

RESEARCH ARTICLE

Molecular phylogenetics of Thymelaeaceae-Thymelaeoideae: Resolving the paraphyly of *Gnidia* and a new monophyletic generic classification for the group

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Abstract Earlier phylogenetic analyses of the family Thymelaeaceae using combined plastid (*matK*, *rbcL*, *rps16*, *trnL-F*) and nuclear (ITS) regions showed that the African-Malagasy genus *Gnidia* was extensively polyphyletic in relation to the southern African genera *Lachnaea*, *Passerina* and *Struthiola*, as well as to other Southern Hemisphere genera such as *Drapetes*, *Kelleria* and *Pimelea*. We present here a robust and well-sampled phylogenetic analysis of the subfamily Thymelaeoideae, with sampling in *Gnidia* increased to 76% of the species, to better resolve the polyphyly of the genus. Our analysis retrieved seven lineages of *Gnidia* nested in four independent evolutionary clades within the “*Gnidia* group” of the subfamily Thymelaeoideae. We analysed the options available for re-circumscribing *Gnidia* as a monophyletic genus, with secondary considerations of nomenclatural stability, phylogenetic and biogeographic information, and ease of identification. The option that we present retains the traditionally recognized genera *Drapetes*, *Kelleria*, *Lachnaea*, *Passerina*, *Pimelea* and *Struthiola* through the recognition of six lineages of *Gnidia* at the generic level. We propose that *Gnidia* be retained as a monotypic genus, including only the type of the genus name *G. pinifolia*. We reinstate the four previously recognized genera *Basutica*, *Craspedostoma*, *Gnidiopsis* and *Thymelina* and recognize the two new genera *Epichroxantha* and *Phidia* for the remaining two lineages of continental African *Gnidia* for which no names were available, plus the monotypic *Zacharia* for an anomalous Malagasy species that was previously excluded from *Lasiosiphon*. A taxonomic key and descriptions are provided for the genera in the “*Gnidia* group”. We also provide the necessary new combinations for names of *Gnidia* species now transferred to other genera.

Keywords generic limits; *Gnidia*; molecular phylogenetic analysis; morphological characters; new genera; polyphyly; Southern Africa; taxonomy; Tropical Africa

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

Thymelaeaceae subfamily Thymelaeoideae, with ca. 780 species in 38 genera (Herber, 2003), is the larger of the two subfamilies recognized by Herber (2003) in his comprehensive review of the family, the other being Octolepidoideae. The more recent subfamilial classification by Colli-Silva & al. (2025), based on molecular data and character reconstruction, has reinstated subfamily Aquilarioideae from Thymelaeoideae and also included *Tepuianthus* Maguire & Steyerl. as a fourth subfamily. Their taxonomy of the

family thus recognizes the four subfamilies Aquilarioideae, Gonystyloideae (= Octolepidoideae p.p.), Tepuianthoideae, and Thymelaeoideae, with *Octolepis* Oliv. *incertae sedis*.

Subfamily Thymelaeoideae is widely distributed worldwide, with centres of diversity in Australia, the Mediterranean region, and South Africa, particularly the Core Cape Floristic Region (Hutchinson, 1967; Herber, 2003; Manning & Goldblatt, 2012). The subfamily is subdivided into three tribes, with tribe Daphneae including all of the southern African representatives. These number some 210 species that are currently distributed among the nine genera *Dais* Royen

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ex L., *Englerodaphne* Gilg, *Gnidia* L., *Lachnaea* L., *Lasiosiphon* Fresen., *Passerina* L., *Peddiea* Harv., *Struthiola* L. and *Synaptolepis* Oliv. (Herber, 2003; Beaumont & al., 2009; Olaniyan & al., 2020).

The southern African genera were all included in the informally ranked “*Gnidia* group” by Herber (2003), along with the South American genus *Drapetes* Banks ex Lam. and the Australasian genera *Kelleria* Endl. and *Pimelea* Banks ex Gaertn. The tribe Daphneae sensu Herber (2003) corresponds to the subfamily Thymelaeoideae of Domke (1934), and the “*Gnidia* group” sensu Herber (2003) is largely congruent with the tribe Gnidiaceae sensu Domke (1934).

