Generic Delimitations and Relationships of the Cape Genera *Capnophyllum, Dasispermum,* and *Sonderina,* the North African Genera *Krubera* and *Stoibrax*, and a New Monotypic Genus of the Subfamily Apioideae (Apiaceae)

Anthony R. Magee,[1,3] Ben-Erik van Wyk,[1] Patricia M. Tilney,[1] and Stephen R. Downie[2]

[1]Department of Botany and Plant Biotechnology, University of Johannesburg, P.O. Box 524,
Auckland Park 2006 South Africa
[2]Department of Plant Biology, University of Illinois at Urbana-Champaign,
Urbana, Illinois 61801 U.S.A.
[3]Author for correspondence (magee@sanbi.org)

Communicating Editor: Mark P. Simmons

Abstract—Generic circumscriptions and phylogenetic relationships of the Cape genera *Capnophyllum, Dasispermum,* and *Sonderina* are explored through parsimony and Bayesian inference analyses of nrDNA ITS and cpDNA *rps16* intron sequences, morphology, and combined molecular and morphological data. The relationship of these genera with the North African genera *Krubera* and *Stoibrax* is also assessed. Analyses of both molecular data sets place *Capnophyllum, Dasispermum, Sonderina,* and the only southern African species of *Stoibrax* (*S. capense*) within the newly recognized *Lefebvrea* clade of tribe Tordylieae. *Capnophyllum* is strongly supported as monophyletic and is distantly related to *Krubera*. The monotypic genus *Dasispermum* and *Stoibrax capense* are embedded within a paraphyletic *Sonderina*. This complex is distantly related to the North African species of *Stoibrax* in tribe Apieae, in which the type species, *Stoibrax dichotomum*, occurs. Consequently, *Dasispermum* is expanded to include both *Sonderina* and *Stoibrax capense*. New combinations are formalized for *Dasispermum capense*, *D. hispidum*, *D. humile*, and *D. tenue*. An undescribed species from the Tanqua Karoo in South Africa is also closely related to *Capnophyllum* and the *Dasispermum–Sonderina* complex. The genus *Scaraboides* is described herein to accommodate the new species, *S. manningii*. This monotypic genus shares the dorsally compressed fruit and involute marginal wings with *Capnophyllum,* but is easily distinguished by its erect branching habit, green leaves, scabrous umbels, and fruit with indistinct median and lateral ribs, additional solitary vittae in each marginal wing, and parallel, closely spaced commissural vittae. Despite the marked fruit similarities with *Capnophyllum*, analyses of DNA sequence data place *Scaraboides* closer to the *Dasispermum–Sonderina* complex, with which it shares the erect habit, green (nonglaucous) leaves, and scabrous umbels.

Keywords—ITS, *Lefebvrea* clade, morphology, phylogeny, *rps16* intron, *Scaraboides manningii*, South Africa.

A more evolutionary classification of the large and taxonomically complex cosmopolitan family Apiaceae is currently emerging as a result of molecular systematic studies, together with rigorous comparisons of morphological and anatomical data. Several small genera of uncertain circumscription and affinity are evident in recent checklists of African Apiaceae (Burtt 1991; Lebrun and Stork 1992; Van Wyk and Tilney 2004). The majority of these genera are either poorly known or have not been studied in recent years but may be extremely important in the understanding of relationships within the family as a whole. The South African endemic genera *Capnophyllum*, *Dasispermum,* and *Sonderina* were identified as three such taxa. Of these, only two species (*Dasispermum suffruticosum* and *Sonderina humilis*) have heretofore been included in molecular systematic studies (Calviño et al. 2006; Winter et al. 2008). In the phylogenetic analysis by Winter et al. (2008) using nuclear ribosomal DNA internal transcribed spacer (ITS) sequences, both species were shown to be closely related to a group of recently circumscribed African peucedanoid genera, here referred to as the *Lefebvrea* clade (viz., *Afroligusticum* C. Norman, *Afrosciadium* P. J. D.Winter, *Cynorhiza*, *Lefebvrea* A. Rich., *Nanobubon,* and *Notobubon*) within tribe Tordylieae.

The monophyly of *Sonderina* has not yet been assessed, nor has its putative relationship with *Stoibrax* been confirmed. *Sonderina* was described by Wolff (1927) to accommodate four of five South African species previously included in *Ptychotis* Koch by Sonder (1862). Wolff (1927) transferred the fifth species, *Ptychotis didyma* Sond., to *Tragiopsis* Pomel (now *Stoibrax*), which already included four North African species. Adamson (1939) considered this geographically disjunct treatment to be unnatural and transferred the South African species, *Tragiopsis didyma* (Sond.) H. Wolff, to *Sonderina*. Burtt (1989), however, argued that such a Cape and North African disjunction was not uncommon and transferred *Sonderina*

didyma (Sond.) Adamson, along with the North African species, back to the genus *Stoibrax,* as *Stoibrax capense*. Burtt (1989, p. 145), furthermore, expressed his doubts about the generic concept of *Sonderina*, stating that the genus was "probably too close to *Stoibrax* for it to be maintained". Burtt (1991), in his checklist of Southern African Umbelliferae, treated five species within *Sonderina*. One of these, the Namibian endemic *Sonderina streyi* Merxm., has subsequently been transferred to the early diverging African genus *Anginon* Raf. (Allison and Van Wyk 1997). As a result, only four closely related species are now recognised within the taxonomically difficult genus *Sonderina*.

A similar disjunction has also been proposed for *Capnophyllum*, with some authors (e.g. Tutin et al. 1968; Dyer 1975) extending the genus to include the Mediterranean *Capnophyllum peregrinum* (L.) Lange. Meikle (1977), however, treated the Mediterranean species as distinct under the monotypic genus *Krubera* Hoffm., a decision maintained by Burtt (1991). A recent taxonomic revision of *Capnophyllum* (Magee et al. 2009b) recognized four species, two of which were newly described, and excluded *Krubera peregrina* Lowe on the basis of important differences in fruit anatomy.

A thorough taxonomic study of the genera *Capnophyllum*, *Dasispermum,* and *Sonderina* along with extensive field work has revealed one new monotypic genus (herein described as *Scaraboides manningii*) and four new species (Magee et al. 2009b; Magee et al. unpublished). The present study is aimed at resolving generic circumscriptions and relationships of these previously neglected South African endemic genera. As the phylogenetic relationships of African Apiaceae genera are often hard to predict on the basis of morphological characters alone, analyses of both morphology and anatomy in combination with molecular data (specifically, ITS and *rps16* intron sequences) are here presented and explored.

Materials and Methods

Morphological Data—All relevant South African genera and a majority of their species were studied and sampled in situ, including two as yet undescribed species of *Sonderina* (here referred to as *S.* sp. 1 and *S.* sp. 2). This material was supplemented by a study of specimens from the following herbaria: BM, BOL, JRAU, K, LE, MO, NBG, PRE, S, SAM, THUNB-UPS. The distribution data for *Scaraboides manningii* was recorded using Quarter Degree Grid Cells (outlined in Leistner and Morris 1976). In this system the basic unit is the one-degree square of latitude and longitude, which is designated by a degree reference number (i.e. degrees of latitude and longitude of the north-west corner) and the district name of that square. Line drawings were made by the first author with the aid of a camera lucida attachment on a Zeiss compound microscope or a Wild M3Z stereomicroscope.

Preserved (FAA; formaldehyde: acetic acid: alcohol: water) and herbarium materials were used to study fruit anatomy. Herbarium material was first rehydrated and then placed in FAA for a minimum of 24 h. This material was subsequently treated according to a modification of the method of Feder and O'Brien (1968) for embedding in glycol methacrylate (GMA). This modification involves a final infiltration in GMA for five days. Transverse sections, about 3 μm thick, were cut using a Porter-Blüm ultramicrotome. The sections were examined for the presence of crystals using a light microscope, after which they were stained according to the periodic acid Schiff/toluidine blue (PAS/TB) method of Feder and O'Brien (1968). To study the three-dimensional structure of the vittae, mature fruit were softened by soaking in boiling water for 24 h. The exocarp was then peeled off while keeping the fruit submerged in water to prevent desiccation. The terminology used to describe the fruit anatomical features follows Kljuykov et al. (2004).

A matrix of 23 morphological and anatomical characters was prepared for 31 species of the *Lefebvrea* clade based on examination of herbarium specimens and literature (Appendices 1 and 2; Magee et al. 2008a; Magee et al. 2008b; Winter et al. 2008; Magee et al. 2009a; Magee et al. 2009b). These data were also combined with ITS sequences from the same taxa for simultaneous phylogenetic analysis (Kluge 1989; Nixon and Carpenter 1996).

Molecular Data—DNA was extracted using the 2 × CTAB method of Doyle and Doyle (1987) from materials collected in the field and from herbarium specimens and used to assess the generic delimitations and phylogenetic relationships of the Cape endemic genera *Capnophyllum* (12 new accessions), *Dasispermum* (two new accessions), *Sonderina* (13 new accessions), the undescribed monotypic genus *Scaraboides* (two new accessions), and the largely North African genus *Stoibrax* (five new accessions). Additional accessions of the *rps16* intron region for the closely related African peucedanoid genera *Cynorhiza* (two new accessions), *Nanobubon* (two new accessions), and *Notobubon* (five new accessions) were also included. The 45 new accessions for which ITS (18 accessions) and *rps16* intron (27 accessions) sequences were obtained are presented in Appendix 3. Previously published *rps16* intron accessions are listed in Appendix 4, and previously published ITS accessions are available in Winter et al. (2008).

For amplification of the ITS and *rps16* intron regions, we used the primers described by Sun et al. (1994) and Oxelman et al. (1997), respectively. Amplified PCR products were purified using a QIAquick PCR purification kit (Qiagen Inc., Valencia, California) according to the manufacturer's instructions and directly sequenced on a 3130 *xl* Genetic Analyzer (Applied Biosystems Inc., Foster City, California) using BigDye Terminator version 3.1 chemistry (Applied Biosystems Inc.). For each molecular data set, complementary strands were assembled and edited using Sequencher version 3.1.2 (Gene Codes Corporation, Ann Arbor, Michigan) and aligned manually in PAUP* version 4.0b10 (Swofford 2002), with gaps positioned so as to minimize nucleotide mismatches.

Phylogenetic Analyses—To assess the phylogenetic positions of the aforementioned genera, the newly obtained ITS sequences were added to the 125 taxon ITS matrix of Winter et al. (2008). This matrix represents all tribes and major clades of the apioid superclade plus outgroups from tribes Smyrnieae and Oenantheae (Downie et al. 2001), with those species of the latter used to root the trees. The newly obtained *rps16* intron sequences were analysed with 27 additional *rps16* intron sequences from GenBank (Appendix 4), the latter also representing several relevant major clades of the apioid superclade. The *rps16* intron trees were rooted with *Sium latifolium* and *Berula erecta* of tribe Oenantheae. To further explore relationships within the *Capnophyllum* group, combined data sets (ITS/*rps16* intron, ITS/morphology, and ITS/*rps16* intron/morphology) for 31 taxa of the *Lefebvrea* clade were analysed, with *Lefebvrea abyssinica* A.Rich. used as the outgroup.

