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, *Afroligusticum* 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: *Afroligusticum* (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 (Burtt, 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; Burtt & Davis, 1949; Kowal & Wojterska, 1973; Reduron, 1984; Pimenov, 1987; Frey, 1989; Hadaček, 1986; Burtt, 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

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

^{*} 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. gal*banum 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. magalismontanum 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 Afroligusticum 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).

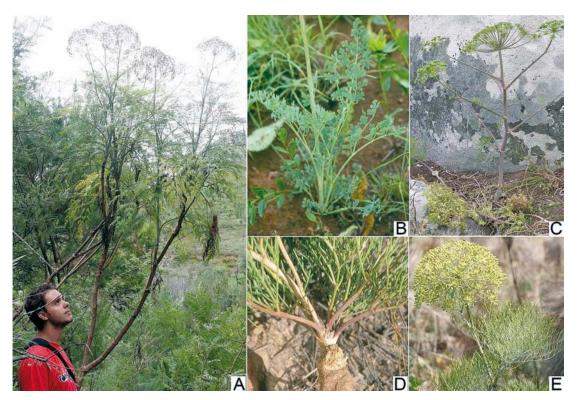


Fig. 1. The African species of *Peucedanum* exhibit an extreme diversity of habit (woody shrubs, shrublets, suffrutices and monocarpic herbs) and to a lesser extent inflorescence structure. A, *P. gummiferum* (woody shrub); B, *P. caffrum* (nonwoody herb); C, *P. sulcatum* (deciduous, non-woody herb 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.,

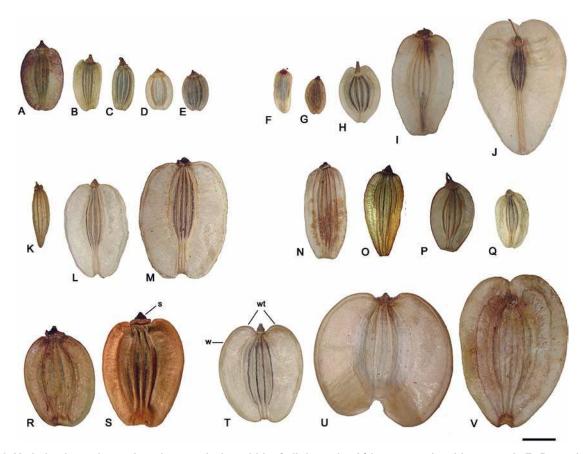


Fig. 2. Variation in mericarp size, shape and wing width of all the major African peucedanoid groups. A–E, Peucedanum galbanum group; F–J, Monocarpic group (including Erythroselinum and Lefebvrea); K–M, Crenato-serrata group (including Afroligusticum); N–Q, P. magalismontanum group; R–S, P. strictum 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. camerunense (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 & Burtt 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

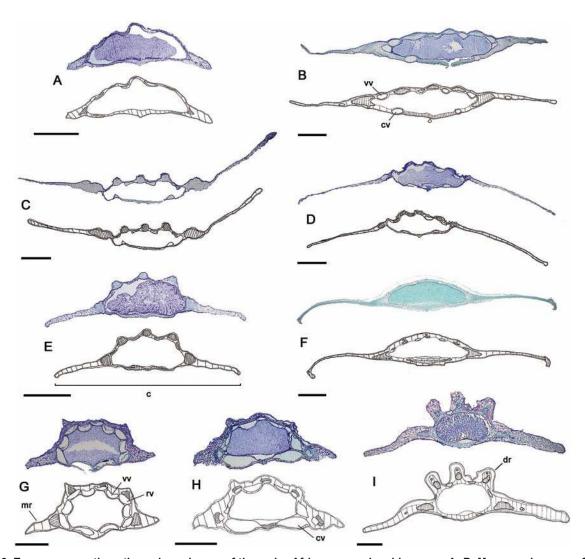
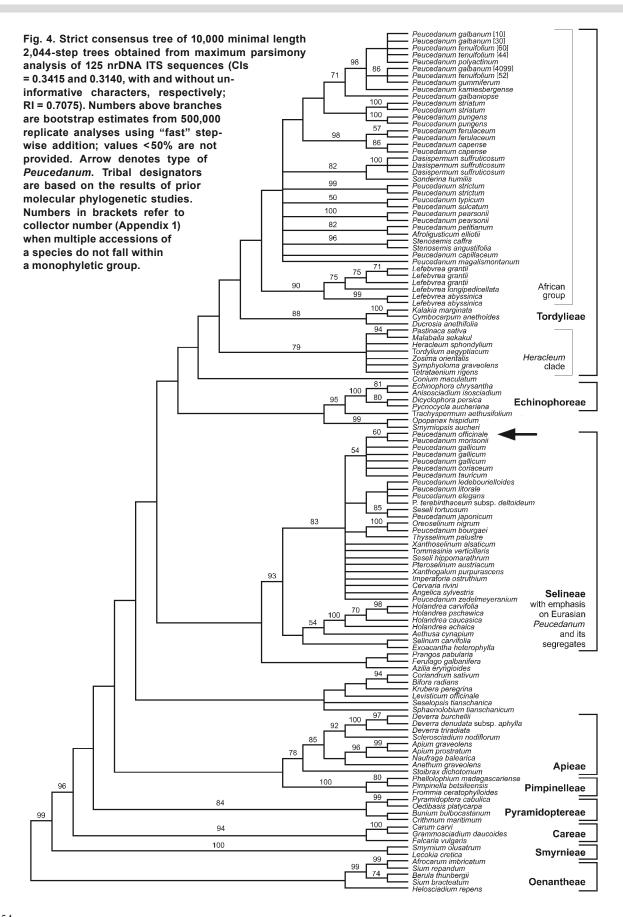


Fig. 3. Transverse sections through mericarps of the major African peucedanoid groups. A–B, Monocarpic group; C–D, Crenato-serrata group; E, P. magalismontanum group; F, Cynorhiza group; G–H, P. galbanum group; I, P. strictum group. A, P. camerunense (Koechlin 7541, P); B, P. upingtoniae (Dinter 7359, 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.