The relationships of *Gnidia* and its presumptive relatives in the “*Gnidia* group”, mostly from southern Africa and Madagascar, have not been clearly understood until now, resulting in widely differing circumscriptions of the genus *Gnidia*. At one extreme the genus has been very broadly circumscribed to include segregates such as *Arthrosolen* C.A.Mey., *Atemnosiphon* Leandri, *Englerodaphne*, and *Lasiosiphon* (Gilg, 1894, 1921; Domke, 1934; Peterson, 1959, 1978, 2006; Dyer, 1975; Robyns, 1975; Herber, 2003; Rogers, 2009) and at the other extreme has been more narrowly circumscribed to accept these genera as distinct from *Gnidia* (Endlicher, 1847; Meisner, 1857; Bentham & Hooker, 1880; Pearson, 1910; Wright, 1915; Marloth, 1925; Burt-Davy, 1926; Phillips, 1944, 1951; Leandri, 1950; Hutchinson, 1967).

This conflict is driven by the difficulty in establishing unique or stable morphological characters that can be used to circumscribe genera in the group. Characters such as floral merosity, presence or absence of petaloid scales (Fig. 1), number of stamens, inflorescence structure (Fig. 2), and the presence or absence of involucral bracts, among others, have all been used to circumscribe genera in the “*Gnidia* group”, although their taxonomic value continues to be a matter of debate (Staner, 1935; Peterson, 1959; Peterson, 2006; Rogers, 2009).

Endlicher (1847), Meisner (1857), and Bentham & Hooker (1880) all regarded the presence or absence of petaloid scales as a fundamental generic character ranking above floral merosity in significance. They thus included both 5-merous and 4-merous taxa in the genus *Arthrosolen*, which they defined by the absence of petaloid scales as a genus separate from *Gnidia* and *Lasiosiphon*, in which petaloid scales were present.

In contrast, Gilg (1894) accepted a much broader circumscription of *Gnidia* based on his investigations into the anatomy, geographical distribution, and structure of the flowers, fruits, and seeds. In his circumscription, *Gnidia* was defined by having twice as many stamens as calyx lobes, and it included all species of *Arthrosolen* and *Lasiosiphon*. Gilg (1894) utilized novel characters such as texture, shape, and hairiness of the leaves, inflorescence size and position, details of the receptacle and involucral bracts, and geographical distribution to recognize groups within his enlarged circumscription of *Gnidia*. He also established *Englerodaphne* for the single species *Gnidia leiosiphon* Gilg (= *Englerodaphne*

subcordata (Meisn.) Engl.) based on its distinctive inflorescence (ebracteate umbel-like heads) and leaf structure (membranous, inconspicuously nerved leaves).

Subsequent authorities (Pearson, 1910; Wright, 1915; Marloth, 1925; Burt-Davy, 1926) largely rejected this broad circumscription of *Gnidia*, reverting to the traditional characters of floral merosity and the presence or absence of scales to separate *Lasiosiphon* and *Arthrosolen* from *Gnidia*, but accepted *Englerodaphne* as a distinct genus.

Phillips (1944, 1951) continued to recognize the genera *Arthrosolen*, *Englerodaphne*, and *Lasiosiphon* but radically altered the circumscription of *Arthrosolen*, rejecting the absence of floral scales as a generic criterion and defining it instead by a capitulate inflorescence subtended by coloured, membranous bracts. This revised circumscription of the genus included mainly 5-merous but also 4-merous species, mostly lacking or rarely with petaloid scales. The remaining species that had been previously included in *Arthrosolen* on the basis of the absence of petaloid scales were transferred to *Gnidia*. Phillips (1944, 1951) also segregated some other species from *Gnidia* based on the number of stamens in relation to the number of calyx lobes, characters that he considered more important than the presence or absence of petaloid scales for defining generic limits. On this basis, he established the new monotypic segregate genera *Basutica* E.Phillips, *Pseudognidia* E.Phillips and *Struthiolopsis* E.Phillips.