Phylogenetic analyses of all data sets were conducted initially using the parsimony (MP) algorithm of PAUP* with gaps treated as missing data. Character transformations were treated as unordered and equally weighted (Fitch parsimony; Fitch 1971). Tree searches were performed using a heuristic search with 500 random sequence additions, tree bisection-reconnection (TBR) branch swapping, and the MULPARS option in effect, but saving no more than 5 of the shortest trees from each search. These equally parsimonious trees were then used as starting trees for TBR branch swapping (MULPARS and STEEPEST DESCENT in effect) with the maximum number of trees saved set at 12,000; these trees were permitted to swap to completion (Downie et al. 1998). Bootstrap percentage values (BP; Felsenstein 1985) for the separate ITS and *rps16* intron data sets were determined from 500,000 replicate analyses using fast stepwise addition of taxa, while BP values for the morphological and combined data sets of the *Lefebvrea* clade were determined from 1,000 bootstrap replicates, holding 10 trees per replicate and with TBR and MULPARS selected. Only values greater than or equal to 50% are reported, and the following scale was applied for support percentages: ≤ 74%, weak; 75–84%, moderate; and 85–100%, strong. All data sets (except the separate morphological data set) were subsequently analysed by Bayesian inference (BI; Yang and Rannala 1997) using MRBAYES version 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). An appropriate model of evolution was selected for each data partition using the program MODELTEST version 3.06 (corrected Akaike information criterion; Akaike 1974; Posada and Crandall 1998). For the combined analysis in which morphological data were included, the datatype = standard option of MRBAYES for the non-nucleotide data partition was used. For the separate ITS and *rps16* intron data sets, the analysis was performed for three million generations of Monte Carlo Markov Chains (MCMC) and a sampling frequency of 100, while for the morphological and combined data sets of the *Lefebvrea* clade only two million generations of MCMC and a sampling frequency of 10 was used. The resulting trees were plotted against their likelihoods in order to determine where the likelihoods converge on a stable plateau. All the trees before this convergence were discarded as the 'burn-in' phase. A majority rule consensus tree was produced from the remaining trees in order to show the posterior probabilities (PP) of all observed bipartitions. The following scale was used to evaluate the PPs: 0.5–0.84, weak; 0.85–0.94, moderate; 0.95–1.0, strong.

To assess congruency of relationships within the *Lefebvrea* clade, as inferred by separate MP analyses of the ITS, *rps16* intron and morphological data sets, the bootstrap consensus trees from each analysis were compared. These trees were considered incongruent only if they displayed 'hard' (i.e. incongruencies with strong bootstrap values) rather than 'soft' (i.e. incongruencies with weak bootstrap values) incongruence (Seelanan et al. 1997; Wiens 1998). In addition, a partition homogeneity test (incongruence length difference test, ILD; Farris et al. 1995) was performed in PAUP*. This test was implemented with 1,000 replicate analyses, using the heuristic search option with simple addition of taxa, and with TBR and MULTREES options selected.

To evaluate the significance of differing topologies, we used the Shimodaira-Hasegawa test (SH; Shimodaira and Hasegawa 1999), as implemented in PAUP* (applying the RELL resampling method with 1,000 bootstrap replicates). All DNA sequences have been submitted to GenBank (Appendix 3) and all PAUP* matrices deposited in TreeBASE (study number S2197).

Morphological characters were reconstructed on the MP trees from the combined ITS/*rps16* intron/morphology data set using parsimony with Mesquite version 2.5 (Maddison and Maddison 2008).

Results

ITS Data Set—The ITS matrix consisted of 633 unambiguously aligned nucleotide positions with 382 variable and 317 parsimony informative characters. Parsimony analyses resulted in the preset maximum tree limit of 12,000 trees, each of 2,113 steps (ensemble consistency indices [CI; Kluge and Farris 1969] of 0.33 and 0.31, with and without uninformative characters, respectively; ensemble retention index [RI; Farris 1989] of 0.72). MODELTEST selected the GTR + I + G model of evolution for use in the BI analysis. The MP strict consensus tree yielded a similar topology as the BI consensus tree (with the differences between these trees summarized in Fig. 1). In both analyses, the same groupings as reported previously by Winter et al. (2008) were retrieved. The *Lefebvrea* clade was weakly supported in both the BI and MP trees (PP = 0.75, BP

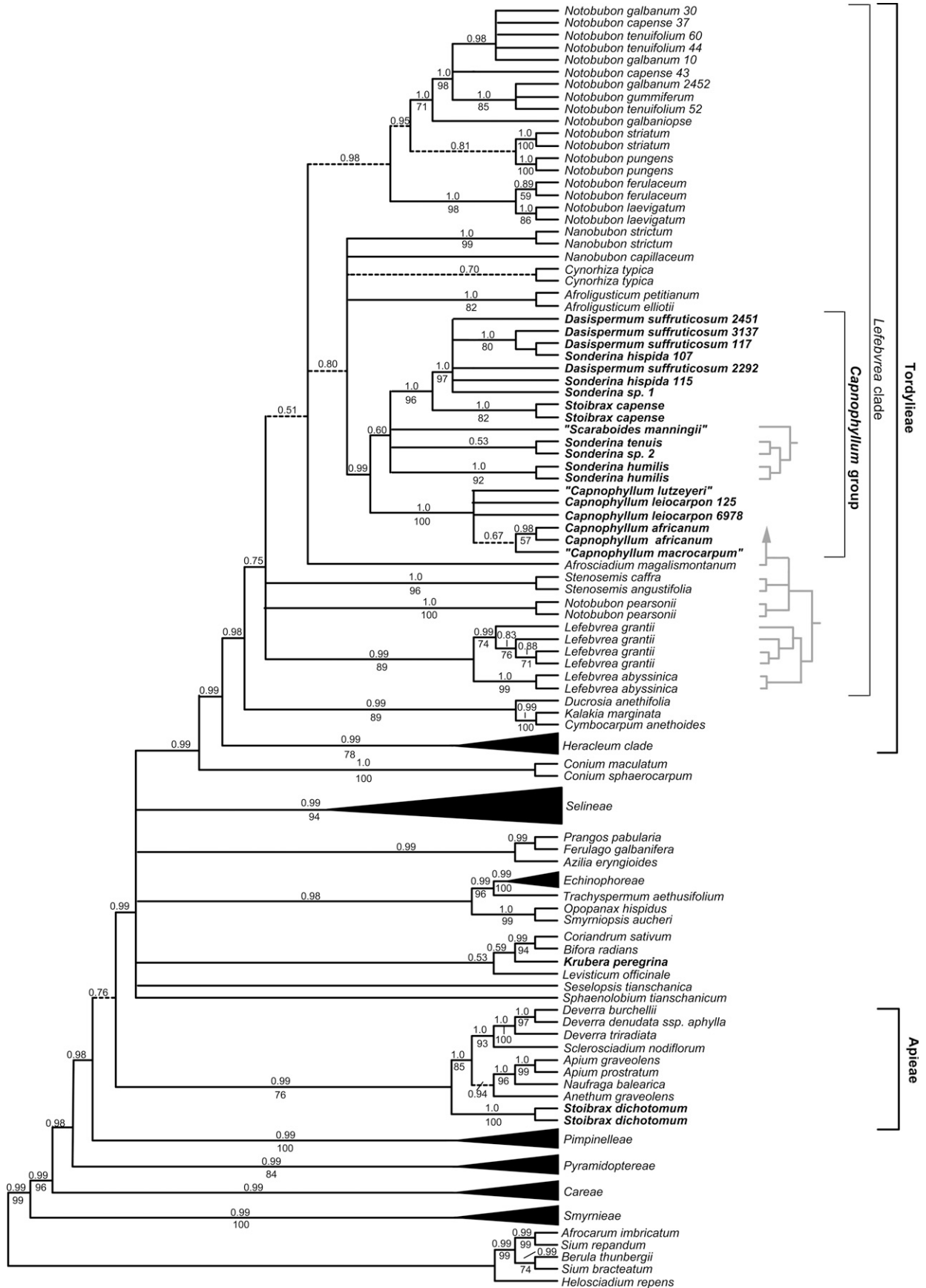FIG. 1.   Bayesian inference (BI) tree of ITS sequence data. Posterior probability (PP) values are presented above the branches. Bootstrap percentage (BP) values are presented below the branches. BP and PP values below 50% and 0.50, respectively, are not indicated. Branches supported only by BI are indicated by dashed lines, those branches that differ in the parsimony strict consensus tree are indicated alongside as gray lines.

< 50). *Lefebvrea* formed the earliest diverging lineage in the MP strict consensus tree, while in the BI tree its position was unresolved.

With the exception of *Notobubon pearsonii*, the woody Cape genus *Notobubon* was strongly supported as monophyletic in the BI tree (PP = 0.98), while in the MP strict consensus tree the latter clade was not resolved. The Cape genera *Capnophyllum*, *Dasispermum,* and *Sonderina*, together with the only South African species of *Stoibrax* (*S. capense*) and the monotypic genus *Scaraboides*, all formed a group (hereafter referred to as the *Capnophyllum* group) within the *Lefebvrea* clade, which was strongly supported in the BI tree (PP = 0.99); however, in the MP strict consensus tree, this clade was supported with a BP value of less than 50%. *Scaraboides manningii* was placed within a weakly supported polytomy with members of the *Dasispermum–Sonderina* complex (PP = 0.60) in the BI tree, while in the MP strict consensus tree it was weakly supported to be sister to the *Sonderina humilis–S. tenuis* group (BP < 50). *Dasispermum suffruticosum* and *Stoibrax capense*, together with *Sonderina hispida* and *Sonderina* sp. 1, comprise a strongly supported clade (PP = 1.0, BP = 96) that arise from within a paraphyletic *Sonderina*. Constraining the *Dasispermum–Sonderina* complex to monophyly so that *Scaraboides manningii* was its sister group resulted in trees that were not significantly different (*p* = 0.261).

The North African species *Krubera peregrina* and *Stoibrax dichotomum*, sometimes considered to be closely related to *Capnophyllum* and *Sonderina* respectively, were inferred to be distantly related to each other and to the *Capnophyllum* group. Both accessions of the type species of *Stoibrax* (*S. dichotomum*) were moderately to strongly placed within tribe Apieae (PP = 0.99, BP = 76), while *Krubera peregrina* was resolved in a clade comprising *Coriandrum sativum* L., *Bifora radians* M.Bieb., and *Levisticum officinale* Koch.

rps16 Intron Data Set—The *rps16* intron matrix consisted of 936 unambiguously aligned nucleotide positions with 191 variable and 92 parsimony informative characters. MP analyses yielded the preset maximum tree limit of 12,000 trees, each of 282 steps (CI = 0.77 and 0.63, with and without uninformative characters, respectively; RI = 0.84). MODELTEST selected the K81uf + G model of evolution for use in the BI analysis. Overall the MP strict consensus tree yielded a similar topology to that of the majority rule consensus tree obtained from the BI analysis (differences between the results of these analyses are presented in Fig. 2). Although the resolution within these trees was poor, a lineage comprising *Capnophyllum*, *Dasispermum*, *Scaraboides*, *Sonderina,* and *Stoibrax capense* (*Capnophyllum* group) was retrieved in both analyses (PP = 0.89, BP < 50). This same *Capnophyllum* group was resolved in the ITS trees with greater taxon sampling (Fig. 1). Similarly, *Dasispermum suffruticosum* and *Stoibrax capense* were again strongly embedded within a subclade of *Sonderina* (PP 1.0, BP < 50) comprising the type species *S. hispida*. *Scaraboides manningii* is placed within a strongly-supported polytomy (PP = 1.0, BP = 87) with members of the *Dasispermum–Sonderina* complex in the BI tree, while in the MP strict consensus tree *Sonderina humilis* and *Sonderina* sp. 2 formed the earliest branching lineages, followed by a polytomy (BP < 50) comprising *Sonderina tenuis, Scaraboides manningii*, and the *Stoibrax capense–Dasispermum suffruticosum* clade. Constraining the *Dasispermum–Sonderina* complex to monophyly so that *S. manningii* was its sister group resulted in trees that were not significantly different (*p* = 0.191).

Notobubon formed a weakly supported clade in the MP strict consensus tree, although without *N. pearsonii*, which in both the BI and MP trees was placed as sister (though supported strongly only in the BI tree with PP = 0.99) to an unresolved *Cynorhiza typica*. *Stoibrax dichotomum* was once again shown to be part of tribe Apieae in both BI (PP = 0.94) and MP trees (BP < 50) and not closely related to its South African congener, *S. capense*, or to its putative relative *Sonderina*. The placement of *Stenosemis* outside of the *Lefebvrea* clade was not consistent with that found in the ITS studies and may be due to the low resolution and limited sampling within the tribe Tordylieae.

Morphological Data Set—MP analysis of 23 morphological and anatomical characters from 31 species of the *Lefebvrea* clade resulted in 10 minimal length trees each of 50 steps (CI = 0.60, RI = 0.88). The relationships among members of the *Lefebvrea* clade were generally better resolved than those inferred from the molecular analyses, although with generally lower BP values (Fig. 3A). *Notobubon pearsonii* was included within a weakly supported clade of *Notobubon* (BP = 54), *Nanobubon* was moderately supported as monophyletic (BP = 80), and *Stenosemis* was strongly supported (BP = 93) as monophyletic. The *Capnophyllum* group comprising the predominantly annual genera *Capnophyllum*, *Dasispermum*, *Scaraboides*, *Sonderina*, and *Stoibrax capense* formed a separate lineage as in the molecular analyses. *Capnophyllum* was strongly supported as monophyletic (BP = 89), with *Scaraboides manningii* as its sister group. *Dasispermum* and *Stoibrax* were again recovered within a paraphyletic *Sonderina* (BP = 72).

