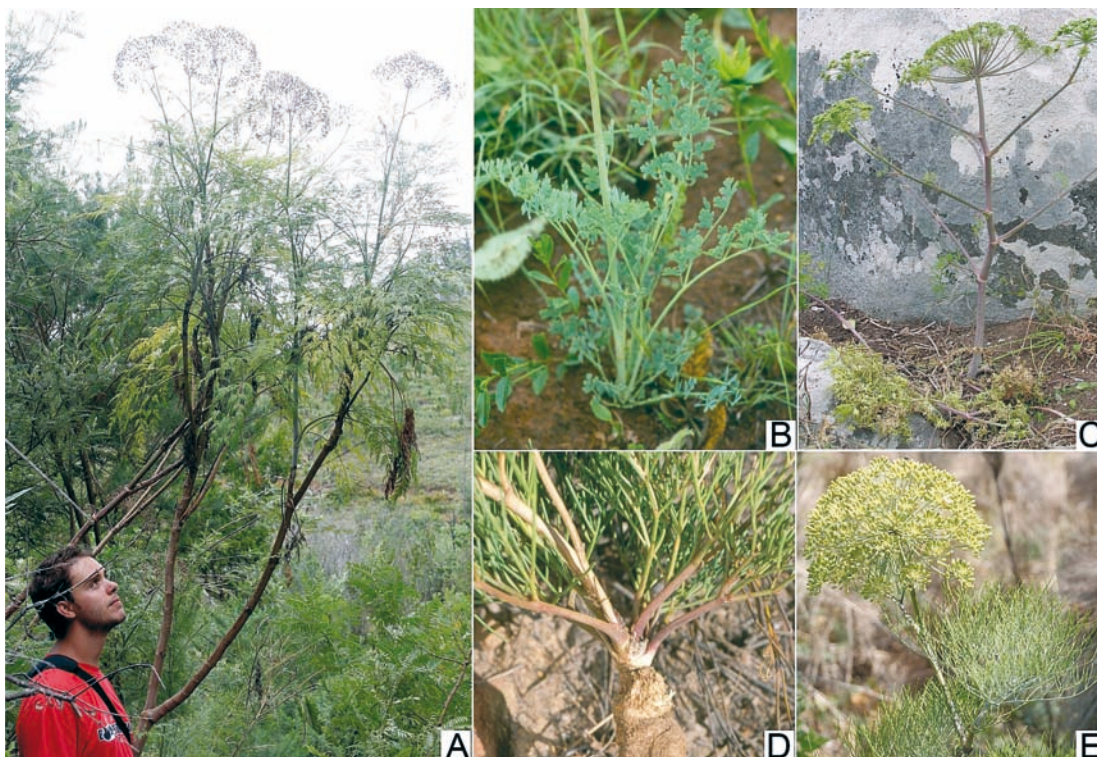


Fig. 1. The African species of *Peucedanum* exhibit an extreme diversity of habit (woody shrubs, shrublets, suffrutices and monocarpic herbs) and to a lesser extent inflorescence structure. A, *P. gummiferum* (woody shrub); B, *P. caffrum* (non-woody herb); C, *P. sulcatum* (deciduous, non-woody herb with leaves senescent at the time of flowering); D, *P. strictum* (suffrutex with woody subterranean stem); E, *P. polyactinum* (woody shrub with large, multiradiate compound umbels borne on short peduncles).

Fruit anatomy. — The fruit anatomy of most species in the *P. galbanum* group is very unusual in the combination of large solitary vallecular vittae as well as solitary vittae below the vascular bundle of each rib (Fig. 3G–H). These “rib vittae” occur in all species of the *P. galbanum* group except in *P. capense*, *P. dregeanum*, *P. pearsonii*, and *P. striatum*. The two commissural vittae of species in this group are furthermore exceptionally wide—as broad as the width of the seed (Fig. 3G–H)—except in four species (*P. capense*, *P. dregeanum*, *P. ferulaceum*, *P. striatum*). In support of the shrubby habit, the vittae features found in the *P. galbanum* group are rare in Apiaceae. No other African species are known to exhibit these characters (or this combination of characters) and in general they have only solitary vittae in the valleculae and usually two small commissural vittae (Fig. 3A–F, I).

Molecular phylogenetic analysis. — Maximum parsimony analysis of 633 unambiguously aligned ITS nucleotide positions resulted in the preset maximum tree limit of 10,000 trees, each of 2,044 steps (consistency indices of 0.3415 and 0.3140, with and without uninformative characters, respectively; retention index of 0.7075). The strict consensus of these trees, with accompanying bootstrap support values, is presented in Fig. 4. The apioid superclade is strongly supported as monophyletic (96% bootstrap) and comprises the African peucedanoid group, the *Heracleum* clade, and tribes Echinophoreae, Selineae, Apieae, Pimpinelleae, Pyramidoptereae, and Careae that have each been defined as monophyletic based on molecular systematic study. In addition, there are several genera of uncertain tribe or clade placement that fall within the apioid superclade, such as *Conium* L.,

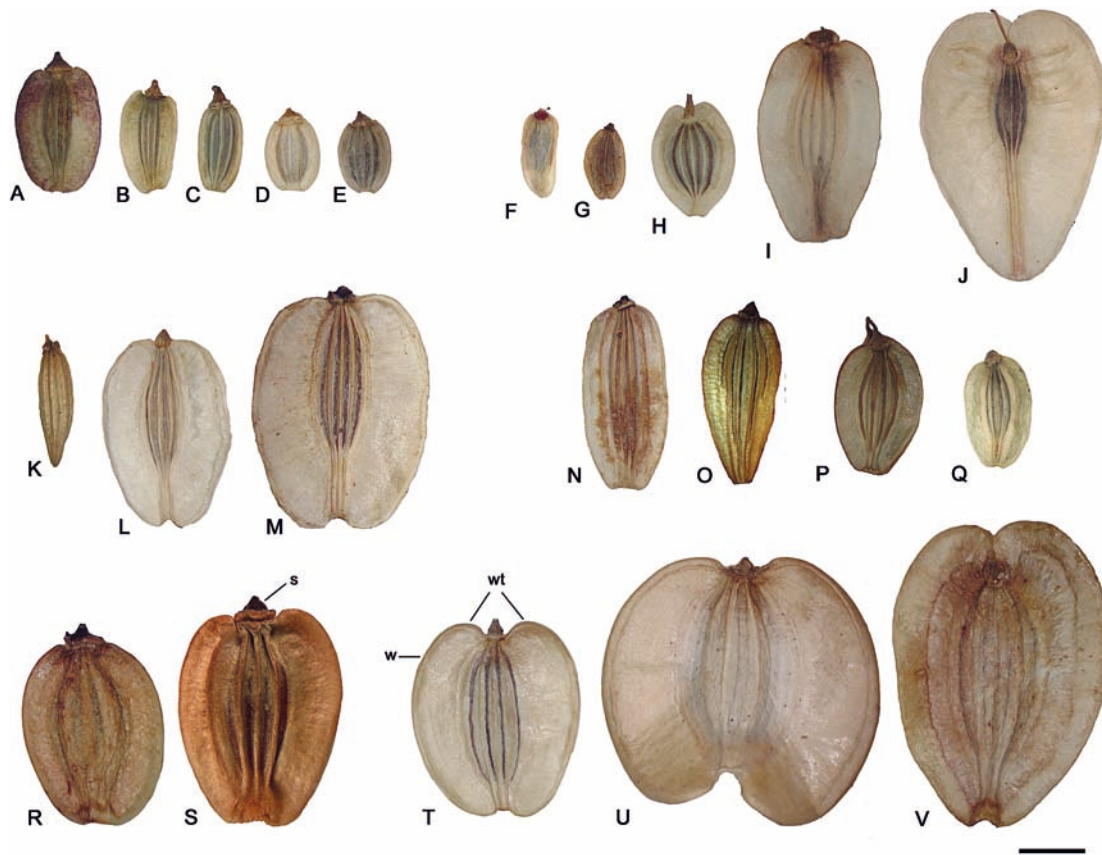


Fig. 2. Variation in mericarp size, shape and wing width of all the major African peucedanoid groups. A–E, *Peucedanum galbanum* group; F–J, Monocarpic group (including *Erythroselinum* and *Lefebvreia*); K–M, *Crenato-serrata* group (including *Afroligusticum*); N–Q, *P. magalismontanum* group; R–S, *P. strictum* group; T–V, *Cynorhiza* group. A, *P. ferulaceum* (Winter 158, JRAU); B, *P. capense* (Magee & Boatwright 7, JRAU); C, *P. galbaniopse* (Taylor 7647, NBG); D, *P. polyactinum* (Compton 21896, NBG); E, *P. galbanum* (Winter 104, JRAU); F, *Erythroselinum atropurpureum* (Lewis 5985, K); G, *P. cameronense* (Koechlin 7541, P); H, *L. abyssinica* (Breteler 481, K); I, *P. oblongisectum* (Robinson 4764, K); J, *L. longipedicellata* (Purseglove 2317, K); K, *Afroligusticum elliotii* (Stauffer s.n., PRE); L, *P. elgonense* (Greenway & Kanuri 13672, K); M, *P. aculeolatum* (Purseglove P2166, K); N, *P. dispersum* (Thomas 1877, K); O, *P. platycarpum* (Hilliard & Burt 11102, PRE); P, *P. rhodesicum* (Torre & Correia 13152, K); Q, *P. kerstenii* (Gilbert & Thulin 1043, K); R, *P. strictum* (Esterhuysen 22772, BOL); S, *P. capillaceum* (Leighton 1563, NBG); T, *P. typicum* (Paterson 5, GRA); U, *P. sulcatum* (Van Jaarsveld 11886, PRE); V, *P. millefolium* (Ecklon & Zeyher 2230, SAM). w = wing; wt = wing tip; s = stylopodium.