Peterson (1959, 1978, 2006) likewise argued that characters such as floral merosity and the presence or absence of petals were too variable within the group to justify the separation of the genera *Arthrosolen*, *Gnidia* and *Lasiosiphon* but also rejected the validity of the relative number of stamens and calyx lobes that had been used to establish *Basutica*, *Pseudognidia* and *Struthiolopsis*. He thus reverted to an even broader circumscription of *Gnidia* than had been adopted by Gilg (1894), including *Arthrosolen*, *Basutica*, *Englerodaphne*, *Lasiosiphon*, *Pseudognidia*, and *Struthiolopsis* as synonyms.

Herber (2002, 2003), in the most comprehensive generic classification of Thymelaeaceae, followed this broad circumscription, citing traditional morphological evidence from pollen and flowers, as well as wood anatomy, in support of his decision to include all of the segregate African genera, plus the monotypic endemic Malagasy *Atemnosiphon*, as elements within *Gnidia*.

Later molecular phylogenetic analyses of *rbcL*, *trnL-F* and ITS regions in the family Thymelaeaceae (Van der Bank & al., 2002; Beaumont & al., 2009) have, however, clearly demonstrated that *Gnidia* in the broad, inclusive sense of Herber (2003) is extensively polyphyletic. These analyses also revealed that pre-molecular authorities had grossly underestimated the complexity of the taxonomic relationships within *Gnidia*. The analyses by Beaumont & al. (2009) revealed that the relationships of *Gnidia* were not limited to its presumptive relatives in the “*Gnidia* group” but also to the other Southern Hemisphere genera *Drapetes*, *Kelleria*, *Lachnaea*, *Passerina*, *Pimelea* and *Struthiola*, none of which