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 petitianum (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 obtained 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

- 2. Perennial or annual herbs with deciduous leaves . . 4
- 3. Suffrutices (with woody subterranean stems); fruits large (more than 10 mm long)....... *Nanobubon*

- 5. Leaves absent (or at least senescent) at fruiting stage, fruit wings broad, Cape species *Cynorhiza*

- 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
- 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 vallecula, 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 (Burtt, 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. Burtt 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 camdebooense* B.L. Burtt 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 lignosibus subterraneis, fructu maiori 10–15 mm longo late-alato differt.

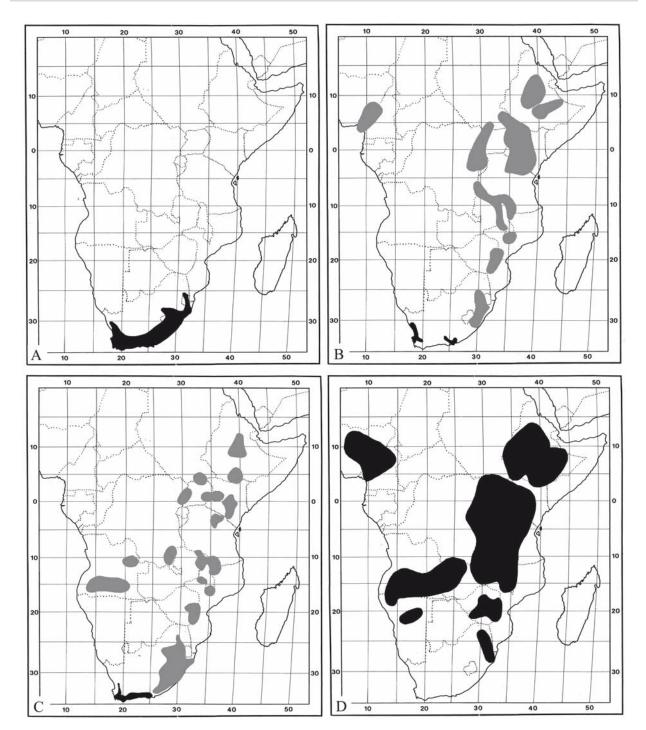


Fig. 5. Distribution ranges of African peucedanoid genera. A, *Notobubon* (black); B, *Cynorhiza* (black), *Afroligusticum* (grey); C, *Nanobubon* (black), *Afrosciadium* (grey); D, *Lefebvrea* (black).

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, Tweny-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!).
- Afroligusticum C. Norman in De Wild., Pl. Bequaert.
 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 Afrosciadium 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 runssoricum, 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 volkensii (Engl.) P.J.D. Winter, comb. nov. ≡ Peucedanum volkensii 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.** *Afrosciadium* P.J.D. Winter, **gen. nov.** Type: *Afrosciadium 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.

Afrosciadium 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, Kondoa dist., hills above Kolo, Burtt 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 magalismontanum (Sond.) P.J.D. Winter, comb. nov. ≡ Peucedanum magalismontanum 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, *Gueinzius* 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).

- Afrosciadium 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).
- Afrosciadium 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 Foumban, Mt Nko Gam, about 2,400 m, Koechlin 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: Nambia, 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, Ufipa 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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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. Burtt, 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, Nuweveldsberge 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, Huíla, 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., AM408865; 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 Wyks.n. (JRAU), South Africa, Khamiesberg, AM408868; Peucedanum petitianum 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 daucoides 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; Kalakia marginata (Boiss.) R. Alava, EU169293; Krubera peregrina (L.) Hoffm., U78390, U78450; Lecokia cretica DC., U78358; Lefebvrea abyssinica A. Rich., DQ516376; Levisticum officinale (Koch), AF077899; Malabaila 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 zedelmeyeranium Manden., AF164834, AF164859; Phellolophium madagascariense Baker, DQ647627; Pimpinella betsileensis Sales & Hedge, DQ647626; Prangos pabularia Lindl., AF077906; Pteroselinum austriacum Rchb., AH012701; Pycnocycla aucheriana Boiss., AF073533; Pyramidoptera cabulica Boiss., AF008631; Sclerosciadium nodiflorum Coss., K. Spalik & S.R. Downie, unpubl; Selinum carvifolia (L.) L., AY179028; Seseli hippomarathrum 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; Smyrnium olusatrum L., U30594; Sphaenolobium tianschanicum (Korov.) Pimenov, AF008622, AF009101; Stoibrax dichotomum (L.) Raf., DQ516366; Symphyoloma graveolens C.A. Mey., DQ010944; Tetrataenium rigens (Wall. ex. DC.) Manden., AH003477; Thysselinum 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.