Trachyspermum Link, *Opopanax* W.D.J. Koch, *Smyrniopsis* Boiss., and that group of taxa immediately basal to tribe Selineae (Downie & al., 2001). *Peucedanum officinale*, the type of the genus, allies with the other Eurasian species of *Peucedanum* in tribe Selineae (Spalik & al., 2004), and this tribe is supported strongly with a 93% bootstrap value. In contrast, the African taxa currently residing in *Peucedanum* and its platyspermous allies (the “African group,” Fig. 4) do not group with the type of *Peucedanum*, but rather comprise a clade, sister group to a small alliance of southwest Asian species (*Kalakia marginata*, *Cymbocarpum anethoides*, *Ducrosia anethifolia*) that together are in turn sister group to the *Heracleum* clade. The results of our ITS analysis show, for the first

time, an association of the African peucedanoids with the *Kalakia-Cymbocarpum-Ducrosia* alliance and the *Heracleum* clade. These lineages collectively correspond well to tribe Tordylieae W.D.J. Koch.

While bootstrap support for the position of the African clade within Tordylieae is extremely weak (<50%), the strong support for Selineae suggests a clear enough separation between those Eurasian and African taxa currently in *Peucedanum*. The evidence that the African peucedanoids are separate from European *Peucedanum* is therefore unconditionally conclusive, despite the known limitations of nrITS data (Álvarez & Wendel, 2003). The reported instances of intra-individual ITS polymorphisms in Apiaceae, and especially in the higher

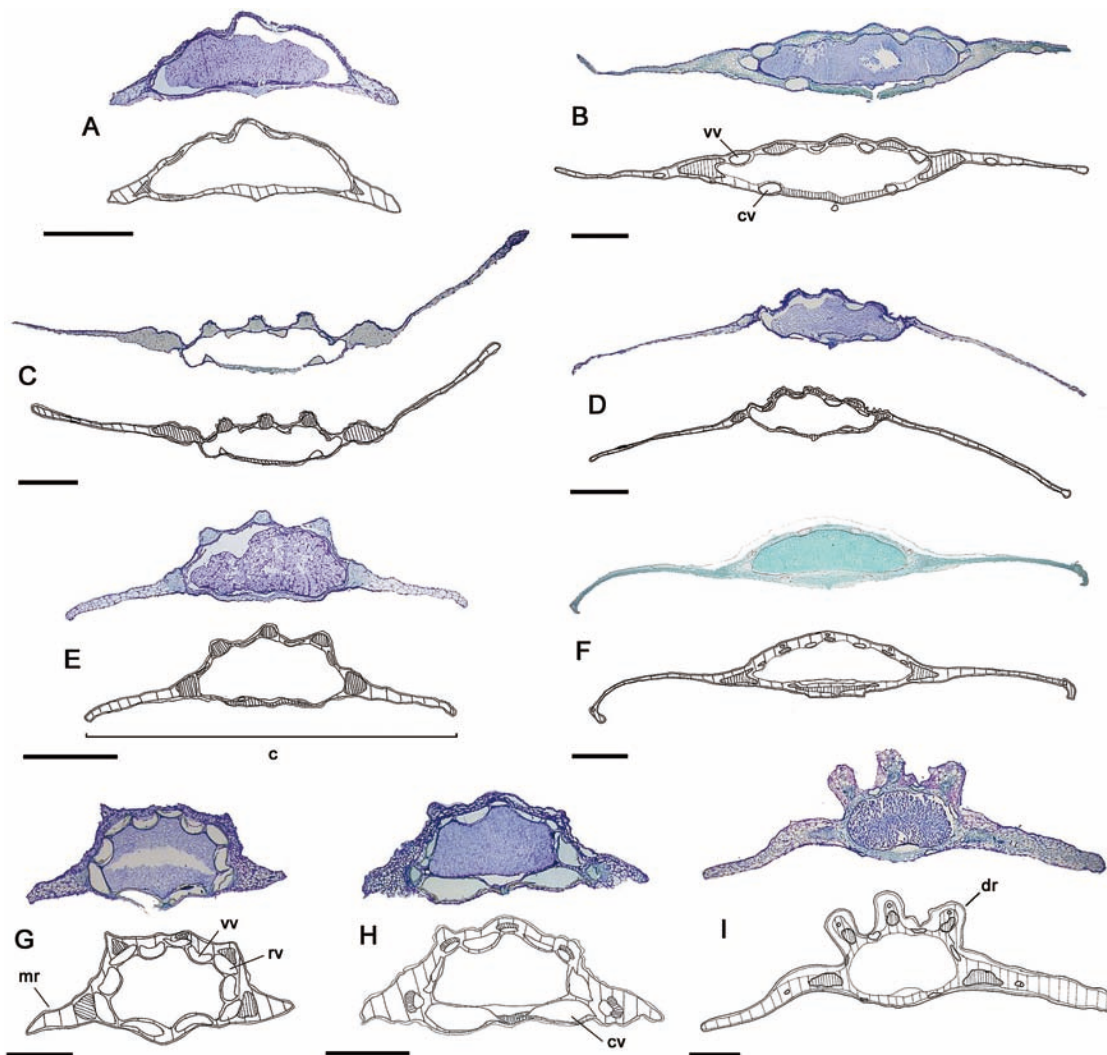
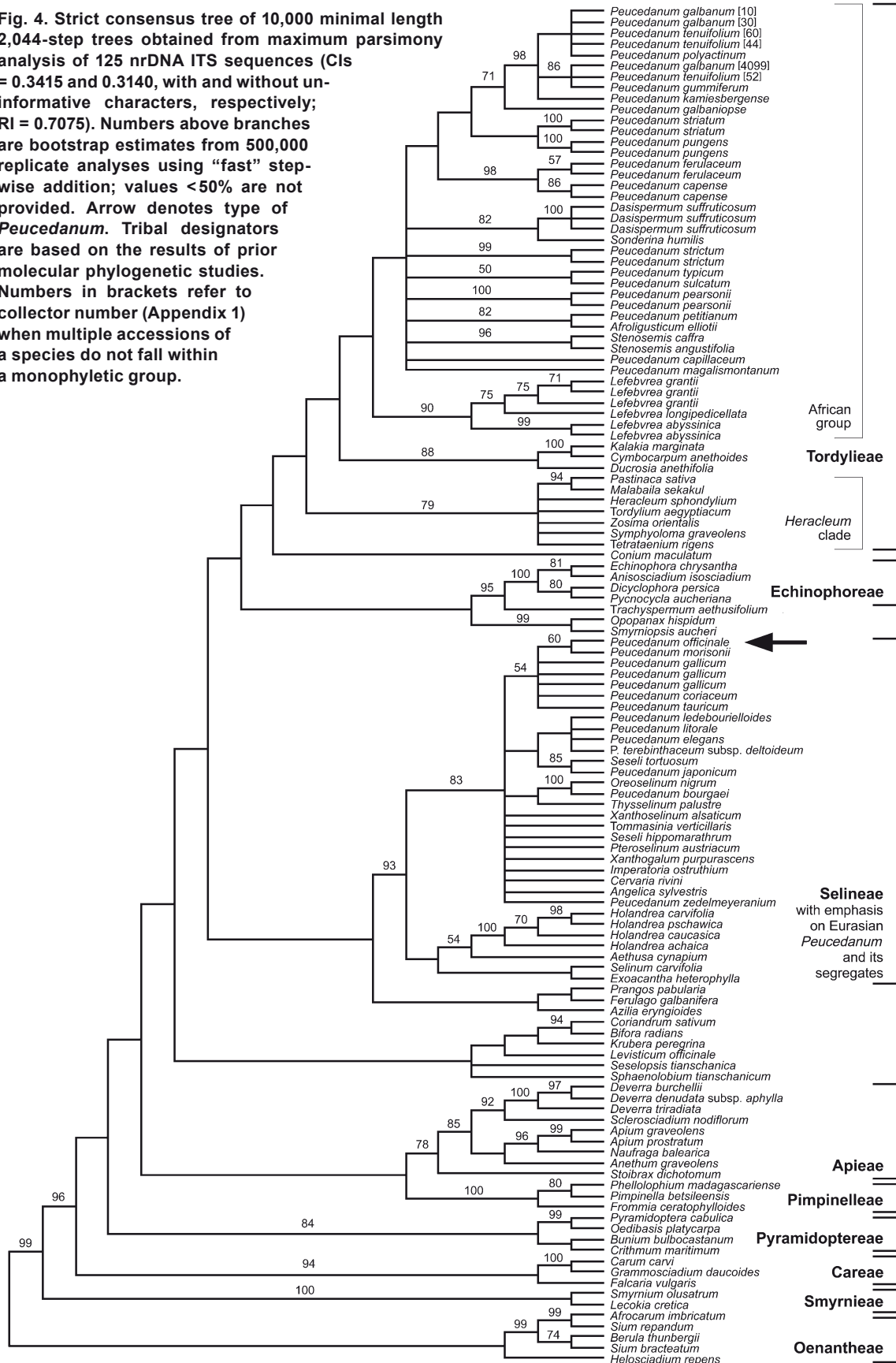


Fig. 3. Transverse sections through mericarps of the major African peucedanoid groups. A–B, Monocarpic group; C–D, *Crenato-serrata* group; E, *P. magalismontanum* group; F, *Cynorhiza* group; G–H, *P. galbanum* group; I, *P. strictum* group. A, *P. camerunense* (Koechlin 7541, P); B, *P. upingtoniae* (Dinter 7359, PRE); C, *P. aculeolatum* (Stauffer 622, PRE); D, *P. claessensii* (Robson 1715, PRE); E, *P. eylesii* (Richardson 8742, P); F, *P. typicum* (Galpin 6413, PRE); G, *P. gummiferum* (Thode 4850, PRE); H, *P. kamiesbergense* (Rourke 1979, NBG); I, *P. capillaceum* (Drewe 892, HER). c, commissure; cv, commissural vittae; dr, dorsal rib; mr, marginal rib; rv, rib vittae; vv, vallecular vittae.

Fig. 4. Strict consensus tree of 10,000 minimal length 2,044-step trees obtained from maximum parsimony analysis of 125 nrDNA ITS sequences (CIs = 0.3415 and 0.3140, with and without uninformative characters, respectively; RI = 0.7075). Numbers above branches are bootstrap estimates from 500,000 replicate analyses using “fast” step-wise addition; values <50% are not provided. Arrow denotes type of *Peucedanum*. Tribal designators are based on the results of prior molecular phylogenetic studies. Numbers in brackets refer to collector number (Appendix 1) when multiple accessions of a species do not fall within a monophyletic group.



apioid umbellifers, have been few and those that have been reported have only differed from one another by a few substitution differences and have not misled phylogenetic inferences (Chung & al., 2005; Spalik & Downie, 2006; Calviño & al., 2006). Constraining the analysis so that *P. officinale* and one accession of *P. galbanum* are monophyletic, results in trees 52 steps longer ($L = 2,096$ steps) than those without the constraint ($L = 2,044$). Our results regarding the divide between Selineae and Tordylieae are consistent with those from previous studies including analyses from different gene regions (Downie & al., 2001; Spalik & al., 2004). We conclude that the current classification is untenable, and that there is now a need to recognise the African species as distinct from *Peucedanum*.