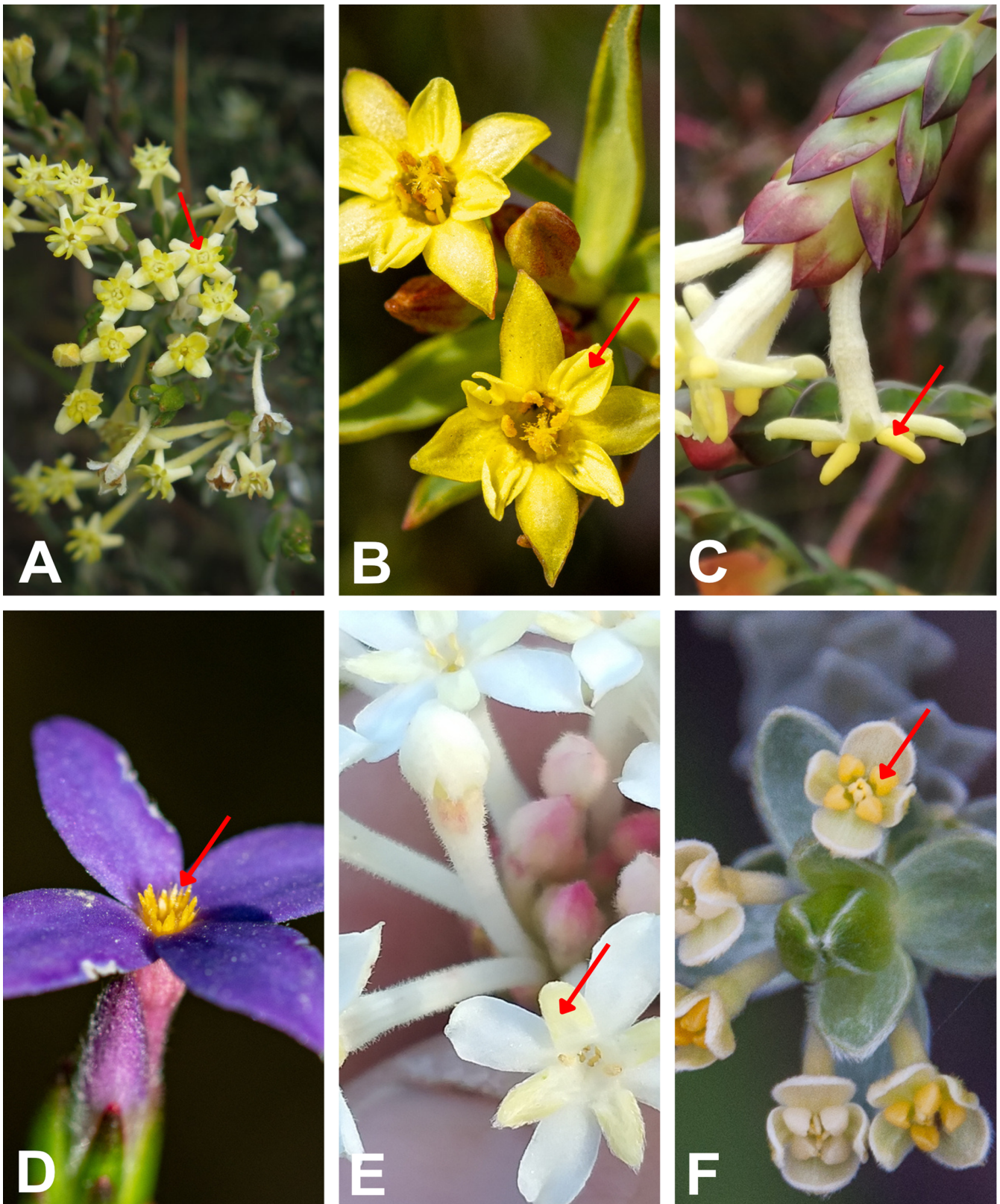


Fig. 1. Diversity of petaloid scales in selected Thymelaeoideae. **A**, Eight fleshy scales in *Gnidia clavata*; **B**, Four membranous scales in *Gnidia juniperifolia*; **C**, Four fleshy scales with involute margins in *Gnidia oppositifolia*; **D**, Lacinate scales interspersed with hairs in *Gnidia penicillata*; **E**, Four densely hairy scales in *Gnidia pinifolia*; **F**, Four fleshy scales in *Gnidia tenella*. — Photos: A, AnneLise Vlok, [iNaturalist](#), CC BY-NC 4.0; B, magriet b, [iNaturalist](#), CC BY-SA 4.0; C, Mashudu, [iNaturalist](#), CC BY-NC 4.0; D, magriet b, [iNaturalist](#), CC BY-SA 4.0; E, Kevin Koen, [iNaturalist](#), CC BY-SA 4.0; F, magriet b, [iNaturalist](#), CC BY-SA 4.0.