Combined ITS/rps16 Intron Data Set—The combined ITS and *rps16* intron matrix for 31 taxa within the *Lefebvrea* clade consisted of 1,593 characters, of which 228 were variable and 112 parsimony informative. Missing data represented 13% of the entire data matrix, as *rps16* intron sequences were unavailable for eight taxa. Visual inspection of the two separate bootstrap consensus trees and results of the ILD test suggested that the two matrices were not significantly incongruent (*p* = 1.0). Parsimony analyses of combined molecular data yielded 97 trees, each of 359 steps (CI = 0.74 and 0.59, with and without uninformative characters, respectively; RI = 0.77). The GTR + I + G and the K81uf + G models were retained for the ITS and *rps16* intron data partitions, respectively. Trees obtained from both the MP and BI analyses yielded the same overall topologies (Fig. 3B). As in the analyses of partitioned molecular data, a lineage comprising the *Capnophyllum* group (incl. *Capnophyllum*, *Dasispermum*, *Scaraboides*, *Sonderina*, and *Stoibrax capense*) was recovered (PP = 1.0, BP = 62). *Capnophyllum* was again strongly supported as monophyletic (PP = 1.0, BP = 100). *Dasispermum suffruticosum* and *Stoibrax capense* were strongly embedded within a subclade of a paraphyletic *Sonderina*, together with *Sonderina hispida* and *Sonderina* sp. 1 (PP = 1.0, BP = 100). *Scaraboides manningii* was again strongly supported as part of a clade comprising *Dasispermum, Stoibrax capense,* and all species of *Sonderina* (PP = 1.0, BP = 91), although its exact position within this clade remained equivocal. In the BI trees *Scaraboides manningii* was weakly supported as a sister group to the subclade comprising *Stoibrax–Dasispermum* (PP = 0.74), while in the MP strict consensus tree it formed one branch of a trichotomy. As in the separate ITS and *rps16* analyses, constraining the *Dasispermum–Sonderina* complex to monophyly so that *S. manningii* was its sister group resulted in trees that were not significantly different (*p* = 0.142).
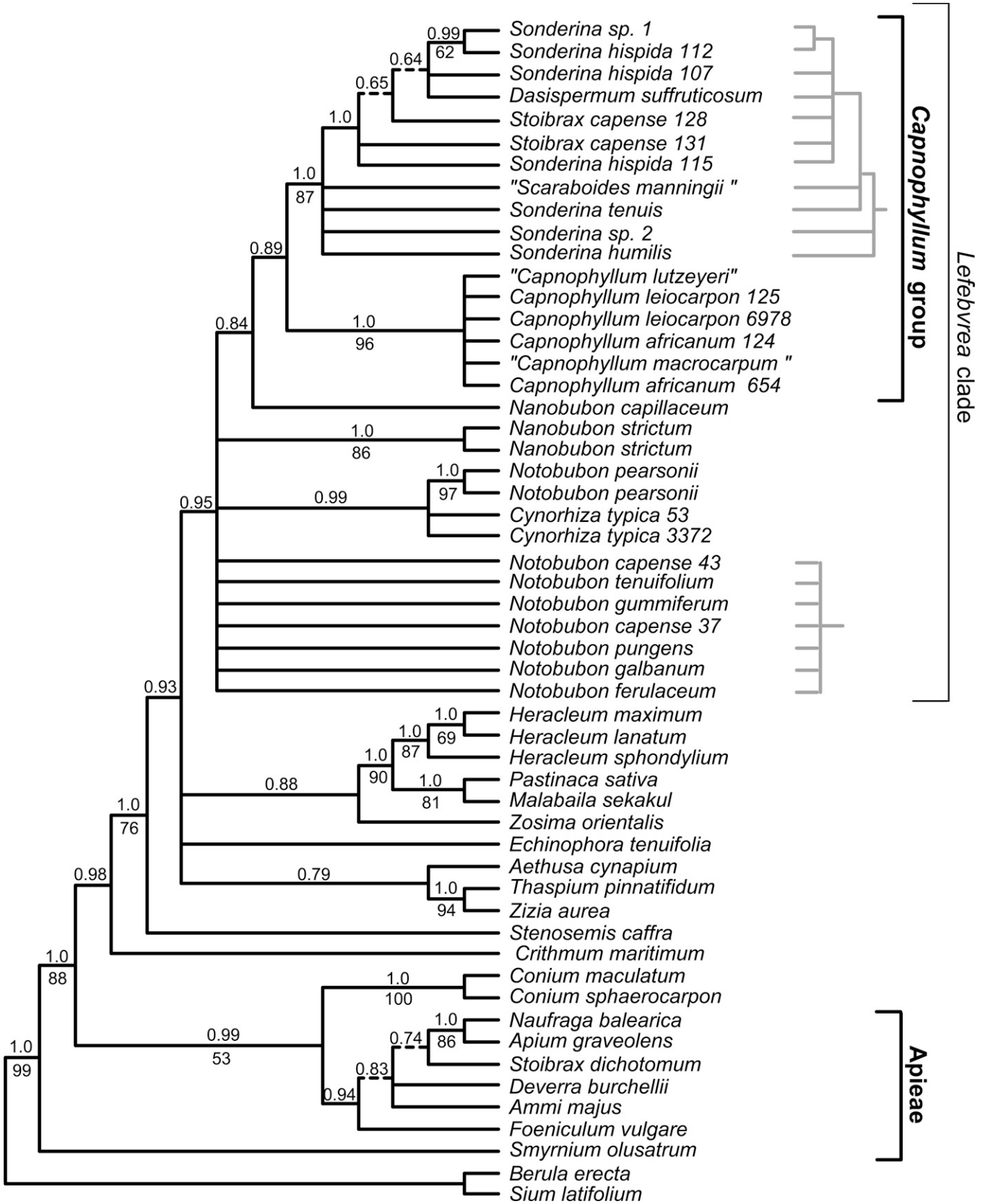
Fig. 2.   Bayesian inference (BI) tree of *rps16* intron sequence data. Posterior probability (PP) values are presented above the branches. Bootstrap percentage (BP) values are presented below the branches. BP and PP values below 50% and 0.50, respectively, are not indicated. Branches supported only by BI are indicated by dashed lines, those branches that differ in the parsimony strict consensus tree are indicated alongside as gray lines.
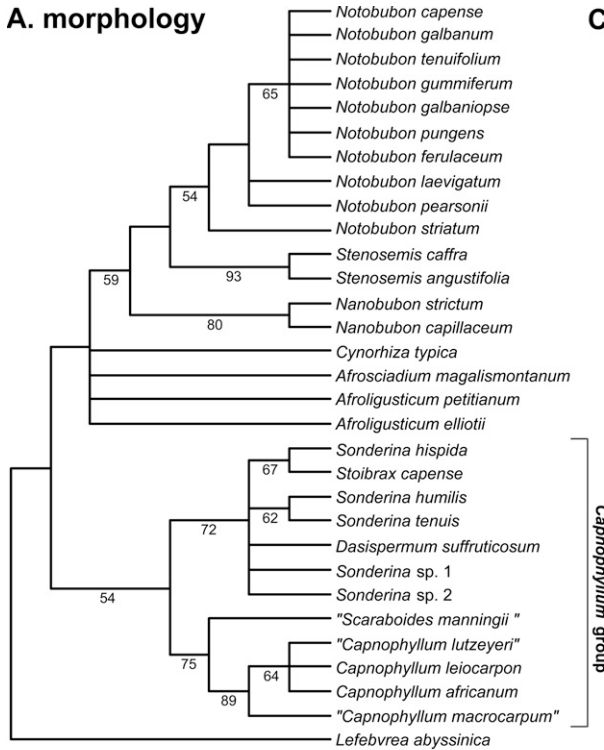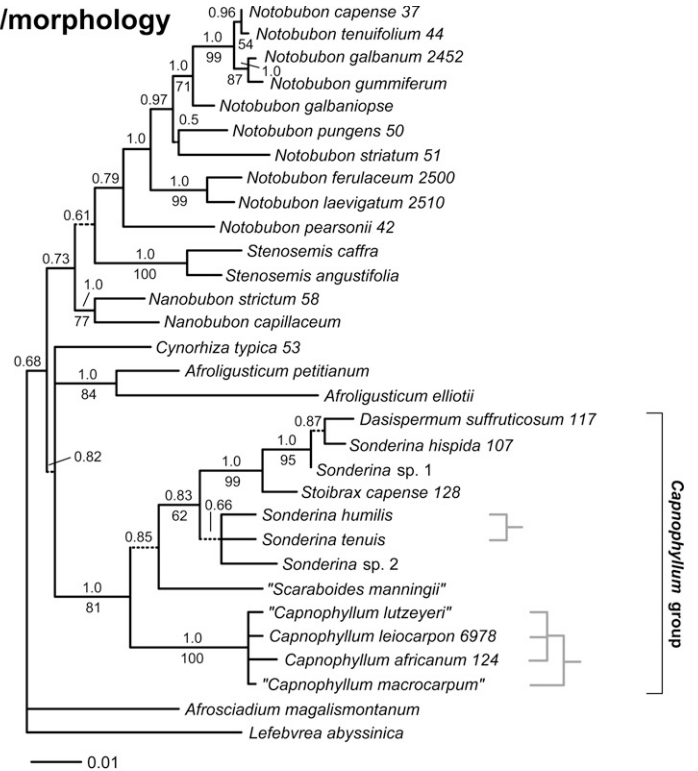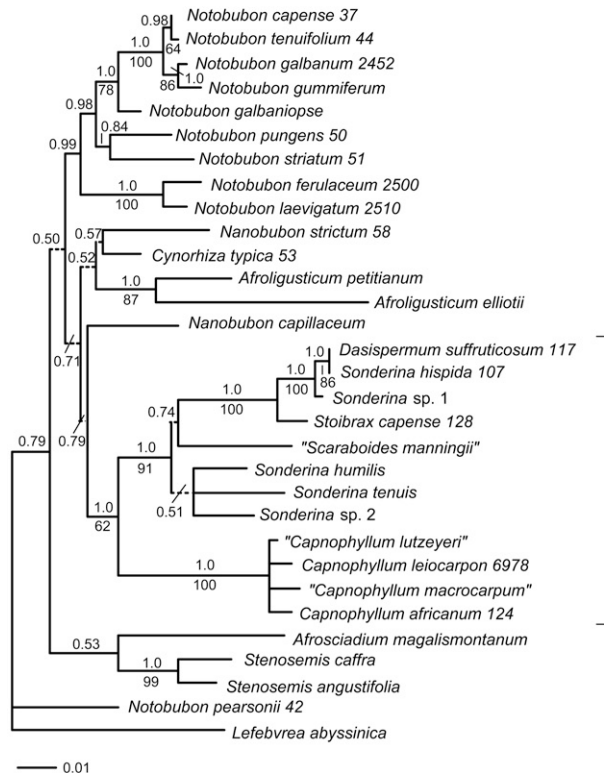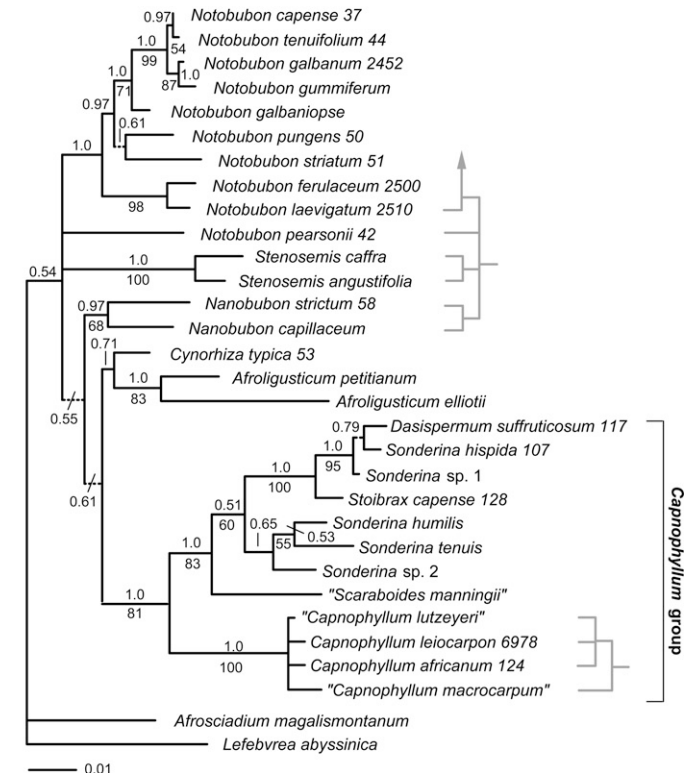
Fig. 3. A. Strict consensus tree of 18 equally most parsimonious trees based on the parsimony analysis of morphological data. B. Bayesian inference (BI) phylogram of the combined ITS/*rps16* intron data sets. C. Bayesian inference phylogram of the combined ITS/morphological data sets. D. Bayesian inference phylogram of the combined ITS/*rps16* intron/morphological data sets. Posterior probability values are presented above the branches. Bootstrap values from the parsimony analysis are presented below the branches. Bootsrap and PP values below 50% and 0.50, respectively, are not indicated. Branches supported only in the BI tree are indicated by dashed lines, those branches that differ in the parsimony strict consensus tree are indicated alongside as gray lines.