The lack of nrITS sequence divergence among the African peucedanoid taxa and the limited sampling of this large group of species imply that any firm conclusions about generic relationships, based on this molecular evidence, would be premature.

The African group is comprised of two major clades: a *Lefebvrea* clade, which is supported strongly as monophyletic (90% bootstrap) and a second clade consisting of the remaining African peucedanoid species together with some taxa not previously associated with *Peucedanum*. This second clade is rendered non-monophyletic by the inclusion of *Afroligusticum*. The moderately well-supported grouping of *Afroligusticum elliotii* with *Peucedanum petitanum* (82% bootstrap) supports our broadened concept of *Afroligusticum*. The positions of *Dasispermum* Raf., *Sonderina humilis*, and *Stenosemis* E. Mey ex Sond. relative to African *Peucedanum* are unresolved (Fig. 4). The latter three genera differ markedly from all other species in their narrow commissures (distinctly narrower than the width of the fruit). As their status remains unaffected by our results, they are not discussed here.

The woody *P. galbanum* group, comprising species *P. galbanum* through *P. capense* in Fig. 4, forms a weakly supported clade; the morphologically similar *P. pearsonii*, however, falls outside of this clade as a separate branch of a large polytomy. Constraining the *P. galbanum* group of species and *P. pearsonii* to monophyly results in maximally parsimonious trees just two steps greater than those without the constraint ($L = 2,046$ steps) and supports the morphology in suggesting that these species are all very closely related. The two included accessions of *P. strictum* are monophyletic with *P. capillaceum* in a subset of the maximally parsimonious topologies ($L = 2,044$ steps). *Sonderina humilis* and *Dasispermum suffruticosum* form a monophyletic group (82% bootstrap), as do the two species of *Stenosemis* (96% bootstrap).

The generic treatment presented here is based on considerable experience of the taxonomy of African Apiaceae and insights into morphological patterns ob-

tained through many years of dedicated study, including laboratory and field work. Detailed taxonomic studies and revisions of *Cynorhiza*, *Notobubon* and *Nanobubon* have been completed and will be submitted for publication in the near future, while further morphological and molecular studies of the remaining taxa are currently underway.

TAXONOMIC TREATMENT

Key to African platyspermous Apiaceae genera

1. Fruit with commissure narrower than the fruit (including the wings): all other African and Madagascar genera and species.
 1. Fruit with commissure as wide as the fruit (including the wings): peucedanoid genera 2
 2. Woody shrubs or suffrutices with persistent, often sclerophyllous or leathery leaves 3
 2. Perennial or annual herbs with deciduous leaves 4
 3. Woody shrubs or shrublets; fruits small (less than 9 mm long) **Notobubon**
 3. Suffrutices (with woody subterranean stems); fruits large (more than 10 mm long). **Nanobubon**
 4. Perennial herbs; stems without purple or red spots near the base; leaf segments with secondary veins more or less uninterrupted before they reach the margin, fruit wings never exceeding the stylopodium 5
 4. Monocarpic herbs (doubtfully perennial in *L. abyssinica*); stems usually with purple or red spots near the base; leaf segments usually with a prominent vein midway between, and parallel with, the midvein and margin; fruit wings sometimes exceeding the stylopodium **Lefebvrea**
 5. Leaves absent (or at least senescent) at fruiting stage, fruit wings broad, Cape species **Cynorhiza**
 5. Leaves present (actively growing) at fruiting stage, fruit wings broad, narrow or absent, widespread except in the Cape 6
 6. Leaflet segments less than 8 mm wide (or if rarely more than 8 mm wide, then plant less than 1 m tall, with few umbels on long thin peduncles—*A. caffrum*, *A. eylesii*, or *A. platycarpum*), lamina coriaceous, veins more or less obscured below; mericarps invariably winged **Afroscidium**
 6. Leaflet segments of basal leaves usually wider than 8 mm (or, if less than 8 mm wide, then leaf segment margin revolute—*A. runssoricum*), lamina thin, veins conspicuous below; mericarps winged or wingless (*A. elliotii*, *A. thodei*) **Afroligusticum**
1. **Notobubon** B.-E. van Wyk, **gen. nov.** – Type: *Notobubon galbanum* (L.) A.R. Magee
Genus novum *Peucedano* L. simile, sed frutices ramis

lignosis persistentibus, foliis persistentibus sclerophyllibus, caulinis, umbellis primariis multiradiatis saepe brevipedunculatis, fructu parvo (infra 9 mm longo) alis marginalibus crassis angustis, et plerumque vittis 11 in quoque mericarpo differt.

Notobubon is similar to *Peucedanum* L. but the species are shrubs with woody permanent branches and cauline, permanent and sclerophyllous leaves. The primary umbel is often multiradiate and borne on a short peduncle. The fruits are small (less than 9 mm long) with the marginal wings thick and narrow, vittae usually eleven in each mericarp (solitary in each vallecule, two in the commissure—usually very broad—and five additional solitary vittae interior to the vascular bundle in each rib).

Twelve species subendemic to the Cape Floristic Region, with one species extending into the eastern parts of South Africa (Fig. 5A).

The segregation of these twelve woody Cape species seems long overdue as their woody branches, permanent cauline leaves and small fruits easily distinguish them. Many of the species in this group were once part of the genus *Bubon* L. (e.g., Sonder, 1862), but the name is unfortunately not available, as it has been typified by a Eurasian species (Burt, 1991). The root of the name is nevertheless retained here, with the Greek prefix “noto” meaning southern. We have followed Magee & al. (2008) in regarding the name *Bubon* as neuter.

Notobubon galbanum (L.) A.R. Magee, **comb. nov.** ≡ *Bubon galbanum* L., Sp. Pl.: 253. 1753 – Type: South Africa, Western Cape Province, *Herb. Clifford: 96, Bubon 3, sheet A* (BM000558280, BM!).

Notobubon capense (Eckl. & Zeyh.) A.R. Magee, **comb. nov.** ≡ *Oreoselinum capense* Eckl. & Zeyh., Enum. Pl. Afric. Austral.: 350. 1837 – Type: South Africa, Western Cape Province, Stellenbosch, Klapmuts, *Ecklon & Zeyher 2239* (S!, SAM!).

= *Peucedanum kamiesbergense* B.L. Burt in Edinb. J. Bot. 48: 232. 1991, **syn. nov.** – Type: South Africa, Northern Cape Province, Namaqualand, Khamiesberg, Rooiberg, *Rourke 1679* (E, NBG!, PRE!).

Notobubon ferulaceum (Thunb.) A.R. Magee, **comb. nov.** ≡ *Oenanthe ferulacea* Thunb., Prodr. Fl. Cap.: 50. 1794 – Type: South Africa, Cape of Good Hope, *Thunberg s.n.* (UPS-sheet 7089, microfiche!, photograph in BM!).

Notobubon galbaniopse (H. Wolff) A.R. Magee, **comb. nov.** ≡ *Peucedanum galbaniopse* H. Wolff in Bot. Jahrb. Syst. 57: 232. 1921 – Type: South Africa, Western Cape Province, Sir Lowry’s Pass, *Schlechter 7213* (BM!, K!, PRE!).

Notobubon gummiferum (L.) A.R. Magee, **comb. nov.** ≡ *Bubon gummiferum* L., Sp. Pl.: 254. 1753 – Type: Commelin, Hort. Med. Amst. 2: 115, t. 58. 1701.

Notobubon laevigatum (Aiton) A.R. Magee, **comb. nov.** ≡ *Bubon laevigatum* Aiton, Hort. Kew. 1: 352. 1789 – Type: Without locality, collector or number, labeled “type of *Bubon laevigatum*” (BM!).

= *Peucedanum camdeboosense* B.L. Burt in Edinb. J. Bot. 48: 228. 1991, **syn. nov.** Type: South Africa, Western Cape Province, Camdeboosberg, 4,000–5,000 ft, *Drège s.n.* (S!, K!, P!).

Notobubon montanum (Eckl. & Zeyh.) A.R. Magee, **comb. nov.** ≡ *Dregea montana* Eckl. & Zeyh., Enum. Pl. Afric. Austral. 351. 1837 – Type: South Africa, Eastern Cape Province, Uitenhage, Winterhoeksberge near Elandsrivier, *Ecklon & Zeyher 2242* (S!, photograph in K!, SAM!, P!).

Notobubon pearsonii (Adamson) A.R. Magee, **comb. nov.** ≡ *Peucedanum pearsonii* Adamson in J. Bot. 76: 345. 1938 – Type: South Africa, Northern Cape Province, Khamiesberg, *Adamson 1438* (BOL!, photograph in K!).

Notobubon pungens (Sond.) A.R. Magee, **comb. nov.** ≡ *Peucedanum pungens* E. Mey. ex Sond., in Harv. & Sond., Fl. Cap. 2: 557. 1862 – Type: South Africa, Western Cape Province, near Genadenthal, *Drège s.n.* (S!, K!, P!).

Notobubon sonderi (M. Hiroe) A.R. Magee, **comb. nov.** ≡ *Seseli sonderi* M. Hiroe, Umbell. World: 1128. 1979 – Type: South Africa, Western Cape Province, Dutoitskloof, *Drège s.n.* (S!, E, G, K!, BM!, PRE!, P!).

Notobubon striatum (Thunb.) A.R. Magee, **comb. nov.** ≡ *Seseli striatum* Thunb., Prodr. Fl. Cap.: 51. 1794 – Type: South Africa, Cape, *Thunberg s.n.* (UPS-sheet 7212, microfiche!).

Notobubon tenuifolium (Thunb.) A.R. Magee, **comb. nov.** ≡ *Peucedanum tenuifolium* Thunb., Prodr. Fl. Cap.: 50. 1794 – Type: South Africa, Western Cape Province, Mosterd Hoek, Cape of Good Hope, *Thunberg s.n.* (UPS-sheet 6924, microfiche!).

2. ***Nanobubon*** A.R. Magee, **gen. nov.** – Type: *Nanobubon strictum* (Spreng.) A.R. Magee.

Genus novum *Notobubo* B.-E. van Wyk simile foliis persistentibus sclerophyllibus, sed habitu suffruticoso caulibus lignosis subterraneis, fructu maiori 10–15 mm longo late-alato differt.

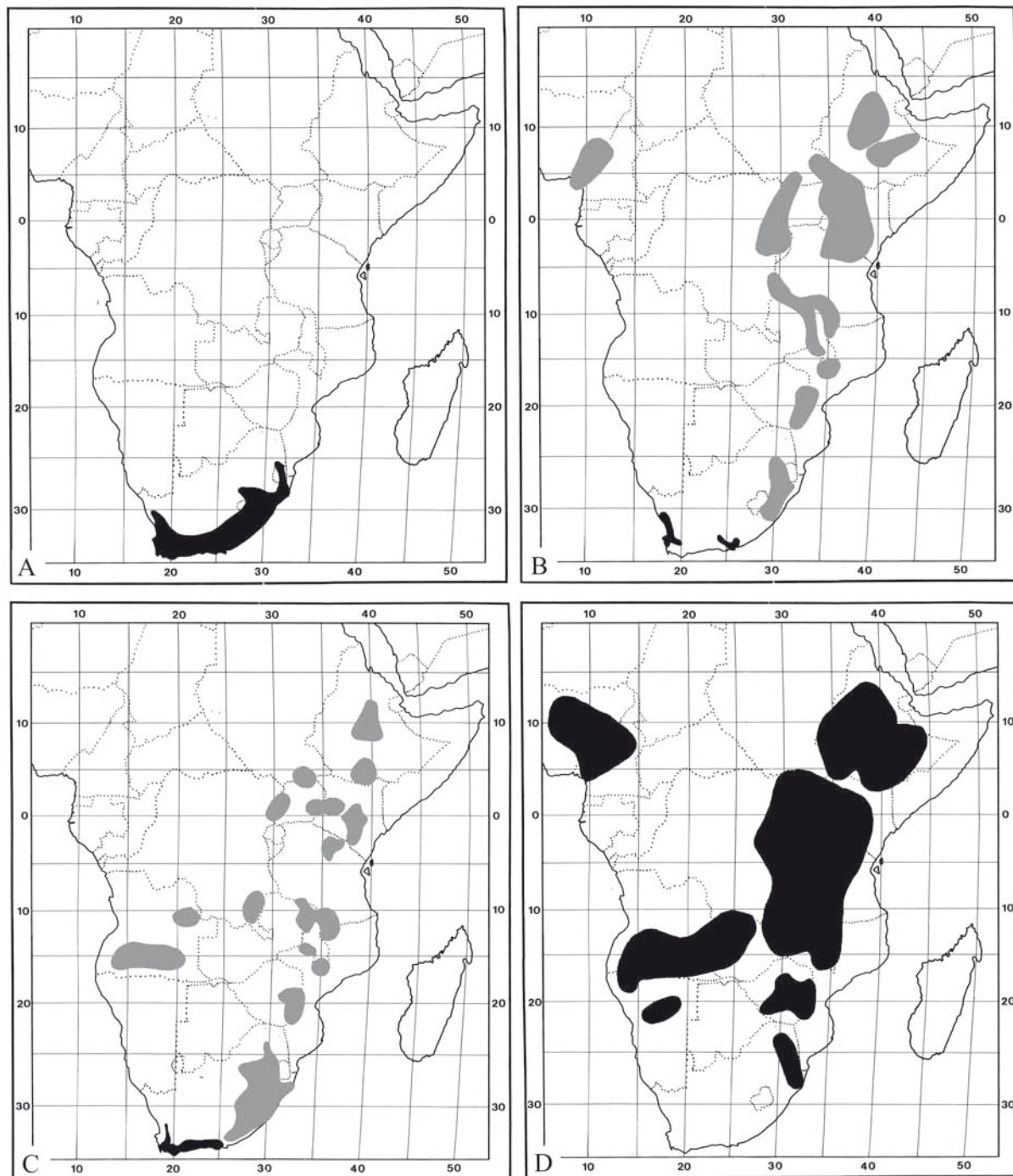


Fig. 5. Distribution ranges of African peucedanoid genera. A, *Notobubon* (black); B, *Cynorhiza* (black), *Afroligusticum* (grey); C, *Nanobubon* (black), *Afroscidium* (grey); D, *Lefebvrea* (black).

Nanobubon is similar to *Notobubon* in the permanent and sclerophyllous leaves, but differs in the suffrutescent habit with woody subterranean stems (woody shrubs in *Notobubon*) and in the larger fruits which are 10–15 mm long (less than 9 mm long in *Notobubon*) with broad wings (narrow in *Notobubon*).

Two species restricted to the Western Cape Province of South Africa and endemic to the Cape Floristic Region. The distribution is shown in Fig. 5C.

The name alludes to the similarity with *Notobubon* and the difference in habit, hence the Greek prefix “nano” (dwarf).

Nanobubon strictum (Spreng.) A.R. Magee, **comb. nov.**
 ≡ *Ferula stricta* Spreng., in Roem. & Schultes, Syst. Veg. 6: 592. 1820 – Type: South Africa, Western Cape Province, Cape of Good Hope, *Hesse s.n.* (photograph in W!).

Nanobubon capillaceum (Thunb.) A.R. Magee, **comb. nov.** ≡ *Peucedanum capillaceum* Thunb., Prodr. Fl. Cap. 50.: 1794 – Type: South Africa, Cape, *Thunberg s.n.* (UPS-sheet 6915, microfiche!, photograph in BM!).

3. *Cynorhiza* Eckl. & Zeyh., Enum. Pl. Afric. Austral.: 351. 1837 – Lectotype (designated here): *C. typica* Eckl. & Zeyh.

Perennial (non-woody) herbs with tuberous roots (?) and hysteranthous leaves (withered at time of fruiting), often with a large terminal umbel and a few, much smaller lateral umbels (or lateral umbels sometimes lacking) and very large fruits (more than 10 mm long) with broad, thin wings that are often apically notched as in *Lefebvrea* (but *Lefebvrea* differs in its monocarpic habit with a weak, non-tuberous taproot and the fertile part of the fruit is usually smaller). *Cynorhiza* has a distinctive combination of characters but the most useful diagnostic feature is the summer-deciduous leaves, which are senescent at the time of flowering and usually completely absent in the fruiting stage. All other African species have actively growing leaves present at the time of fruiting. In the Eastern Cape Province, *C. typicum* often responds to sporadic summer rains, and may therefore flower earlier or later than the other species. However, even in this species, leaves are invariably withered at the time of fruiting.

Three species with a restricted and disjunct distribution in the Western, Northern and Eastern Cape Provinces of South Africa (Fig. 5B). The third species is very poorly known and our attempts at locating plants have thus far failed.

The concept of the genus *Cynorhiza* is broadened here to include two poorly known species (one of which is undescribed) that have the same combination of characters as is found in *Cynorhiza* s.str. (the latter here for the first time considered to be monotypic). The new circumscription corresponds with Drude's (1897–98) concept that included *Peucedanum millefolium* in an unranked *Cynorhiza* group.

Cynorhiza typica Eckl. & Zeyh., Enum. Pl. Afric. Austral.: 352. 1837 – Type: South Africa, Eastern Cape Province, Uitenhage, Swartkops River, *Ecklon & Zeyher 2244* (SAM!, S!, P!).

= *Cynorhiza olifantiana* Koso-Pol. in Bull. Jard. Bot. Petersb. 16: 230. 1916, **syn. nov.** – Type: South Africa,

Eastern Cape Province, Uitenhage, near mouths of Koega and Swartkops rivers, *Zeyher 2692 p.p.* (photograph in LE!).

= *Peucedanum sulcatum* Eckl. & Zeyh. ex. Sond. in Harv. & Sond., Fl. Cap. 2: 559. 1862, **syn. nov.** – Type: South Africa, Northern Cape Province, Khamiesberg, *Ecklon & Zeyher 2247* (S!, SAM!).

Cynorhiza meifolia (Eckl. & Zeyh.) A.R. Magee, **comb. nov.** ≡ *Ferula meifolia* Eckl. & Zeyh., Enum. Pl. Afric. Austral.: 348. 1837 – Type: South Africa, Western Cape Province, Worcester, Tweney-Four Rivers, *Ecklon & Zeyher 2230* (S!, SAM!, K!, W!, HAL!).

Cynorhiza sp. *Bolus 8617* (BOL!); *Bolus s.n.* sub BOL 23408 (BOL!, NBG!, PRE!, BM!); *Barker 10142* (NBG!).

4. *Afroligusticum* C. Norman in De Wild., Pl. Bequaert. 4: 301. 1927 – Type: *Afroligusticum elliotii* (Engl.) C. Norman.

Afroligusticum has leaves similar to broad-leaved forms of *Lefebvrea* species, but it differs in the perennial habit and the mericarp wings not extending beyond the stylopodium. From *Afroscidium* it differs in the leaflet segments that are usually wider than 8 mm, the thin lamina and the prominent abaxial veins.

Thirteen species restricted to the Afromontane archipelago in tropical Africa from Ethiopia to South Africa, with an outlying part of the range in Cameroon and Bioko. The centre of diversity is in tropical East Africa, where plants grow in Afromontane grassland or forest habitats. The distribution is shown in Fig. 5B.

The concept of the monotypic *Afroligusticum* is here expanded by the transferral of twelve *Peucedanum* species. Of these species, seven were known to Engler (1921), six of which were in his *Crenato-serrata* group. The seventh species, *Peucedanum runsoricum*, was treated in a group of its own (Engler, 1921; Norman, 1934) due to its uniquely entire and revolute leaf segment margins, here postulated as an autapomorphy for the species, and thus considered of no value for grouping. Although *Afroligusticum elliotii* has a very different appearance from other African peucedanoid species due to its wingless mericarps and few-rayed umbels, it shares several characters with the other species in Engler's (1921) *Crenato-serrata* group. The mericarps of *A. elliotii* are indeed orthospermous (Townsend, 1989: fig. 27), the habit is the same, and the leaves show the broad segments with a thin lamina and prominent veins on the undersurface that are typical of our expanded *Crenato-serrata* group. A striking feature is the fern-like vestiture (scale-like trichomes) of stems and leaf axes in *A. elliotii*, *A. aculeolatum*, and to a lesser extent, *A. mattirolii*.