Combined ITS/Morphological Data Set—The combined ITS and morphological matrix for 31 taxa within the *Lefebvrea* clade consisted of 712 characters, of which 206 were variable and 115 parsimony informative. Visual inspection of the two separate MP bootstrap consensus trees revealed no hard incongruence, however, the ILD test suggested that the two were significantly incongruent ($p = 0.001$). Following the suggestions of Seelenan et al. (1997) and Wiens (1998), the two matrices were still combined for simultaneous analyses. Parsimony analysis yielded 200 trees, each of 364 steps (CI = 0.68 and 0.55, with and without uninformative characters, respectively; RI = 0.76). The GTR + I + G model was retained

for the ITS data. Overall, the MP strict consensus tree yielded a similar topology as those retrieved from the BI analysis (differences between the results of these analyses are presented in Fig. 3C). As in the morphological analysis, subclades comprising the Cape genera *Notobubon* (PP = 0.79, BP < 50), *Nanobubon* (PP = 1.0, BP = 77), and *Stenosemis* (PP = 1.0, BP = 100) were supported as monophyletic (PP = 0.73, BP < 50). The *Capnophyllum* group was again recovered (PP = 1.0, BP = 81), with *Capnophyllum* strongly supported as monophyletic (PP = 1.0, BP = 100). *Dasispermum* and *Stoibrax capense* again arose from within a paraphyletic *Sonderina*. This broadened *Dasispermum–Sonderina* complex was weakly to moderately
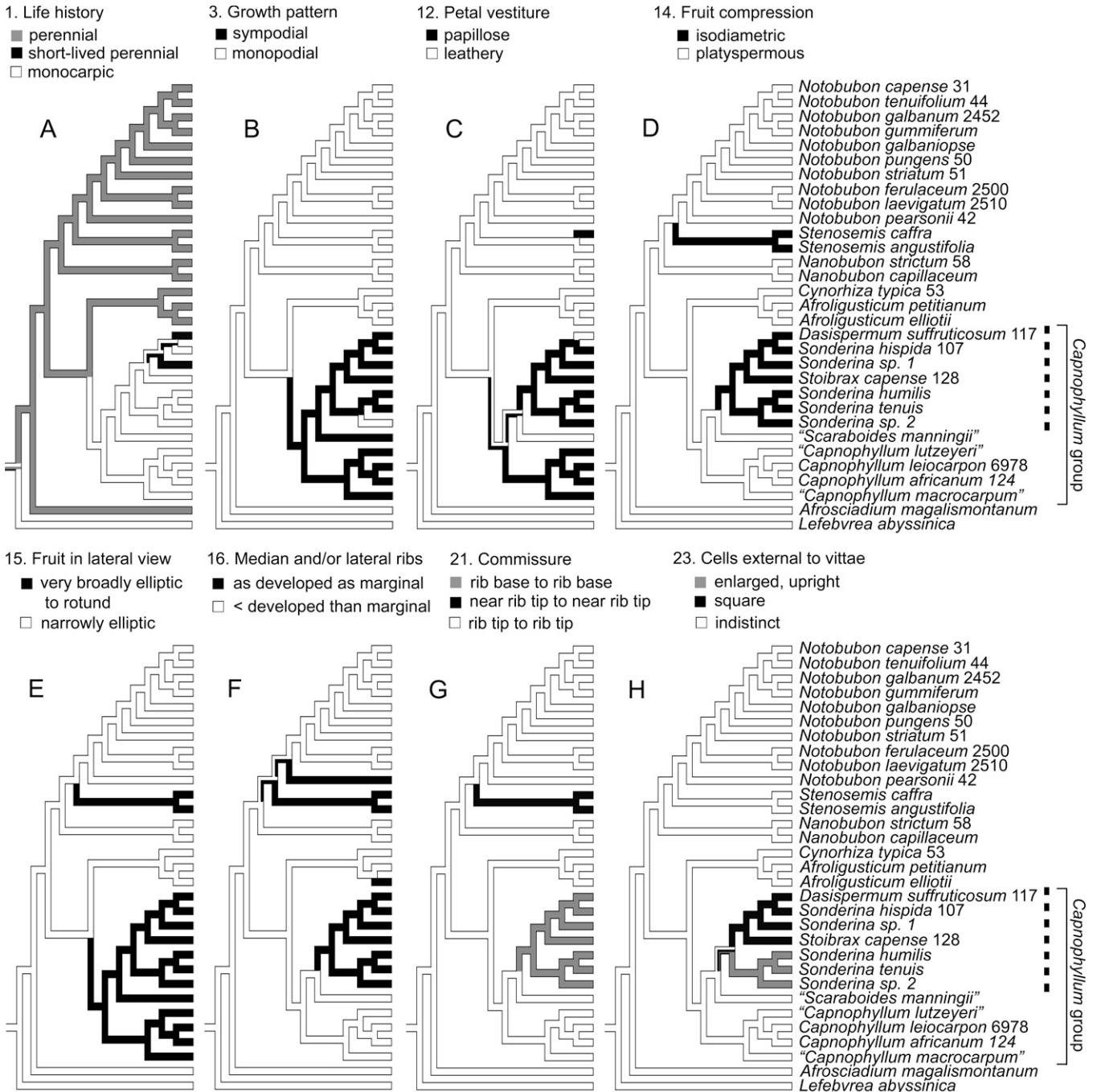
FIG. 4. Reconstruction of eight morphological characters supporting either the *Capnophyllum* group or the *Dasispermum–Sonderina* complex (indicated with a dashed line), when optimized over the ten minimal length trees inferred from MP analysis of combined ITS/*rps16* intron/morphology data.

supported (PP = 0.83, BP = 62), with *Scaraboides* as its sister group (PP = 0.85), although in the MP strict consensus tree a trichotomy comprising *Capnophyllum*, *Scaraboides*, and the *Dasispermum–Sonderina* complex was retrieved.

***Combined ITS/rps16 Intron/Morphology Data Set*—**The combined ITS, *rps16* intron and morphological matrix for 31 taxa within the *Lefebvrea* clade consisted of 1,616 characters, of which 251 were variable and 135 parsimony informative. Missing data represented 8.6% of the entire data matrix, as *rps16* intron sequences were unavailable for eight taxa. Visual inspection of the three separate MP bootstrap trees revealed no hard incongruencies. Parsimony analyses yielded 10 trees, each of 425 steps (CI = 0.69 and 0.56, with and without uninformative characters, respectively; RI = 0.77). Trees obtained from both the MP and BI analyses yielded similar overall topologies (differences between the results of these analyses are presented in Fig. 3D). The topology resolved from the combined ITS/*rps16* intron/morphology analyses was generally similar to those obtained from analyses of the combined ITS/morphology dataset. The genera *Capnophyllum* (PP = 1.0, BP = 100), *Nanobubon* (PP = 0.97, BP = 68), and *Stenosemis* (PP = 1.0, BP = 100) were each recovered as monophyletic. The *Capnophyllum* group (i.e. *Capnophyllum*, *Dasispermum*, *Scaraboides*, *Sonderina*, and *Stoibrax capense*) was again retrieved (PP = 1.0, BP = 81).

The clade comprising *Scaraboides* and the *Dasispermum–Sonderina* group was strongly supported (PP = 1.0, BP = 83). As in all prior analyses, *Sonderina* is rendered paraphyletic by the inclusion of *Dasispermum* and *Stoibrax capense*.

***Morphological Character Evolution*—**Parsimony-based reconstructions of eight morphological characters supporting either the *Capnophyllum* group or the *Dasispermum–Sonderina* complex are each summarized onto one of the ten minimal length trees inferred from MP analysis of combined ITS/*rps16* intron/morphology data (Fig. 4). Monocarpic life history (character 1, Fig. 4A), sympodial growth pattern (character 3, Fig. 4B), and the broadly elliptic to rotund fruit in lateral view (character 15, Fig. 4E) were reconstructed as synapomorphies for the *Capnophyllum* group. Petal vestiture (character 12, Fig. 4C) was ambiguously reconstructed at the base of the *Capnophyllum* group; this character can either be interpreted as a synapomorphy for the *Capnophyllum* group with reversals in *Scaraboides manningii* and *Dasispermum suffruticosum*, or as a convergent character supporting both *Capnophyllum* as well as the *Dasispermum–Sonderina* complex, with a reversal in *Dasispermum suffruticosum*. Reconstruction of the short-lived perennial habit (character 1) differed slightly among the 10 minimal length trees depending on the relative position of *Sonderina* sp. 1. In eight of the trees, this character was recon-
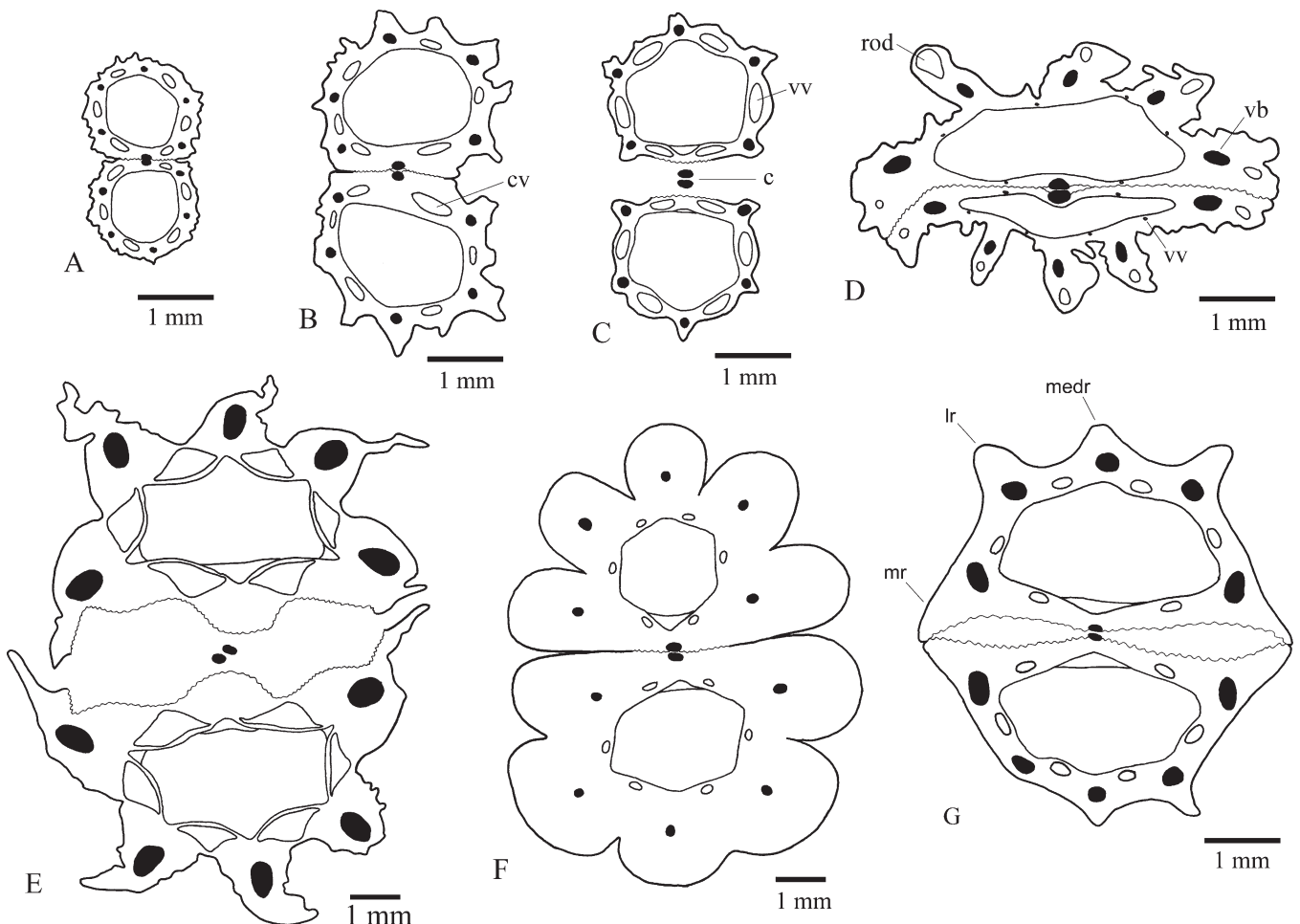
FIG. 5. Transverse sections through the fruit of A. *Stoibrax hanotei*, *Wall s.n.* (S); B. *Stoibrax capense*, *Boatwright et al. 212* (JRAU); C. *Sonderina hispida*, *Van Wyk 3539* (JRAU); D. *Krubera peregrina*, *Lippert 22959* (PRE); E. *Stenosemis caffra*, *MacOwen s.n.* sub South African Exchange Club 904 (GRA); F. *Dasispermum suffruticosum*, *Winter 78* (JRAU); and G. *Capnophyllum africanum*, *Winter 110* (JRAU). c - carpophore; cv - commissural vitta; lr - lateral rib; mr - marginal rib; medr - median rib; rod - rib oil duct; vb - vascular bundle; vv - vallecular vitta.