- Afroligusticum elliotii* (Engl.) C. Norman in J. Linn. Soc., Bot. 49: 516. 1934 ≡ *Peucedanum elliotii* Engl. in Engl. & Drude, Veg. Erde 9, Band 3(2): 825. 1921 – Type: Uganda, Ruwenzori, Yeria R., *Scott Elliot 7802* (B†, K!).
- Afroligusticum aculeolatum* (Engl.) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum aculeolatum* Engl. in Bot. Jahrb. Syst. 19, Beibl. 47: 42. 1894 – Type: Tanzania, Kilimanjaro, Marangu, *Volkens 718* (K!).
- Afroligusticum claessensii* (C. Norman) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum claessensii* C. Norman, in De Wild., Pl. Bequaert. 4: 352. 1928 – Type: D. R. Congo, Djukwa, *Claessens 1409* (BR).
- Afroligusticum elgonense* (H. Wolff) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum elgonense* H. Wolff in Notizbl. Bot. Gart. Berlin-Dahlem 8: 230. 1922 – Type: Kenya, Elgon, *Lindblom [s.n.]* (S).
- Afroligusticum linderi* (C. Norman) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum linderi* C. Norman in J. Linn. Soc., Bot. 49: 511. 1934 – Type: D. R. Congo, Mt. Niragongo, *Linder 2080* (K!).
- Afroligusticum mattirolii* (Chiov.) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum mattirolii* Chiov. in Nuovo Giorn. Bot. Ital. 3: 365. 1929 – Type: Ethiopia, Arsi region, Bekoji, Galamavalley, *Basile 61* (TO).
- Afroligusticum petitianum* (A. Rich.) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum petitianum* A. Rich., Tent. Fl. Abyss. 1: 327. 1848 – Type: Ethiopia, Gonder region, Wedgera [Oedgerate], *Petit s.n.* (P, photograph in K!).
- Afroligusticum runssoricum* (Engl.) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum runssoricum* Engl. in Bot. Jahrb. Syst. 19, Beibl. 47: 44. 1894 – Type: Uganda, Runssoro, Marangu, *Stuhlmann [s.n.]* (B†).
- Afroligusticum scottianum* (Engl.) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum scottianum* Engl. in Engl. & Drude, Veg. Erde 9, Band 3(2): 826. 1921 – Type: Uganda, Ruwenzori, *Scott Elliot 7631* (B†, BM!, K!).
- Afroligusticum thodei* (T.H. Arnold) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum thodei* T.H. Arnold in Bothalia 12: 441. 1978 – Type: South Africa, Kwazulu-Natal, Cathedral Peak Forest Research Station, Bergville dist., *Killick 1227* (K!, PRE!).
- Afroligusticum townsendii* (Charpin & Fern. Casas) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum townsen-*
- dii* Charpin & Fern. Casas in Anales Jard. Bot. Madrid, 54: 276. 1996 – Type: Bioko, “cumbre del pico Basilé”, Jul 1986, *Fernández Casas 10151* (MA, AAU, B, BM!, BR, COI, G, H, FI, K![2], LG, MO, P, S, U, UPS, WAG).
- Afroligusticum volkensisii* (Engl.) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum volkensisii* Engl. in Bot. Jahrb. Syst. 19, Beibl. 47: 43. 1894 – Type: Tanzania, Kilimanjaro, *Volkens 1364* (B†).
- Afroligusticum wilmsianum* (H. Wolff) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum wilmsianum* H. Wolff in Bot. Jahrb. Syst. 48: 280. 1912 – Type: South Africa, Kwazulu-Natal, Mzinto dist., Umgaye, *Rudatis 812* (E, K!, S).
5. *Afroscidium* P.J.D. Winter, **gen. nov.** – Type: *Afroscidium harmsianum* (H. Wolff) P.J.D. Winter.
- Genus novum *Nanobubo* A.R. Magee simile, sed foliis non persistentibus nec sclerophyllibus differt. Ab *Afroligustico* segmentis foliorum angustioribus, 1–4(–8) mm latis, laminis coriaceis, nervis subtus obscuribus differt. Similis est speciebus nonnullis *Peucedani* Asiae, sed fructu plerumque maiori differt.
- Afroscidium* is similar to *Nanobubon* but differs in that the leaves are neither permanent nor sclerophyllous. From *Afroligusticum*, it differs in the narrower leaf segments 1–4(–8) mm wide, acute apices, coriaceous lamina and veins more or less obscured below. It is similar to some Asian *Peucedanum* species but the fruits are generally larger.
- Eighteen species, mostly along the eastern part of Africa, from Ethiopia to the Amatola mountain range in South Africa, with an extension to Angola along the Congo-Zambezi watershed (Fig. 5C).
- This relatively large number of tropical African species (represented in the ITS analysis by a single species, *P. magalismontanum*) is distinguished from the other African herbaceous perennial groups either by narrower, coriaceous leaves with obscure venation, or by generally smaller fruits without apically-lobed mericarp wings, and by retaining the leaves throughout the flowering and fruiting periods, rather than with senescent or sclerophyllous leaves as is typical of the Cape species. Wolff (1927) considered several of these species to be closely related, a notion formalized by Norman (1934) as *Peucedanum* sect. *Cervaria*. This group is more difficult to distinguish morphologically from Eurasian *Peucedanum* species and their allies in the Selineae, than any of the other African groups. A comparison of fruit size showed that the African species generally have larger fruits (more than 8 mm long). The few African species with smaller fruits (*A. friesiorum*, *A. kerstenii*, *A. thodei*) each show a unique combination of

characters and can therefore easily be distinguished from Eurasian *Peucedanum* species using leaf division, petiole dilation, flower colour and fruit wing thickness.

The name is derived from *Afer* (Africa) and *sciadium* (umbel).

Afrosciadium harmsianum (H. Wolff) P.J.D. Winter, **comb. nov.**

- a. *Afrosciadium harmsianum* subsp. *harmsianum* ≡ *Peucedanum harmsianum* H. Wolff in Notizbl. Bot. Gart. Berlin-Dahlem 9: 1121. 1927 – Type: Kenya, N. Nyeri dist., Cole's mill, *R.E. & T.C.E. Fries 1031* (UPS, photograph in K!).
- b. *Afrosciadium harmsianum* subsp. *australis* (C.C. Towns.) P.J.D. Winter ≡ *Peucedanum harmsianum* subsp. *australe* C.C. Towns. in Kew Bull. 42: 593. 1987 – Type: Tanzania, Kondo dist., hills above Kolo, *Burt 1189* (K!).

Afrosciadium abyssinicum (Vatke) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum abyssinicum* Vatke in Linnaea 40: 187. 1876 – Type: Ethiopia, Gonder region, Gafat, c. 2,700 m, 1863–1868, *Schimper 1147* (BM!, K!).

Afrosciadium articulatum (C.C. Towns.) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum articulatum* C.C. Towns. in Kew Bull. 42: 602, fig. 5. 1987 – Type: Malawi, Northern Province, Nyika Plateau, *Pawek 11203* (K!, MAL, MO, PRE!, SRGH, UC).

Afrosciadium caffrum (Meisn.) P.J.D. Winter, **comb. nov.** ≡ *Seseli caffrum* Meisn. in Lond. J. Bot. 2: 533. 1843 – Type: South Africa, Kwazulu-Natal, Durban area, *Krauss 403* (BM!).

Afrosciadium dispersum (C.C. Towns.) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum dispersum* C.C. Towns. in Kew Bull. 42: 596. 1987 – Type: Tanzania, Poroto Mountains, Igoma to Kitulo, W of road to Matamba, 29 May 1980, *Hooper, Townsend & Mwasumbi 1758* (K!).

Afrosciadium englerianum (H. Wolff) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum englerianum* H. Wolff in Notizbl. Bot. Gart. Berlin-Dahlem 9: 1122. 1927 – Type: Kenya, Aberdare Mountains near Kinangop, *R.E. & T.C.E. Fries 2694* (UPS, photograph in K!).

Afrosciadium eylesii (C. Norman) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum eylesii* C. Norman in J. Bot. 70: 138. 1932 – Type: Zimbabwe, Eastern Highlands, Macheke, *Eyles 2006* (PRE!, K!, SRGH).

Afrosciadium friesiorum (H. Wolff) P.J.D. Winter, **comb. nov.**

- a. *Afrosciadium friesiorum* var. *friesiorum* ≡ *Peucedanum friesiorum* H. Wolff in Notizbl. Bot. Gart. Berlin-Dahlem 9: 1119, fig. 15. 1927 – Type: Kenya, Mt Kenya, *R.E. & T.C.E. Fries 1301* (UPS, K!).
- b. *Afrosciadium friesiorum* var. *bipinnatum* (C.C. Towns.) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum friesiorum* H. Wolff var. *bipinnatum* C.C. Towns. in Kew Bull. 42: 591. 1987 – Type: Kenya, Aberdare Mountains, above Wanderi's Camp, *Townsend 2405* (K!).

Afrosciadium gossweileri (C. Norman) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum gossweileri* C. Norman in J. Bot. 60: 120. 1922 – Type: Angola, Mumua, Right bank of Lunga River, *Gossweiler 3011* (BM!).

Afrosciadium kerstenii (Engl.) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum kerstenii* Engl. in Bot. Jahrb. Syst. 19, Beibl. 47: 43. 1894 – Neotype: Tanzania, Kilimanjaro, 4,200 m, *Hedberg 1206* (EA, K!, S, UPS).

Afrosciadium lundense (Cannon) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum lundense* Cannon in Bol. Soc. Brot. ser. 2., 44: 99, tab. 1. 1970 – Type: Angola, between Vila Henrique de Carvalho and Dala, 1,100–1,300 m, 24/4/1937, *Exell & Mendonça 1058* (BM!, photograph in K!, COI).