structed as an autapomorphy for both *Sonderina* sp. 1 and *Dasispermum suffruticosum* (as shown in Fig. 4A), while in the remaining two trees where *Sonderina* sp. 1 and *Dasispermum suffruticosum* were sister, it was reconstructed as a synapomorphy. The *Dasispermum–Sonderina* complex was supported by an isodiametric fruit compression (character 14, Fig. 4D), median and/or lateral ribs as developed as the marginal ribs (character 16, Fig. 4F), commissure extending from at most rib base to rib base (character 21, Fig. 4G), and square or enlarged, upright cells external to the vittae (character 23, Fig. 4H). Flimsy leaf texture (character 6) and concolorously glaucous leaves (character 7) were both reconstructed as synapomorphies for *Capnophyllum* (not shown).

DISCUSSION

Lefebvrea clade—Winter et al. (2008) reported that the African species previously attributed to *Peucedanum* and its platyspermous allies comprise a clade sister to a small alliance of southwest Asian species (*Ducrosia anethifolia* Boiss., *Kalakia marginata* (Boiss.) R. Alava, *Cymbocarpum anethoides* DC.) within tribe Tordylieae. Within their African group, here referred to as the *Lefebvrea* clade, the nonplatyspermous, South African endemic species *Dasispermum suffruticosum*, *Sonderina humilis*, *Stenosemis caffra*, and *Stenosemis angustifolia* E. Mey. ex. Harv. & Sond. were also included. Our broadened analyses show that the *Lefebvrea* clade also includes all species of *Sonderina* and *Capnophyllum*, the monotypic genus *Scaraboides*, and the Cape species *Stoibrax capense*. Winter et al. (2008) separated *Dasispermum*, *Sonderina*, and *Stenosemis* E. Mey. ex. Harv. & Sond. from the peucedanoid genera by their narrower commissure, not extending to the tips of each marginal rib/wing. *Capnophyllum* and *Scaraboides* also have dorsally compressed fruit with prominent marginal wings and a broad commissure. These three characters are all plesiomorphies based on the distribution of characters states (Fig. 4D, F, G). The fruit of *Stenosemis* differ from those of *Dasispermum*, *Sonderina*, and *Stoibrax* in that the commissure, though not as broad as found in *Capnophyllum*, *Scaraboides*, and the peucedanoid genera, is much broader and extends to beyond the base of the marginal wings, often somewhere between the tip and the centre of the wing/rib. This feature was reconstructed as a synapomorphy for the genus *Stenosemis* (Fig. 4G).

Capnophyllum and Krubera—Although the genus *Capnophyllum* has sometimes been extended to include the Mediterranean species *Krubera peregrina*, Magee et al. (2009b) maintained the two genera as distinct, in agreement with Meikle (1977) and Burtt (1991). The fruit of both genera (Fig. 5D, G) are superficially similar; they have dorsally compressed mericarps, a broad commissure, marginal ribs extended into wings, and prominent ridges on the dorsal surface. However, on close examination of the fruit, Magee et al. (2009b) found diagnostic differences between the two genera in terms of the size and prominence of both vittae and rib oil ducts and the shape of the marginal wings. *Krubera* and *Capnophyllum* were widely separated in the ITS-derived trees (Fig. 1), with *Krubera* placed in a clade sister to *Coriandrum sativum* and *Bifora radians*, and *Capnophyllum* placed in the *Lefebvrea* clade of tribe Tordylieae. In all trees presented herein, *Capnophyllum* is strongly supported as monophyletic and occupies a position within a broader lineage comprising other largely annual, sympatric, Cape endemic genera (viz., *Dasispermum*, *Sonderina*, *Stoibrax capense*, and *Scaraboides*).
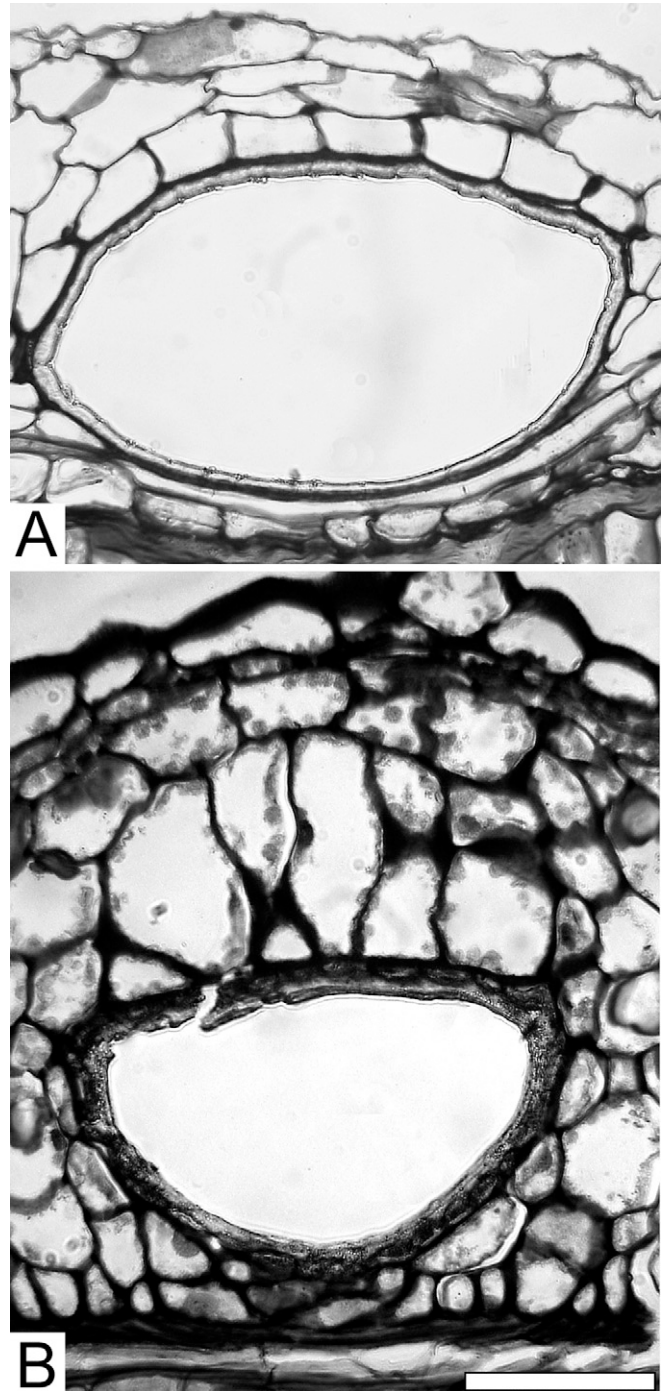
FIG. 6. Transverse sections through the fruit of *Sonderina* showing the A. square, *Sonderina* sp. 1 (*Magee & Boatwright 105*, JRAU), or B. upright *Sonderina tenuis* (*Van Wyk et al. 3433*, JRAU) cells external to the vittae. Scale: 0.07 mm

Dasispermum, Sonderina, and Stoibrax—Burtt (1989) suggested that the South African endemic genus *Sonderina* may be insufficiently distinct at the generic level from the largely North African genus *Stoibrax*. Previous molecular systematic studies have shown the type species of *Stoibrax* (*S. dichotomum*) to be placed in tribe Apieae (e.g. Downie et al. 2001). Our analyses of both ITS and *rps16* intron data clearly show *Sonderina* to form part of the *Lefebvrea* clade together with the only South African species of *Stoibrax*, *S. capense.* Such a relationship was proposed by Adamson

(1939, 1950) who treated *Stoibrax capense* (then *Stoibrax didyma*) as *Sonderina didyma*.

The monotypic genus *Dasispermum* is strongly supported in all analyses as embedded within *Sonderina.* The single species, *Dasispermum suffruticosum*, is a perennial dune endemic, distinguished by its usually fleshy leaves and often prominently winged fruit (Fig. 5F) which can be either homo- or heteromericarpic. The genus is plastic with regard to both of these characters (Tilney and Van Wyk 1995). Leaves may be less fleshy in some individuals within a population, especially those in more shaded sites and the ribs of some fruits may not be expanded into wings. Both characters appear to be adaptations to harsh littoral conditions and wind dispersal. *Dasispermum* shares the sympodial growth habit, a synapomorphy for the *Capnophyllum* group (Fig. 4B), as well as the isodiametric fruit, median and/or lateral ribs as well developed as the marginal ribs, narrow commissure (Fig. 5A, B, C, F), and the square or upright cells external to the vittae of the fruit (Fig. 6A, B) with *Sonderina* and *Stoibrax.* These character states are all synapomorphies for the *Dasispermum–Sonderina* complex (Fig. 4D, F, G, H). Furthermore, the close relationship between *Dasispermum suffruticosum* and *Stoibrax capense* is supported by a chromosome number of $n = 9$, an unusual number for the subfamily (Constance et al. 1976). An expanded circumscription of the genus *Dasispermum* to include *Sonderina* and *Stoibrax capense*, therefore, seems to be unavoidable.

Scaraboides—While revising the genus *Capnophyllum* (Magee et al. 2009b), the authors were alerted to an unusual species from the arid Tanqua Karoo region. Although this species shares numerous fruit characters with *Capnophyllum*, such as dorsally compressed mericarps, broad commissures, concave commissural surfaces, and involute marginal wings (Fig. 7E–G), it also has morphological characters in common with species of *Sonderina*, such as an erect habit (Fig. 7A), green ultimate leaf segments, scabrous often sessile umbels (Fig. 7A, D), and the absence of involucral and involucel bracts (Fig. 7D). The sympodial habit is weakly expressed in young plants of this species and is therefore not clearly visible in Fig. 7A. The species is easily distinguished by the presence of additional wing vittae (not known in any other genus within the family) and parallel, closely-spaced commissural vittae in the fruit (Fig. 7E–G).