Afrosciadium lynesii (C. Norman) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum lynesii* C. Norman in J. Bot. 74: 171. 1936 – Type: Tanzania, Iringa dist. side of Mt Luhoto [Lukota], *Lynes I.H.83* (K!).

Afrosciadium magalimontanum (Sond.) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum magalimontanum* Sond. in Harv. & Sond., Fl. Cap. 2: 558. 1862 – Syntypes: South Africa, Transvaal, Magalisberg and near Vaal R., *Burke 277* (K?, S?) & *Zeyher 118, 744* (K?, S!, SAM!).

Afrosciadium natalense (Sond.) P.J.D. Winter, **comb. nov.** ≡ *Seseli natalense* Sond. in Harv. & Sond., Fl. Cap. 2: 550. 1862 – Type: South Africa, Kwazulu-Natal, near Durban, *Gueinzus 535* (S).

Afrosciadium nyassicum (H. Wolff) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum nyassicum* H. Wolff in Bot. Jahrb. Syst. 48: 282. 1912 – Type: Malawi, Mt Mulanje, 1891, *Whyte s.n.* (B†, photographs in BM!, K!, BM!, K!).

Afrosciadium platycarpum (Sond.) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum platycarpum* Sond. in Harv. & Sond., Fl. Cap. 2: 557. 1862 – Type: South Africa,

E. Cape Province, Kachu or Geelhoutriver, *Drège s.n.* (S).

Afroscidium rhodesicum (Cannon) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum rhodesicum* Cannon in Garcia de Orta, Sér. Bot. 1: 47, tab. 1. 1973 – Type: Zimbabwe, Nyanga dist., Mt Nyangani, *Wild 4931* (BM!, K!, SRGH).

Afroscidium trisectum (C.C. Towns.) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum trisectum* C.C. Towns. in Kew Bull. 32: 601. 1978 – Type: D. R. Congo, Shaba Province: Kundelungu Plateau, 3–4 km beyond N boundary of National Park on track to Katshupa, c. 1,700 m, 4/3/1975, *Hooper & Townsend 504* (BM!, K!, LSHI).

6. ***Lefebvrea*** A. Rich. in Ann. Sci. Nat., Bot., sér. 2, 14: 260, tab. 15/1. 1840. – Type: *Lefebvrea abyssinica* A. Rich.
= *Erythroselinum* Chiov. in Ann. Bot. (Rome) 9: 64. 1911, **syn. nov.** – Type: *Lefebvrea atropurpurea* (Hochst. ex A. Rich.) P.J.D. Winter

Lefebvrea can be distinguished from all indigenous African platyspermous genera by the monocarpic habit. The stems are usually red or purple-spotted near the base and petals often have some degree of red or purple pigmentation. Leaf segments of most species have a prominent vein midway between, and almost parallel with, the midvein and margin, that further helps to distinguish this genus from others, though this is not always apparent, particularly in the broader leaf segments often present in forms of certain species.

The concept of *Lefebvrea* is here expanded to now comprise ten monocarpic species in tropical and subtropical Africa (Fig. 5D). It occurs in woodland or wooded grassland.

We found six *Peucedanum* species that share a monocarpic habit with *Lefebvrea*, but lack the distinctive apically-lobed mericarp wings that exceed the stylopodium, as found in all other species traditionally placed in that genus. The only genus other than *Lefebvrea* in this alliance with a monocarpic habit is *Erythroselinum*. The fruits of these species agreed more with those of the monotypic *Erythroselinum* than those of *Lefebvrea*, and we considered transferring these six species to the former. Three of the species (*P. madense*, *P. upingtoniae*, *P. wildemanianum*) seem to have been treated in *Peucedanum* simply because it was not clear whether they should be placed in *Erythroselinum* or *Lefebvrea*. They were found to correspond to Townsend's (1989) expanded concept of *L. grantii*, a widespread and very variable aggregate species that has already accumulated a myriad of synonyms including several from *Peucedanum*, in the regions where this complex has been studied. These remaining three occur in areas that have

not had recent Flora treatments, but they can now readily be absorbed into this complex. The continuous variation in the extent of wing lobes in the Monocarpic group, already reported by Cannon (1978) in *L. grantii*, effectively closes the gap that was perceived to exist between *Lefebvrea* and *Erythroselinum*, and we find no reason to retain the latter as a separate genus. The monocarpic *Peucedanum* species that were kept out of *Lefebvrea* on the basis of this character state are here transferred to that genus. We postulate the monocarpic habit as a synapomorphic character for this group. Two of these species (*Peucedanum camerunense*, *P. kupense*) were distinguished from *P. angustisectum* (Engl.) C. Norman on the basis of leaf and fruit characters that are known to be variable at species level for most, if not all of the species. Though species rank may later be confirmed, we think it prudent not to make new combinations for species of doubtful status, and have thus chosen to reduce them to synonymy. As this has implications for the conservation status of *P. kupense*, there is some urgency for a revision of *Lefebvrea*, in which the taxonomic status of such species can be evaluated in a relevant context.

Lefebvrea abyssinica A. Rich. in Ann. Sci. Nat., Bot., sér. 2, 14: 260, tab. 15/1. 1840 – Type: Ethiopia, Tigray region, Hica, *Quartin-Dillon & Petit s.n.* (P, photograph in K!).

Lefebvrea angustisecta Engl. in Engl. & Drude, Veg. Erde 9, Band 3(2): 829. 1921 – Type: Cameroon, Mt Cameroon, *Preuss 969* (HBG, K!—as *969a*).

= *Peucedanum camerunense* Jacq.-Fél. in Adansonia 10: 47, tab. 1. 1970, **syn. nov.** – Type: Cameroon, region de Fouban, Mt Nko Gam, about 2,400 m, *Koehlin 7541* (P, photograph in K!).

= *Peucedanum kupense* I. Darbyshire & Cheek in Kew Bull. 59: 133. 2004, **syn. nov.** – Type: Cameroon, Southwest Province, Mt Kupe summit, peak 2, c. 1,900 m, 31/10/1995, *Cheek 7586* (K!, MO, P, SCA, WAG, YA).

Lefebvrea atropurpurea (Hochst. ex A. Rich.) P.J.D. Winter, **comb. nov.** ≡ *Pastinaca atropurpurea* Hochst. ex A. Rich., Tent. Fl. Abyss. 1: 329. 1848 – Type: Ethiopia, Tigray region, near Gapdia, *Schimper II: 788* (K!).

Lefebvrea brachystyla Hiern ex Oliver in Trans. Linn. Soc. London 29: 80. 1873 – Type: Tanzania, Tabora dist. Unyamwezi, *Grant [s.n.]* (K!).

Lefebvrea droopii C.C. Towns. in Kew Bull. 42: 589. 1987 – Type: Tanzania, Uluguru mts, Lukwangule Plateau above Chenzema Mission, *Drummond & Hemsley 1530* (K!).

- Lefebvrea grantii* (Hiern) S. Droop in Troupin, Fl. Rwanda 2: 575. 1983 – Type: Uganda, Bunyoro [Unyoro], *Grant 581* (K!).
- = *Lefebvrea upingtoniae* Schinz in Bull. Herb. Boissier 2: 206. 1894, **syn. nov.** – Type: Namibia, SE Ondonga, farm Upingtonia, *Schinz 1034* (=“1033”) (Z, photograph in K!).
- = *Peucedanum madense* C. Norman in J. Bot. 74: 513. 1934, **syn. nov.** – Type: N Nigeria, Mada Hills, Wana, *Hepburn 93* (K!).
- = *Peucedanum wildemanianum* C. Norman in De Wild., Contr. fl. Katanga, Suppl. 2: 99. 1929, **syn. nov.** – Type: D. R. Congo, Shaba Province, Munama, 4/1928, *Quarre 1110* (BR, sketch in BM!).

Lefebvrea longipedicellata Engl. in Pflanzenw. Ost-Afrikas C: 300. 1895 – Type: Tanzania, Kilimanjaro, Marangu, *Volkens 2269* (BM!, K!).

Lefebvrea oblongisecta (C.C. Towns.) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum oblongisectum* C.C. Towns. in Kew Bull. 42: 598, fig. 3. 1987 – Type: Tanzania, Ufupa dist., Luiche escarpment, *Richards 15788* (K!).

Lefebvrea stenosperma (C.C. Towns.) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum stenospermum* C.C. Towns. in Kew Bull. 42: 600. 1987 – Type: Zambia, Northern region: 8 km E of Shiva Ngandu, 1,460 m, 18/1/1972, *Kornás 0897* (K!).

Lefebvrea tenuis (C.C. Towns.) P.J.D. Winter, **comb. nov.** ≡ *Peucedanum tenue* C.C. Towns. in Kew Bull. 42: 602. 1987 – Type: Zambia, Northern region: between Mbala & Kasama, N’tingila Ranch, 8/6/1980, *Hooper & Townsend 1892* (K!).

Species insufficiently known

Peucedanum princeae (Engl. & H. Wolff) M. Hiroe ≡ *Malabaila princeae* Engl. & H. Wolff in Engl. & Drude, Veg. Erde 9, Band 3(2): 830. 1921.

Peucedanum quarrei (C. Norman) M. Hiroe ≡ *Malabaila quarrei* C. Norman in De Wild., Contr. Fl. Katanga, Suppl. 2: 96. 1929.

Peucedanum winkleri H. Wolff in Bot. Jahrb. Syst. 48: 278. 1912 – Lectotype (designated by Townsend, 1987): Tanzania, Kilimanjaro, Marangu, *Winkler 3862* (B⁺). We tentatively follow Townsend (1987) regarding the exclusion of this name despite his arguments that it is conspecific with *Afroligusticum linderi*. Townsend’s lectotypification and conclusions require critical assessment, preferably as part of a revision of *Afroligusticum*.

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LITERATURE CITED

- Ajani, Y., Ajani, A., Cordes, J.M., Watson, M.F. & Downie, S.R. 2008. Phylogenetic analysis of nrDNA ITS sequences reveals relationships within five groups of Iranian Apiaceae subfamily Apioideae. *Taxon* 57: 383–401.
- Álvarez, I. & Wendel, J.F. 2003. Ribosomal ITS sequences and plant phylogenetic inference. *Molec. Phylog. Evol.* 29: 417–434.
- Burt, B.L. & Davis, P.H. 1949. *Glaucosciadium*: a new Mediterranean genus of Umbelliferae. *Kew Bull.* 2: 225–230.
- Burt, B.L. 1991. Umbelliferae of southern Africa: an introduction and annotated checklist. *Edinburgh J. Bot.* 48: 133–282.
- Calestani, V. 1905. Contributo alla sistematica delle Ombrellifere d’Europa. *Webbia* 1: 89–280.
- Calviño, C.I., Tilney, P.M., Van Wyk, B.-E. & Downie, S.R. 2006. A molecular phylogenetic study of southern African Apiaceae. *Amer. J. Bot.* 93: 1832–1833.
- Cannon, J.F.M. 1978. Umbelliferae. Pp. 555–621 in: Launert, E. (ed.), *Flora Zambesiaca*, vol. 4. Flora Zambesiaca Managing Committee, London.
- Chung, K.-F., Peng, C.-I., Downie, S.R., Spalik, K. & Schaal, B.A. 2005. Molecular systematics of the trans-Pacific Alpine genus *Oreomyrrhis* (Apiaceae): phylogenetic affinities and biogeographic implications. *Amer. J. Bot.* 92: 2054–2071.
- Downie, S.R. & Katz-Downie, D.S. 1996. A molecular phylogeny of Apiaceae subfamily Apioideae: evidence from nuclear ribosomal DNA internal transcribed spacer sequences. *Amer. J. Bot.* 83: 234–251.
- Downie, S.R., Plunkett, G.M., Watson, M.F., Spalik, K., Katz-Downie, D.S., Valiejo-Roman, C.M., Terentieva, E.I., Troitsky, A.V., Lee, B.-Y., Lahham, J. & El-Oqlah, A. 2001. Tribes and clades within Apiaceae subfamily Apioideae: the contribution of molecular data. *Edinburgh J. Bot.* 58: 301–330.
- Downie, S.R., Ramanath, S., Katz-Downie, D.S. & Llanas, E. 1998. Molecular systematics of Apiaceae subfamily Apioideae: phylogenetic analyses of nuclear ribosomal DNA internal transcribed spacer and plastid *rpoCl* intron sequences. *Amer. J. Bot.* 85: 563–591.
- Downie, S.R., Watson, M., Spalik, K. & Katz-Downie, D.S. 2000. Molecular systematics of Old World Apioideae (Apiaceae): relationships among some members of the tribe Peucedaneae sensu lato, the placement of several island-

- endemic species, and resolution within the apiooid superclade. *Canad. J. Bot.* 78: 506–528.
- Doyle, J.J. & Doyle, J.L.** 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull.* 19: 11–15.
- Drude, O.** 1897–1898. Umbelliferae. Pp. 63–250 in: Engler, A. & Prantl, K. (eds.), *Die natürlichen Pflanzenfamilien*, 3(8). Engelmann, Leipzig.
- Ecklon, C.F. & Zeyher, C.** 1837: *Enumeratio plantarum Africae australis extratropicae*. Perthes & Besser, Hamburg. [Umbelliferae: 330–355]
- Engler, A.** 1921. Die Pflanzenwelt Afrikas 3 (2). Pp. 821–831 in: Engler, A. & Drude, O. (eds.), *Die Vegetation der Erde* 9. Engelmann, Leipzig.
- Feder, N. & O'Brien, T.P.** 1968. Plant microtechnique: some principles and new methods. *Amer. J. Bot.* 55: 123–142.
- Felsenstein, J.** 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.
- Frey, R.** 1989. Taxonomische Revision der Gattung *Peucedanum*: Sektion *Peucedanum* und Sektion *Palimbioidea* (Umbelliferae). *Candollea* 44: 257–327.
- Hadaček, F.** 1986. Vergleichende phytochemische Untersuchungen in der Gattung *Peucedanum* (Apiaceae-Apioideae). *Stapfia* 18: 1–190.
- Jacques-Félix, H.** 1970. Contribution à l'étude des Umbelliflorae du Cameroun. *Adansonia* 10: 35–94.
- Jeanmougin, F., Thompson, J.D., Gouy, M., Higgins, D.G. & Gibson, T.J.** 1998. Multiple sequence alignment with Clustal X. *Trends Biochem. Sci.* 23: 403–405.
- Kowal, T. & Wojterska, H.** 1973. Morfologiczne i anatomiczne cechy diagnostyczne owocow wybranych gatunkow rodzaju *Peucedanum* L. *Prace Komis. Biol.* 35: 33–67.
- Magee, A.R., Van Wyk, B.-E. & Tilney, P.M.** 2008. The identity of the type of *Bubon gummiferum* (*Peucedanum gummiferum*) (Apiaceae). *Taxon* 57: 615–618.
- Norman, C.** 1934. *Peucedanum* and *Steganotaenia* in Tropical Africa. *Bot. J. Linn. Soc.* 49: 503–516.
- Ostroumova, T.A. & Pimenov, M.G.** 1997a. Carpological diversity of African *Peucedanum* s.l. (Umbelliferae) I. The species of southern Africa. *Feddes Repert.* 108: 299–318.
- Ostroumova, T.A. & Pimenov, M.G.** 1997b. Carpological diversity of African *Peucedanum* s.l. (Umbelliferae) II. The species of Tropical Africa. *Feddes Repert.* 108: 533–547.
- Pimenov, M.G. & Leonov, M.V.** 1993. *The Genera of the Umbelliferae*. Royal Botanic Gardens, Kew.
- Pimenov, M.G.** 1987. *Leutea, Demavendia, Cervaria, Johreniopsis, Zeravschania*. Pp. 445–461 in: Rechinger, K.H. (ed.), *Flora Iranica*, vol. 162. Akademische Druck- u. Verlagsanstalt, Graz.
- Reduron, J.-P.** 1984. Biologie florale de quatre espèces de *Peucedanum* (Umbelliferae) de la flore française; conclusions pluri-disciplinaires et implications taxonomiques. *Bull. Mus. Natl. Hist. Nat., B, Adansonia* 6: 119–145.
- Schur, P.J.F.** 1866. *Enumeratio plantarum Transilvaniae exhibens*. Guilielmum Braumüller, Vindobonae.
- Shneyer, V.S., Kutayvina, N.G. & Pimenov, M.G.** 2003. Systematic relationships within and between *Peucedanum* and *Angelica* (Umbelliferae-Peucedaneae) inferred from immunological studies of seed proteins. *Pl. Syst. Evol.* 236: 175–194.
- Sonder, O.W.** 1862. Umbelliferae. Pp. 524–567 in: Harvey, W.H. & Sonder, O.W. (eds.), *Flora Capensis*, vol. 2. Hodges Smith, Dublin.
- Spalik, K., Reduron, J.-P. & Downie, S.R.** 2004. The phylogenetic position of *Peucedanum* sensu lato and allied genera and their placement in tribe Selineae (Apiaceae, subfamily Apioideae). *Pl. Syst. Evol.* 243: 189–210.
- Spalik, K. & Downie, S.R.** 2006. The evolutionary history of *Sium* sensu lato (Apiaceae): dispersal, vicariance, and domestication as inferred from ITS rDNA phylogeny. *Amer. J. Bot.* 93: 747–761.
- Spalik, K. & Downie, S.R.** 2007. Intercontinental disjunctions in *Cryptotaenia* (Apiaceae, Oenantheae): an appraisal using molecular data. *J. Biogeogr.* 34: 2039–2054.
- Sun, Y., Skinner, D.Z., Liang, G.H. & Hulbert, S.H.** 1994. Phylogenetic analysis of *Sorghum* and related taxa using internal transcribed spacers of nuclear ribosomal DNA. *Theor. Appl. Genet.* 89: 26–32.
- Swofford, D.L.** 2002. *PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods)*, version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.
- Townsend, C.C.** 1987. Notes on *Peucedanum* (Umbelliferae) and allied genera in Central and East Africa. *Kew Bull.* 42: 587–604.
- Townsend, C.C.** 1989. Umbelliferae. Pp. 1–127 in: Polhill, R.M. (ed.), *Flora of Tropical East Africa*. Balkema, Rotterdam.
- Wolff, H.** 1927. Umbelliferae. Pp. 1107–1124 in: Fries, R.E. & Fries, T.C.E. Beiträge zur Kenntnis der Flora des Kenia, Mt. Aberdare und Mt. Elgon IX. *Notizbl. Bot. Gart. Berlin-Dahlem* 9: 1103–1124.

Appendix 1. New accessions of Apiaceae from which nrDNA ITS sequences were obtained, with corresponding voucher information and GenBank reference numbers.

Dasispermum suffruticosum (P.J. Bergius) B.L. Burt, *Downie 2451* (ILL), South Africa, Betty's Bay, AM408870; *Goldblatt & Manning 9522A* (MO), South Africa, Glentana, AM408871; *Hugo 1908* (MO), South Africa, Witsand, AM408872; *Deverra burchellii* (DC.) Eckl. & Zeyh., *Van Wyk & Tilney 4114* (JRAU), South Africa, Polokwane, AM408887; *Deverra denudata* (Viv.) Pfisterer & Podlech subsp. *aphylla* (Cham. & Schltdl.) Pfisterer & Podlech, *Vlok 2270* (JRAU), South Africa, Beaufort West, Nuwevelsberge plateaux, AM408888; *Lefebvrea longipedicellata* Engl. (= *L. brevipes* H. Wolff), *Banda & al. 3477* (MO), Malawi, Mulanje, slopes of Mulanje Mountain, AM408877; *Lefebvrea grantii* (Hiern) S. Droop, *Malaisse 13815* (PRE), Zaire, Kakands-Kambove, AM408878; *Lefebvrea grantii* (Hiern) S. Droop (= *Peucedanum angolense* (Welw.) Cannon), *Henriques 393* (MO), Angola, Huila, Sá da Bandeira, Tchivinguire, AM408881; *Lefebvrea grantii* (Hiern) S. Droop (= *Peucedanum zenkeri* H. Wolff), *Leeuwenberg 10670* (MO), Cameroon, 6 km W of Bandjoun, cult. in medicinal plant garden, AM408880; *Lefebvrea abyssinica* A. Rich., *Gilbert & Thulin 790* (MO), Ethiopia, Wollega Region, AM408879; *Peucedanum capense* (Thunb.) Sond., *Winter 6832* (JRAU), South Africa, Valley of Desolation, AM408861; *Van Wyk & Van Wyk 42* (JRAU), South Africa, Zuurberg National Park, AM408860; *Peucedanum capillaceum* Thunb., *Magee & Boatwright 14* (JRAU), South Africa, Fernkloof Nature Reserve, AM408864; *Peucedanum elegans* (Spreng.) Sweet, *Constance C-970* (ISU), Russia, Vladivostok 451-672, cult. University of California Botanical Garden, Berkeley, U.S.A., AM408885; *Peucedanum ferulaceum*

Appendix 1. Continued.