Separate and combined analyses of ITS and *rps16* intron data sets place *Scaraboides* either within the *Dasispermum–Sonderina* complex (but with weak support values) or are equivocal in its placement. Shimodaira-Hasegawa tests indicate that a sister group relationship of *Scaraboides* to this complex (as retrieved in the analyses of the ITS/morphology and ITS/*rps16* intron/morphology data sets) cannot be rejected. In the analysis of morphological data, the genus was moderately supported (BP = 75) as sister to *Capnophyllum*. When combined with the molecular data sets, the position of *Scaraboides* was either unresolved (MP strict consensus tree, Fig. 3C) or sister to the *Dasispermum–Sonderina* complex (Fig. 3C and D). The genus is morphologically distinct from the *Dasispermum–Sonderina* complex, which has isodiametric fruit with a narrow commissure (Fig. 5B, C, F). The inclusion of *Scaraboides* within an expanded circumscription of *Dasispermum* would result in a group that would be impossible to delimit based on observed morphological characters. Despite the superficial similarity between the fruits of *Scaraboides manningii* and *Capnophyllum*, neither the molecular nor the combined molecular/morphological analyses place these taxa together. It is therefore clear that *Scaraboides* represents an independent, easily recognizable lineage.

Capnophyllum Group—All analyses presented herein indicate a broader lineage within the *Lefebvrea* clade, comprising *Capnophyllum*, *Dasispermum*, *Scaraboides*, *Sonderina*, and *Stoibrax capense*. These taxa share a unique combination of characters, namely the monocarpic or rarely short-lived perennial life history, the sympodial growth pattern, the papillose petals, and the broadly elliptic to rotund fruit in lateral view. The clade is therefore defined herein as the *Capnophyllum* group.

Key to Genera of the *Capnophyllum* Group

1. Fruit isodiametric; if homomericarpic then with the median and lateral ribs as well developed as the marginal ribs, if heteromericarpic then with either median or lateral ribs as well developed as the marginal ribs, prominent or winged; commissure narrow, extending to the base of each rib . . . . *Dasispermum*
1. Fruit dorsally compressed; homomericarpic with the median and lateral ribs not as well developed as the marginal ribs, marginal ribs prominently winged, median and lateral ribs inconspicuous or prominent but not winged; commissure broad, extending to the tip of each wing . . . . 2.
   2. Involucral and involucel bracts absent; rays and raylets scabrous; fruit with indistinct median and lateral ribs; additional vittae in the marginal wings; commissural vittae close together; ultimate leaflet segments more than 1.5 mm broad (never subterete), green . . . . *Scaraboides*
   2. Involucral and involucel bracts present; rays and raylets glabrous; fruit with prominent median and lateral ribs; additional vittae in the marginal wings absent; commissural vittae widely separate; ultimate leaflet segments less than 1 mm broad (often subterete), glaucous . . . . *Capnophyllum*

Taxonomic Treatment

1. **Dasispermum** Raf., Good Book 56 (1840) emend. Magee & B.-E. van Wyk, emend. nov.—TYPE: *Dasispermum maritimum* Raf., nom illeg. (= *Dasispermum suffruticosum* (Berg.) B. L. Burtt).

Sonderina H. Wolff in Pflanzenr. Heft 90: 92. 1927, syn. nov.— TYPE: *Sonderina hispida* (Thunb.) H. Wolff

Carum sect. *Brachyapium* Baill., Hist. Pl. 7: 118. 1879. *Brachyapium* (Baill.) Maire in Bull. Soc. Hist. Nat. Afr. Nord 23: 186. 1932, syn. nov.—TYPE: *Ptychotis didyma* Sond.

The concept of the genus *Dasispermum*, which has nomenclatural priority, is here expanded to include three species previously treated as *Sonderina*, as well as the only South African species of *Stoibrax*, namely *S. capense*. As a result, this previously monotypic genus now consists of seven South African endemic species, two of which are as yet undescribed (Magee et al. in prep.). The genus can be distinguished from all other genera within the *Lefebvrea* clade by a combination of characters, namely the sympodial growth habit (resulting in leaf-opposed umbels), papillose petals, isodiametric fruit with the median and/or lateral ribs as prominent as the marginal ribs, the narrow commissure extending to, at the most, the base of
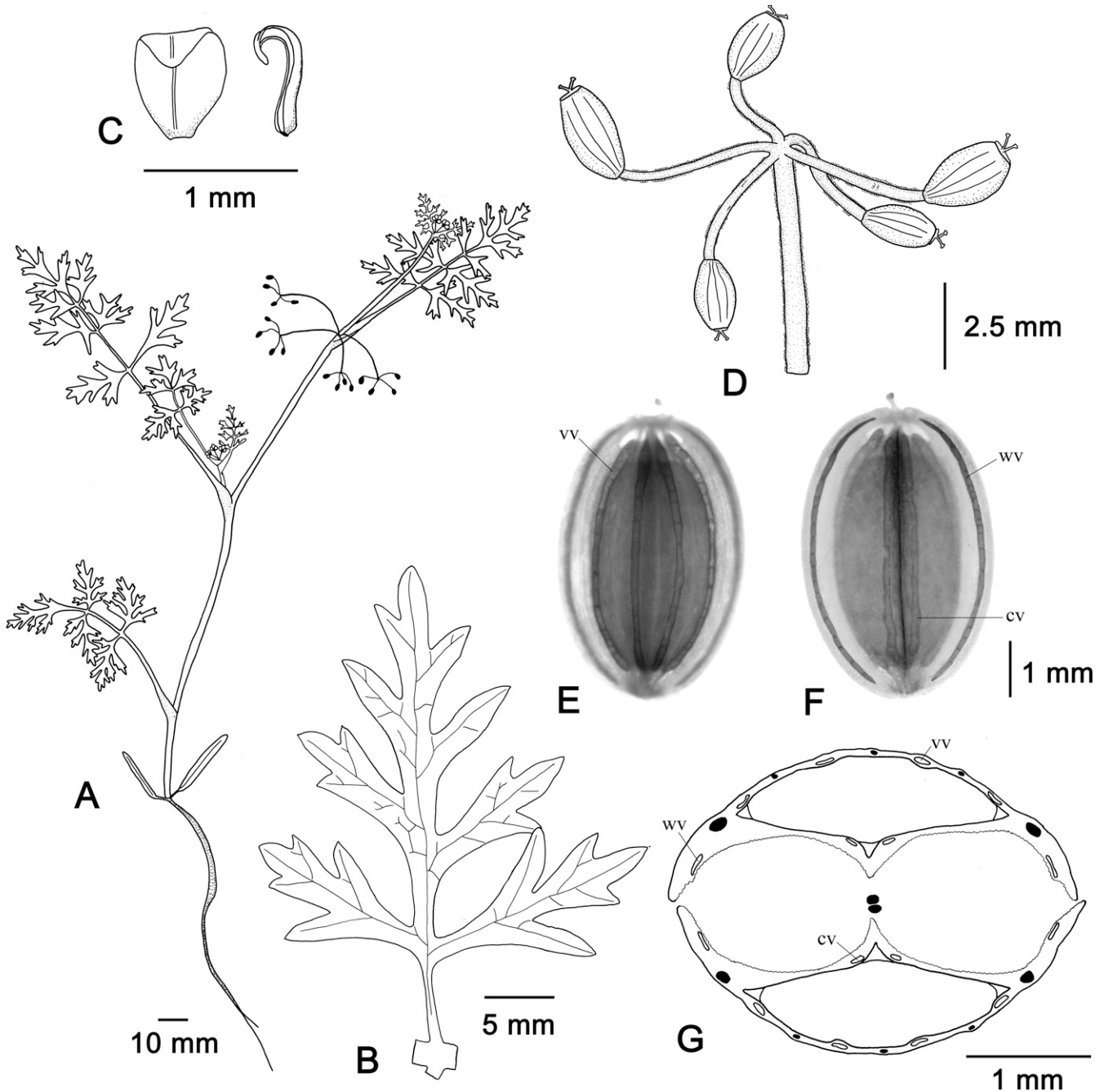
Fig. 7.   *Scaraboides manningii*. A. habit, B. lower leaf pinnae, C. petal in ventral and lateral view, D. umbellule, E. fruit, dorsal surface, F. fruit, commissural surface, G. transverse section through the mature fruit. A–D: *Manning 3010* (NBG); E–G. *Manning 3061* (NBG). cv - commissural vitta; vv - vallecular vitta; wv - additional wing vitta.

each rib and the presence of square or upright cells external to the vittae of the fruit.

DASISPERMUM SUFFRUTICOSUM (Berg.) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 45: 93. 1988. *Conium suffruticosum* Berg., Pl. Cap. 77. 1767.—TYPE: SOUTH AFRICA. Cape of Good Hope, *Grubb s.n.* (STB!).

Dasispermum capense (Lam.) Magee & B.-E. van Wyk, comb. nov. *Caucalis capensis* Lam., Encycl. 1: 658. 1785.—TYPE: SOUTH AFRICA. Cape, *Sonnerat s.n.* (P-LAM!).

Dasispermum hispidum (Thunb.) Magee & B.-E.van Wyk, comb. nov. *Sium hispidum* Thunb., Prodr. 51. 1794.—TYPE: SOUTH AFRICA. Cape, *Thunberg s.n.* (UPS-sheet 7046!).

Sonderina caruifolia (Sond.) H. Wolff, Pflanzenr. Heft 90:94. 1927, syn. nov.— TYPE: SOUTH AFRICA. Cape, Riebeekkasteel, *Zeyher 729* (K!, LE!, NBG!, S!).

Dasispermum humile (Meisn.) Magee & B.-E. van Wyk, comb. nov. *Petroselinum humile* Meisn. in Hook., Lond. J. Bot. 2: 531. 1843.—SYNTYPE: SOUTH AFRICA. Natal, near Port Natal, *Krauss 418* (BM!, K!, MO!); *Drège 9545* (not located).

Dasispermum tenue (Sond.) Magee & B.-E. van Wyk, comb. nov. *Ptychotis tenuis* Sond., Fl. Cap. 2: 537. 1862.—TYPE: SOUTH AFRICA. Cape, Buffeljagdrivier to Rietkuil, *Zeyher 2672* (LE!, S!).
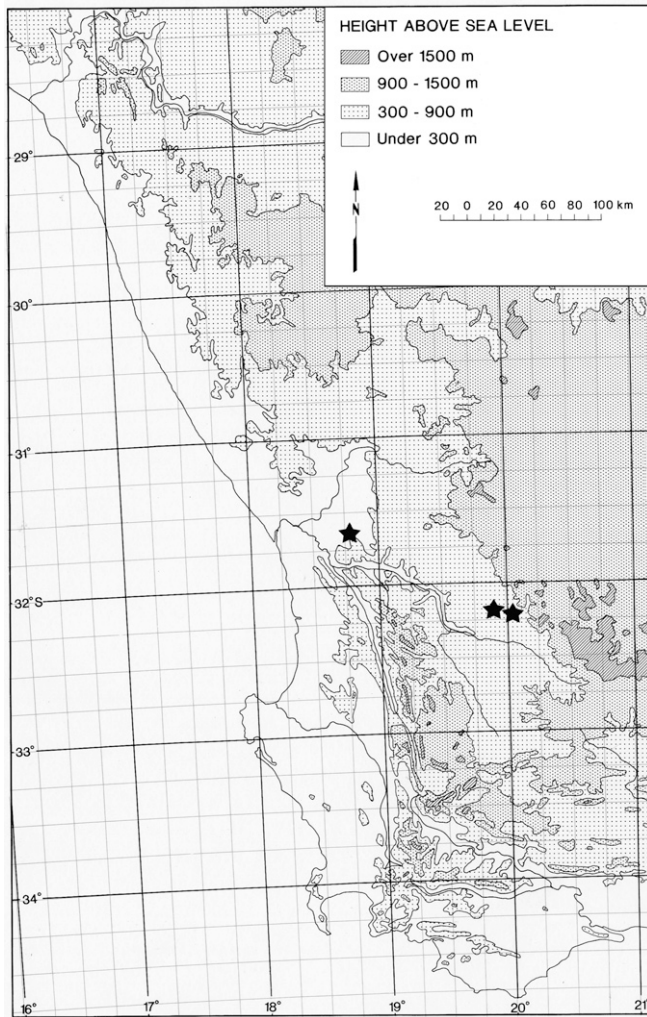
FIG. 8.   The known geographical distribution of *Scaraboides manningii*.

DASISPERMUM SP. 1. *Esterhuysen 28979* (BOL!), *34312* (BOL!); *Magee & Boatwright 105* (JRAU!), *Winter 3850* (JRAU!, PRE!).

DASISPERMUM SP. 2. *Lutzeyer s.n.* (JRAU!, NBG!).

2. **Scaraboides** Magee & B.-E. van Wyk, gen. nov.—TYPE: *S. manningii* Magee & B.-E. van Wyk.

A combined generic and specific description (*descriptio generico-specifica*) is provided under *S. manningii* below.

Etymology—The generic name is derived from the distinctive dark color and the strongly convex, smooth outline of the fruits (making them distinctly beetle-like in appearance), hence *Scaraboides* [from the Greek, *scarabeus* (beetle) and *–oides* (like)].

Scaraboides manningii Magee & B.-E. van Wyk, sp. nov.—TYPE: SOUTH AFRICA. Sutherland district: Tanqua Karoo National Park, NE slopes of Elandsberg; 06 August 2006; *B. Sachse 116* (holotype: PRE!; isotypes: BOL!, JRAU!, K!, KMG!, KSAN!, NBG!).

Descriptio generico-specifica: Capnophyllo Gaertn. habitu annuali, commissura lata fructus, mericarpiis dorsaliter compressis, superficiebus commissurialibus concavis, alis marginalibus involitis similis sed ramis erectis (non prostratis nec decumbentibus), segmentis ultimis foliorum latis viridis

(non angustis glaucis), umbellis scabris (non glabris) saepe sessilibus, bracteis involucralibus involucellaribusque deficientibus, costis dorsalibus fructus indistinctis, vittis additis solitariis in quoque alo marginali fructus et vittis paralelis crebris commissurialibus differt.

Erect herb, 0.2–0.4 m tall. Stem single, rarely slightly branched at the base, erect. Leaves 50–120 mm × 20–60 mm, pinnate, glabrous, green. Petioles 20–60 mm long, basal sheaths 7–12 mm × 3–5 mm. Ultimate leaflets broadly ovate, 12–30 mm × 10–28 mm, venation pinnate; segments narrowly oblong, 2–9 mm × 1.5–3 mm, flat. Umbels compound; peduncle sessile or rarely short, 0(–30) mm long; involucre absent; rays 4–6, 10–30 mm long at anthesis, slightly scabrous; involucel absent; raylets 6–9, 5–8 mm long at anthesis, scabrous. Flowers pentamerous; petals ± 0.5 mm long and broad, papillose, inflexed tips obtuse, septum absent on inner face, apex truncate; ovary glabrous; stylopodium flat, level with or slightly sunken below the fruit apex; styles not markedly elongated in mature fruit, 0.2–0.4 mm long, remaining erect or rarely becoming somewhat reflexed up to the base of the stylopodium. Fruit broadly elliptic, 5.5–6.0 mm × 3.0–3.5 mm; base obtuse or shallowly concave; apex obtuse; mericarps strongly concave on the commissural surface; median and lateral ribs indistinct; marginal ribs distinctly involute; additional solitary vittae present in the marginal wings.

Diagnostic Characters—The fruit is most similar to those of *Capnophyllum* in the broad commissure, the dorsally compressed mericarps with concave commissural surfaces and the involute marginal wings, but differs in the indistinct median and lateral ribs, the additional solitary vittae in each marginal wing and the parallel, closely spaced commissural vittae. When in flower, this species may be confused with *Dasispermum humile* but it is geographically isolated and can easily be distinguished by the flattened stylopodium and the petals which are not keeled on the adaxial face and which have only a short, acute tip (not slender and attenuate – the typical *lobulum inflexum* as is found in most other Apioideae).

Distribution and Habitat—*Scaraboides manningii* is restricted to the Succulent Karoo of the Western Cape Province, where it is known from only two localities, the Tanqua Karoo National Park and Mauwerskop near Vanrhynsdorp (Fig. 8). The species grows in seasonally damp, dolerite or clay soils.

Etymology—This species is named in honour of Dr. John Manning (NBG) who brought it to our attention and who also provided the first complete collection.

Additional Specimens Examined—SOUTH AFRICA. 3118 (Calvinia): Mauwerskop, NW of Matsikammaberg (–DB), *Snijman 1056* (PRE, MO). 3219 (Wuppertal): Top of Boulderkoppie, E of Leeuberg (–BB), *Sachse 71* (PRE), Tanqua Karoo National Park. 3220 (Sutherland): NE slopes of Remhoogte, ca. 1 km S from Maansedam, Tanqua Karoo National Park (–AA), *Bester 7171* (PRE); E foot of Elandsberg, Tanqua Karoo National Park (–AA), *Manning 3010* (NBG); E foot of Elandsberg, Tanqua Karoo National Park (–AA), *Manning 3061* (NBG); Elandsberg, Wilderness chalets (–AA), *Sachse 628* (PRE).

Literature Cited

Adamson, R. S. 1939. Some changes in nomenclature II. *The Journal of South African Botany* 5: 53–58.

Adamson, R. S. 1950. Umbelliferae. Pp. 623–625 in *Flora of the Cape Peninsula*, eds. R. S. Adamson and T. M. Salter. Cape Town: Juta and Co.

Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19: 716–723.

Allison, I. and B.-E. van Wyk. 1997. A revision of the genus *Anginon* (Apiaceae). *Nordic Journal of Botany* 17: 561–577.

Burtt, B. L. 1989. The adoption of *Stoibrax* for *Tragiopsis* and *Brachyapium* (Umbelliferae), and its N-S African disjunction. Pp. 143–147 in *The Davis and Hedge Festschrift*, ed. K. Tan. Edinburgh: Edinburgh University Press.

Burtt, B. L. 1991. Umbelliferae of southern Africa: an introduction and annotated checklist. *Edinburgh Journal of Botany* 48: 133–282.

Calviño, C. I., P. M. Tilney, B.-E. van Wyk, and S. R. Downie. 2006. A molecular phylogenetic study of southern African Apiaceae. *American Journal of Botany* 93: 1828–1847.

Constance, L., T.-L. Chuang, and C. R. Bell. 1976. Chromosome numbers in Umbelliferae V. *American Journal of Botany* 63: 608–625.

Downie, S. R. and D. S. Katz-Downie. 1999. Phylogenetic analysis of chloroplast *rps16* intron sequences reveals relationships within the woody southern African Apiaceae subfamily Apioideae. *Canadian Journal of Botany* 77: 1120–1135.

Downie, S. R., G. M. Plunkett, M. F. Watson, K. Spalik, D. S. Katz-Downie, C. M. Valiejo-Roman, E. I. Terentieva, A. V. Troitsky, B.-Y. Lee, J. Lahham, and A. El-Oqlah. 2001. Tribes and clades within Apiaceae subfamily Apioideae: the contribution of molecular data. *Edinburgh Journal of Botany* 58: 301–330.

Downie, S. R., S. Ramanath, D. S. Katz-Downie, and E. Llanas. 1998. Molecular systematics of Apiaceae subfamily Apioideae: phylogenetic analyses of nuclear ribosomal DNA internal transcribed spacer and plastid *rpoC1* intron sequences. *American Journal of Botany* 85: 563–591.

Downie, S. R., M. F. Watson, K. Spalik, and D. S. Katz-Downie. 2000. Molecular systematics of Old World Apioideae (Apiaceae): relationships among some members of tribe Peucedaneae sensu lato, the placement of several island endemic species, and resolution within the apioid superclade. *Canadian Journal of Botany* 78: 506–528.

Doyle, J. J. and J. L. Doyle. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin* 19: 11–15.

Dyer, R. A. 1975. *The genera of Southern African flowering plants.* Vol 1: Dicotyledons. Pretoria: Botanical Research Institute.

Farris, J. S. 1989. The retention index and the rescaled consistency index. *Cladistics* 5: 417–419.

Farris, J. S., M. Källersjö, A. G. Kluge, and C. Bult. 1995. Constructing a significance test for incongruence. *Systematic Biology* 44: 570–572.

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

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.

Fitch, W. M. 1971. Towards defining the course of evolution: minimal change for a specific tree topology. *Systematic Zoology* 20: 406–416.

Huelsenbeck, J. P. and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17: 754–755.

Kljuykov, E. V., M. Liu, T. A. Ostroumova, M. G. Pimenov, P. M. Tilney, and B.-E. van Wyk. 2004. Towards a standardised terminology for taxonomically important morphological characters in the Umbelliferae. *South African Journal of Botany* 70: 488–496.

Kluge, A. G. 1989. A concern for evidence and a phylogenetic hypothesis for relationships among *Epicrates* (Boidae, Serpentes). *Systematic Zoology* 38: 7–25.

Kluge, A. G. and J. S. Farris. 1969. Quantitative phyletics and the evolution of Anurans. *Systematic Zoology* 18: 1–32.

Lebrun, J.-P. and A. L. Stork. 1992. *Enumération des plantes à fleurs d'Afrique tropicale*, Vol. 2. Genève: Ville de Genève Editions.

Leistner, O. A. and J. M. Morris. 1976. Southern African place names. *Annals of the Cape Province Museum* 12: 1–565.

Maddison, W. P. and D. R. Maddison. 2008. Mesquite: a modular system for evolutionary analysis. Version 2.5. http://mesquiteproject .org.

Magee, A. R., B.-E. van Wyk, and P. M. Tilney. 2008a. A taxonomic revision of the genus *Nanobubon* (Apiaceae: Apioideae). *South African Journal of Botany* 74: 713–719.

Magee, A. R. B.-E. van Wyk, and P. M. Tilney. 2008b. A taxonomic revision of the genus *Cynorhiza* (Apiaceae: Apioideae). *South African Journal of Botany* 74: 726–734.

Magee, A. R., B.-E. van Wyk, P. M. Tilney, and S. R. Downie. 2008c. *Ezosciadum* (Apiaceae): A taxonomic revision of yet another early diverging South African apioid genus. *Plant Systematics and Evolution* 276: 167–175.

Magee, A. R., B.-E. van Wyk, and P. M. Tilney. 2009a. A taxonomic revision of the woody South African genus *Notobubon* (Apiaceae: Apioideae). *Systematic Botany* 34: 220–242.

Magee, A. R. B.-E. van Wyk, P. M. Tilney, and S. R. Downie. 2009b. A taxonomic revision of *Capnophyllum* (Apiaceae: Apioideae). *South African Journal of Botany* 75: 283–291.

Meikle, R. D. 1977. *Flora of Cyprus.* Vol. 1. London: The Bentham-Moxon Trust.

Nixon, K. C. and J. M. Carpenter. 1996. On simultaneous analysis. *Cladistics* 12: 221–242.

Oxelman, B., M. Lidén, and D. Berglund. 1997. Chloroplast *rps16* intron phylogeny of the tribe Sileneae (Caryophyllaceae). *Plant Systematics and Evolution* 206: 393–410.

Posada, D. and K. A. Crandall. 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.

Ronquist, F. and J. P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.

Seelanan, T., A. Schnabel, and J. F. Wendel. 1997. Congruence and consensus in the cotton tribe (Malvaceae). *Systematic Botany* 22: 259–290.

Shimodaira, H. and M. Hasegawa. 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Molecular Biology and Evolution* 16: 1114–1116.

Sonder, W. 1862. Umbelliferae. Pp. 524–567 in *Flora Capensis*, Vol. 2, eds. W. H. Harvey and W. Sonder. Dublin: Hodges, Smith and Co.

Sun, F.-J. and S. R. Downie. 2004. A molecular systematic investigation of *Cymopterus* and its allies (Apiaceae) based on phylogenetic analyses of nuclear (ITS) and plastid (rps16 intron) DNA sequences. *South African Journal of Botany* 70: 407–416.

Sun, Y., D. Z. Skinner, G. H. Liang, and S. H. Hulbert. 1994. Phylogenetic analysis of *Sorghum* and related taxa using internal transcribed spacers of nuclear ribosomal DNA. *Theoretical and Applied Genetics* 89: 26–32.