(Thunb.) Eckl. & Zeyh., *Magee 59* (JRAU), South Africa, Camps Bay, AM408859; *Van Wyk 3881a* (JRAU), South Africa, Knysna, Perdekop, AM408858; *Peucedanum galbaniopse* H. Wolff, *Magee & al. 49* (JRAU), South Africa, Harold Porter National Botanical Garden, AM408853; *Peucedanum galbanum* (L.) Drude, *Van Wyk 4099* (JRAU), South Africa, Noordhoek Pass, AM408846; *Magee & Boatwright 10* (JRAU), South Africa, De Hoop Nature Reserve, AM408844; *Magee & Boatwright 30* (JRAU), South Africa, Jonkershoek Nature Reserve, AM408845; *Peucedanum gallicum* Latour., *Constance C-1045* (ISU), Germany, Halle University Botanical Garden, cult. University of California Botanical Garden, Berkeley, U.S.A., AM408883; *Constance C-884* (ISU), France, Botanical Gardens, Versailles 2111, cult. University of California Botanical Garden, Berkeley, U.S.A., AM408882; *Peucedanum gummiferum* (L.) D.O. Wijnands, *Magee & al. 61* (JRAU), South Africa, Marloth Nature Reserve, AM408852; *Peucedanum kamiesbergense* B.L. Burtt, *Magee & al. 43* (JRAU), South Africa, Khamiesberg, Stalberg summit, AM408851; *Peucedanum magalismontanum* Sond., *Magee & Boatwright 54* (JRAU), South Africa, Gauteng, Honeydew, AM408876; *Peucedanum pearsonii* Adamson, *Magee & al. 42* (JRAU), South Africa, Khamiesberg, 1 km N of Windpoort, AM408867; *Van Wyk s.n.* (JRAU), South Africa, Khamiesberg, AM408868; *Peucedanum petitiunum* A. Rich., *Constance C-462* (ISU), Ethiopia, Kaffa Province, 7 km N of Jimma on Addis Ababa road, cult. University of California Botanical Garden, Berkeley, U.S.A., AM408869; *Peucedanum polyactinum* B.L. Burtt, *Magee & al. 37* (JRAU), South Africa, Harold Porter National Botanical Garden, AM408850; *Peucedanum pungens* E. Mey. ex Sond., *Helme 1865* (JRAU), South Africa, Caledon, Farm Welgemoed 113, AM408857; *Magee & al. 50* (JRAU), South Africa, Spes Bona, AM408856; *Peucedanum striatum* (Thunb.) Sond., *Helme 1896* (JRAU), South Africa, Bredasdorp district, AM408855; *Magee & al. 51* (JRAU), South Africa, Potberg, AM408854; *Peucedanum strictum* (Spreng.) B.L. Burtt, *Magee & al. 58* (JRAU), South Africa, Noordhoek Pass, AM408863; *Winter & Van Wyk 171* (JRAU), South Africa, Du Toit's Kloof, AM408862; *Peucedanum sulcatum* Eckl. & Zeyh. ex Sond., *Magee & al. 53* (JRAU), South Africa, 4.8 km from Lamberts Bay to Elands Bay, AM408866; *Peucedanum tauricum* M. Bieb., *Constance C-930* (ISU), Russia, Komarov Botanical Institute, Moscow 1968/1514, cult. University of California Botanical Garden, Berkeley, U.S.A., AM408884; *Peucedanum tenuifolium* Thunb., *Magee & Van Wyk 60* (JRAU), South Africa, Montagu, AM408848; *Magee & al. 44* (JRAU), South Africa, Pakhuis Pass, AM408849; *Magee & al. 52* (JRAU), South Africa, Seweweekspoort, AM408847; *Peucedanum terebinthaceum* Fisch. ex Rchb. subsp. *deltoideum*, *Constance C-969* (ISU), Russia, Botanical Garden, Vladivostok 450-682, cult. University of California Botanical Garden, Berkeley, U.S.A., AM408886; *Peucedanum typicum* (Eckl. & Zeyh.) B.L. Burtt, *Van Wyk 3372* (JRAU), South Africa, Addo Elephant National Park, AM408865; *Sonderina humilis* (Meisn.) H. Wolff, *Hilliard & Burtt 14861* (E), South Africa, East London District, AM408873; *Stenosemis angustifolia* E. Mey ex Sond., *Hilliard & Burtt 16324* (MO), South Africa, Transkei, above Mhlanfane Forest Station, AM408875; *Stenosemis caffra* (Eckl. & Zeyh.) Sond., *Van Wyk & Van Wyk 1210* (JRAU), South Africa, Zuurberg National Park, AM408874.

Appendix 2. Previously published nrDNA ITS accessions of Apiaceae obtained from GenBank.

Aethusa cynapium L., U30582, U30583; *Afrocarum imbricatum* (Schinz) Rauschert, AY360228; *Afroligusticum elliotii* (Engl.) C. Norman, DQ516377; *Anethum graveolens* L., AY548225; *Angelica sylvestris* L., U78414, U78474; *Anisosciadium isosciadium* Bornm., EU169244; *Apium graveolens* L., U30552, U30553; *Apium prostratum* Ventenat, K. Spalik & S.R. Downie, unpubl; *Azilia eryngioides* (Pau) Hedge & J.M. Lamond, AF008620, AF009099; *Berula thunbergii* H. Wolff, AY353975; *Bifora radians* M. Bieb., U78408, U78468; *Bunium bulbocastanum* L., DQ443722, DQ443724; *Carum carvi* L., AF077878; *Cervaria caucasica* (M. Bieb.) Pimenov, AF008618, AF009097; *Cervaria rivini* Gaertn., AF008608, AF009087; *Conium maculatum* L., AH006070; *Coriandrum sativum* L., U30586, U30587; *Crithmum maritimum* L., AH003474; *Cymbocarpum anethoides* DC., EU169253; *Deverra triradiata* Hochst. ex Boiss., AF073561; *Dicyclophora persica* Boiss., AF073539; *Ducrosia anethifolia* Boiss., EU169266; *Echinophora chrysantha* Freyn & Sint., AF077883; *Exoacantha heterophylla* Labill., AF008617, AF009096; *Falcaria vulgaris* Bernh., AF077888; *Ferulago galbanifera* Koch, AF077889; *Frommia ceratophylloides* H. Wolff, DQ647630; *Grammosciadium daucooides* DC., AF073559; *Helosciadium repens* Koch, AY360241; *Heracleum sphondylium* L., U30544, U30545; *Holandrea carvifolia* (Vill.) Reduron, Charpin & Pimenov, AH012694; *Holandrea pschawica* (Boiss.) Reduron, Charpin & Pimenov, AF008619, AF009098; *Imperatoria ostruthium* L., AF077896; *Kalackia marginata* (Boiss.) R. Alava, EU169293; *Kruberia peregrina* (L.) Hoffm., U78390, U78450; *Lecokia cretica* DC., U78358; *Lefebvreia abyssinica* A. Rich., DQ516376; *Levisticum officinale* (Koch), AF077899; *Malaibaila sekakul* Boiss., AF008627, AF009106; *Naufraga balearica* Constance & Cannon, AF073563; *Oedibasis platycarpa* Koso-Pol., AF008632, AF009111; *Opopanax hispidum* Griseb., AF008624, AF009103; *Oreoselinum nigrum* Delarbre, AH012698; *Pastinaca sativa* L., U30546, U30547; *Peucedanum achaicum* Halácsy, AF164832, AF164857; *Peucedanum bourgaei* Lange, AH012689; *Peucedanum coriaceum* Rchb., AH012692; *Peucedanum gallicum* Latour., AH012688; *Peucedanum japonicum* Thunb., AH012693; *Peucedanum ledebourielloides* K.T. Fu, DQ270200; *Peucedanum litorale* Vorosch. & Gorovoi, AH008032; *Peucedanum morisonii* Bess. ex Schult., AF077903; *Peucedanum officinale* L., AH012690; *Peucedanum zedelmeyerianum* Manden., AF164834, AF164859; *Phellolophium madagascariense* Baker, DQ647627; *Pimpinella betsileensis* Sales & Hedge, DQ647626; *Prangos pabularia* Lindl., AF077906; *Pteroselinum austriacum* Rchb., AH012701; *Pyncocycla aucheriana* Boiss., AF073533; *Pyramidoptera cabulica* Boiss., AF008631; *Sclerosciadium nodiflorum* Coss., K. Spalik & S.R. Downie, unpubl; *Selinum carvifolia* (L.) L., AY179028; *Seseli hipopomarathrum* Jacq., AY179033; *Seseli tortuosum* L., AY179031; *Seselopsis tianschanica* Schischk., AY328955, AY330521; *Sium bracteatum* (Roxb.) Q.C.B. Cronk, AY353982; *Sium repandum* Welw. ex Hiern, DQ005680; *Smyrniopsis aucheri* Boiss., AF077909; *Smyrniolum olusatrum* L., U30594; *Sphaenolobium tianschanicum* (Korov.) Pimenov, AF008622, AF009101; *Stoibrax dichotomum* (L.) Raf., DQ516366; *Symphyloloma graveolens* C.A. Mey., DQ010944; *Tetrataenium rigens* (Wall. ex DC.) Manden., AH003477; *Thysselium palustre* Hoffm., AY179035; *Tommasinia verticillaris* Bertol., AF008609, AF009088; *Tordylium aegyptiacum* (L.) Lam., U78392, U78452; *Trachyspermum aethusifolium* Chiov., AF164845, AF164870; *Xanthogalum purpurascens* Avé-Lall., AF008611, AF009090; *Xanthoselinum alsaticum* (L.) Schur, AH012697; *Zosima orientalis* Hoffm., AF008628.