Swofford, D. L. 2002. PAUP*: Phylogenetic analysis using parsimony (*and other methods). Version 4.0 beta 10. Sunderland: Sinauer Associates.

Tilney, P. M. and B.-E. van Wyk. 1995. Unusual structural variation in the fruit of *Dasispermum suffruticosum* (Apiaceae): A new record of heteromorphic fruits in the family. *South African Journal of Botany* 61: 245–248.

Tutin, T. G., V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters, and D. A. Webb. 1968. *Flora Europaea.* Vol. 2. Cambridge: Cambridge University Press.

Van Wyk, B.-E. and P. M. Tilney. 2004. Diversity of Apiaceae in Africa. *South African Journal of Botany* 70: 433–445.

Wiens, J. J. 1998. Combining data sets with different phylogenetic histories. *Systematic Biology* 47: 568–581.

Winter, P. J. D., A. R. Magee, N. Phephu, P. M. Tilney, S. R. Downie, and B.-E. van Wyk. 2008. A new generic classification for African peucedanoid species (Apiaceae). *Taxon* 57: 347–364.

Wolff, H. 1927. Umbelliferae-Apioideae-Ammineae-Carinae, Ammineae Novemjugatae et Genuinae. Pp. 1–398 in Das Pflanzenreich, Heft 90 (IV. 228), ed. A. Engler. Berlin: W. Engelmann.

Yang, Z. and B. Rannala. 1997. Bayesian phylogenetic inference using DNA sequences: a Markov Chain Monte Carlo method. *Molecular Biology and Evolution* 14: 717–724.

Appendix 1. Morphological and anatomical characters and states used in the phylogenetic analysis of the Lefebvrea clade. [1]Field observations of *Dasispermum suffruticosum* and *Sonderina* sp. 1 indicate that these species are not monocarpic annuals but rather short-lived perennials

lasting for only a few seasons depending on rainfall, possibly an adaptation to the dune habitat in which they both occur. Perennials include all shrubs and also species with permanent fleshy roots. [2]Some species of *Sonderina* are distinct in that their involucre and involucel bracts are usually absent or at best strongly reduced and rudimentary. [3]*Sonderina hispida*, *Sonderina* sp. 1, and *Stoibrax capense* are unusual in that at least some of the involucre and involucel bracts are pinnately divided, thus resembling the leaves.

1. Life history[1] (monocarpic = 0; short-lived perennial = 1; perennial = 2); **2.** Habit (herbs = 0; rhizomatous = 1; suffrutices = 2; shrubs or shrublets = 3); **3.** Growth pattern (monopodial = 0; sympodial = 1); **4.** Leaf persistence (one-seasoned or deciduous = 0; permanent, evergreen = 1); **5.** Leaf arrangement (radical or if somewhat cauline then borne on deciduous branches = 0; cauline, borne on permanent branches =1); **6.** Leaf texture (coriaceous = 0; flimsy = 1; sclerophyllous =2); **7.** Leaf color (concolourously green or green above = 0; glacous =1); **8.** Inflorescence vestiture (glabrous = 0; scabrous = 1); **9.** Ratio of functionally male flowers (equal ratio of male to female flowers in all raylets of the umbellule = 0; inner raylets of umbellules functionally male =1); **10.** Involucre and involucel bracts[2] (present = 0; absent or much reduced = 1); **11.** Involucre and involucel bracts type[3] (absent or all simple = 0; at least some compound, resembling the leaves = 1); **12.** Petal vestiture (leathery = 0; papillose = 1); **13.** Fruit length (more than 9 mm = 0; less than 9 mm = 1); **14.** Fruit compression (platyspermous = 0; isodiametric = 1); **15.** Fruit in lateral view (narrowly elliptic = 0; broadly elliptic to rotund = 1); **16.** Ribs (median and lateral ribs markedly less developed than the marginal ribs = 0; median and/or lateral ribs as well developed as the marginal ribs = 1); **17.** Ribs (obtusely tipped = 0; almost trifid with prominent tapering tips = 1); **18.** Secondary ribs (absent = 0; usually present = 1); **19.** Marginal wings (absent or flat = 0; involute = 1); **20.** Commissural surface (flat = 0; concave = 1); **21.** Commissure (100% from rib tip to rib tip = 0; from near rib tip to near rib tip = 1; from at most rib base to rib base = 2); **22.** Rib vittae (absent = 0; present at base of all ribs = 1; present in marginal wings = 2); **23.** Cells external to vittae (indistinct =0; square = 1; enlarged, upright = 2).

APPENDIX 2.

Capnophyllum Gaertn.**:** *C. africanum* (L.) Gaertn. — FM201528, FM201546; *Magee 124* (JRAU). *C. africanum* (L.) Gaertn. — FM201527, FM201548; *Forest et. al. 654* (NBG). *C. leiocarpon* (Sond.) J.C.Manning & Goldblatt — FM201525, FM201545; *Bester 6978* (PRE). *C. leiocarpon* (Sond.) J.C.Manning & Goldblatt — FM201526, FM201544; *Magee & Boatwright 125* (JRAU). *C. lutzeyeri* Magee & B.-E.van Wyk — FM201524, FM201543; *Magee et al. 106* (JRAU). *C. macrocarpum* Magee & B.-E.van Wyk — FM201529, FM201547; *Magee et al. 133* (JRAU). ***Conium*** L.**:** *C. sphaerocarpum* Hilliard & Burtt— FM201530, FM201558; *Magee at al. 129* (JRAU). ***Cynorhiza*** Eckl. & Zeyh.**:** *C. typica* Eckl. & Zeyh. — *, FM201556; *Magee et al. 53* (JRAU). *C. typica* Eckl. & Zeyh. —*, FM201557; *Van Wyk 3372* (JRAU). ***Dasispermum*** Raf.**:** *D. suffruticosum* (Berg.) B. L. Burtt — FM201514, FM201541; *Magee & Boatwright 117* (JRAU). ***Nanobubon*** Magee**:** *N. capillaceum* (Thunb.) Magee — *, FM201549; *Magee & Boatwright 14* (JRAU). *N. strictum* (Spreng.) Magee — *, FM201550; *Magee et al. 58* (JRAU). ***Notobubon*** B.-E.van Wyk**:** *N. capense* (Eckl. & Zeyh.) Magee — *, FM201551; *Magee et al. 43* (JRAU). *N. capense* (Eckl. & Zeyh.) Magee — *, FM201555; *Magee et al. 37* (JRAU). *N. gummiferum* (L.) Magee — *, FM201554; *Magee et al. 61* (JRAU). *N. pearsonii* (Adamson) Magee — *, FM201552; *Magee et al 42* (JRAU). *N. tenuifolium* (Thunb.) Magee — *, FM201553; *Magee et al. 44* (JRAU). ***Scaraboides*** Magee & B.-E.van Wyk**:** *S. manningii* Magee & B.-E.van Wyk — FM201523, FM201542; *Manning 3010* (NBG). ***Sonderina*** H.Wolff **:** *S. hispida* (Thunb.) H. Wolff — FM201520, FM201537; *Magee & Boatwright 115* (JRAU). *S. hispida* (Thunb.) H.Wolff — –, FM201536; *Magee et al. 112* (JRAU). *S. hispida* (Thunb.) H.Wolff — FM201521, FM201535; *Magee et al. 107* (JRAU). *S. humilis* (Meisn.) H.Wolff — FM201518, FM201538; *Van Wyk & Van Wyk 1883* (JRAU). *S. sp.1* — FM201519, FM201534; *Magee & Boatwright 105* (JRAU). *S. sp. 2* — FM201522, FM201540; *Lutzeyer s.n.* (JRAU). *S. tenuis* (Sond.) H.Wolff — FM201517, FM201539; *Van Wyk et al. 3433* (JRAU). ***Stoibrax*** Raf.**:** *S. capense* (Lam.) B.L.Burtt — FM201516, FM201532; *Magee et al. 128* (JRAU). *S. capense* (Lam.) B.L.Burtt — FM201515, FM201533;

Matrix of morphological character states used in the phylogenetic analysis of the *Lefebvrea* clade.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Afroligusticum elliotii	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Afroligusticum petitianum	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Afrosciadium magalismontanum	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Capnophyllum africanum	0	0	1	0	0	1	1	0	0	0	0	1	1	0	1	0	0	1	1	1	0	0	0
Capnophyllum leiocarpon	0	0	1	0	0	1	1	0	0	0	0	1	1	0	1	0	0	1	1	1	0	0	0
Capnophyllum lutzeyeri	0	0	1	0	0	1	1	0	0	0	0	1	1	0	1	0	0	1	1	1	0	0	0
Capnophyllum macrocarpum	0	0	1	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0
Cynorhiza typica	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dasispermum suffruticosum	1	2	1	1	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	2	0	1
Lefebvrea abyssinica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nanobubon capillaceum	2	1	0	1	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nanobubon strictum	2	1	0	1	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Notobubon capense	2	3	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Notobubon ferulaceum	2	3	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Notobubon galbaniopse	2	3	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Notobubon galbanum	2	3	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Notobubon gummiferum	2	3	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Notobubon laevigatum	2	3	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Notobubon pearsonii	2	3	0	1	1	2	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0
Notobubon pungens	2	3	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Notobubon striatum	2	3	0	1	1	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Notobubon tenuifolium	2	3	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Scaraboides manningii	0	0	1	0	0	0	0	1	0	1	0	0	1	0	1	0	0	1	1	0	2	0	0
Sonderina hispida	0	0	1	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0	0	2	0	1
Sonderina humilis	0	0	1	0	0	0	0	0	0	1	0	1	1	1	1	1	0	0	0	0	2	0	2
Sonderina tenuis	0	0	1	0	0	0	0	0	0	1	0	1	1	1	1	1	0	0	0	0	2	0	2
Sonderina sp. 1	1	2	1	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	2	0	1
Sonderina sp. 2	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	2	0	2
Stenosemis caffra	2	1	0	1	0	2	0	0	1	0	0	1	1	1	1	1	1	0	0	0	1	0	0
Stenosemis angustifolia	2	1	0	1	0	2	0	0	1	0	0	1	1	1	1	1	1	0	0	0	1	0	0
Stoibrax capense	0	0	1	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0	2	0	1

Magee et al. 131 (JRAU). *S. dichotomum* (L.) Raf. — FM201531, –; *Sanchez-Mata & Molina Abril s.n.* (K).

APPENDIX 4. Previously published *rps16* intron accessions of Apiaceae obtained from GenBank.[1] Downie and Katz-Downie (1999);[2] Downie et al. (2000);[3] Sun and Downie (2004);[4] Calviño et al. (2006);[5] Magee et al. (2008c);[6] McNeill and Kemper (unpubl.).

Aethusa cynapium L. AF110539[1]; *Ammi majus* L. AF164814[2]; *Apium graveolens* L. AF110545[1]; *Berula erecta* (Huds.) Coville AF164819[2]; *Conium maculatum* L. AF110546[1]; *Crithmum maritimum* L. AF110540[1]; *Deverra burchelli* (DC.) Eckl. & Zeyh. AY838418[4]; *Echinophora tenuifolia* L. AF164812[2]; *Foeniculum vulgare* Mill. AF110543[1]; *Heracleum lanatum* Michx. AF110537[1]; *Heracleum maximum* Bartr. EF426691[6]; *Heracleum spondylium* L. AF164800[2]; *Malabaila sekakul* Boiss. AF164802[2]; *Nanobubon strictum* (Spreng.) Magee AY838438[4]; *Naufraga balearica* Constance & Cannon AF164816[2]; *Notobubon ferulaceum* (Thunb.) Magee AY838434[4]; *Notobubon galbanum* (L.) Magee AY838435[4]; *Notobubon pearsonii* (Adamson) Magee AY838436[4]; *Notobubon pungens* (E.Mey. ex Sond.) Magee AY838437[4]; *Pastinaca sativa* L. AF110538[1]; *Sium latifolium* L. AF110552[1]; *Smyrnium olusatrum* L. AF110551[1]; *Stenosemis caffra* Sond. AY838444[4]; *Stoibrax dichotomum* (L.) Raf. AM982518[5]; *Thaspium pinnatifidum* (Buckley) A.Gray AY372896[3]; *Zizia aurea* Koch AF110535[1]; *Zosima orientalis* Hoffm. AF164806[2].