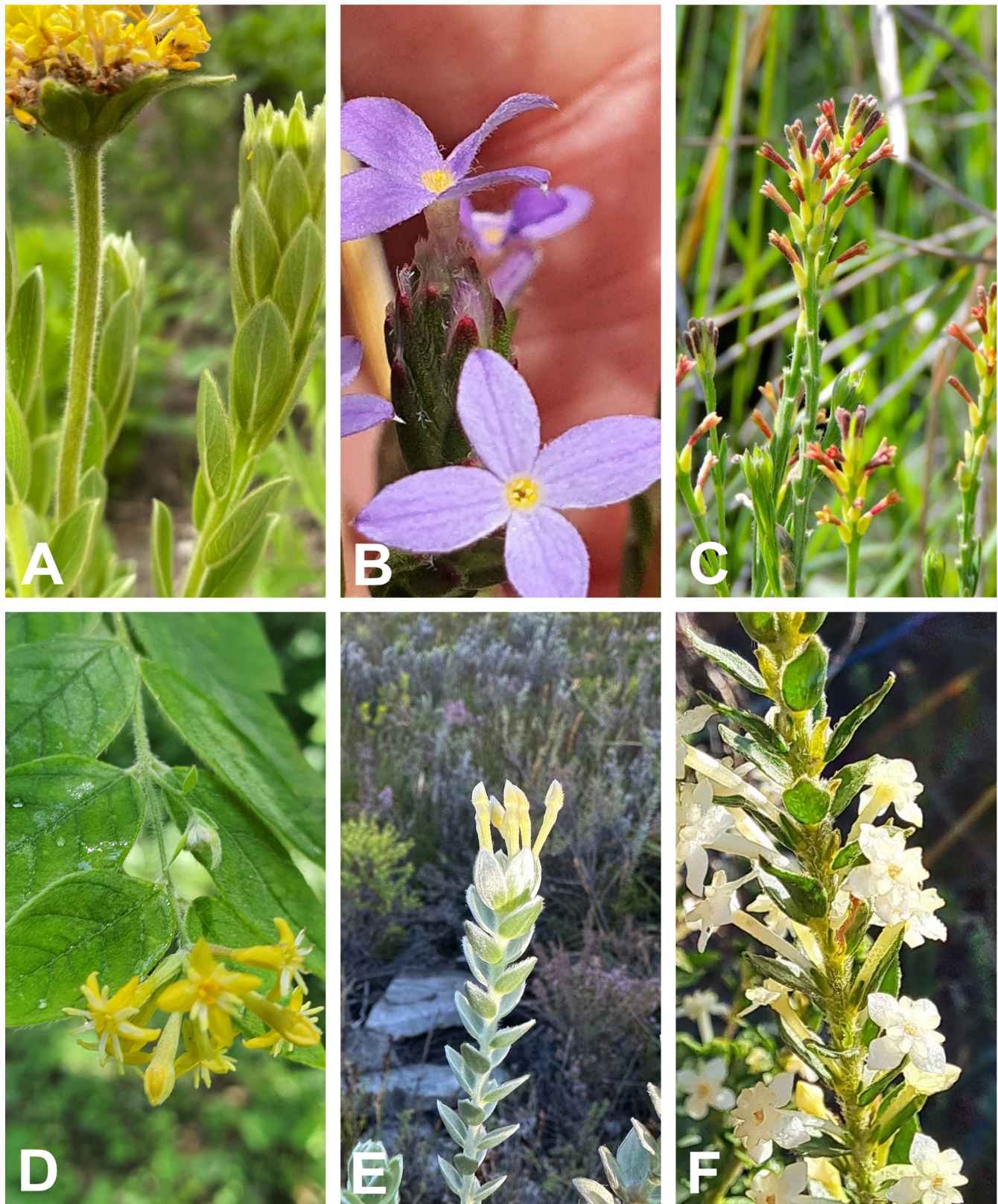


Fig. 2. Inflorescence morphology in selected Thymelaeoideae. **A**, Capitulate inflorescence in *Laiosiphon kraussianus*; **B**, Solitary terminal flower in *Gnidia penicillata*; **C**, Spiciform raceme inflorescence in *Gnidia gymnostachya*; **D**, Ebracteate umbel in *Englerodaphne pilosa*; **E**, Bracteate terminal umbel in *Gnidia anomala*; **F**, Racemose inflorescence in *Struthiola hirsuta*. — Photos: A, Linda Löffler, [iNaturalist](#), CC BY-NC 4.0; B, Jean Stephenson, [iNaturalist](#), CC BY-NC 4.0; C, graham_g, [iNaturalist](#), CC BY-NC 4.0; D, julie braby, [iNaturalist](#), CC BY-NC-SA 4.0; E, Derek Silberblatt, [iNaturalist](#), CC BY-NC 4.0; F, Lynn M., [iNaturalist](#), CC BY-NC 4.0.

have previously been synonymized with *Gnidia*. These genera were all retrieved as monophyletic but nested within the polyphyletic lineages of *Gnidia*. In addition, all species of *Lasiosiphon*, along with *Arthrosolen* sensu Phillips (1944, 1951) and some *Gnidia* species, were retrieved as a well-supported clade outside the remaining genera of the “*Gnidia* group”. This clade included all of the 5-merous species in the group plus various 4-merous taxa that were all morphologically diagnosable by an involucre inflorescence. Beaumont & al. (2009), therefore, argued for the reinstatement of the genus *Lasiosiphon* with an expanded circumscription as a preliminary step to redefining *Gnidia*. Their sampling was, however, too sparse to adequately analyse the complex relationships of the remaining species of *Gnidia* and facilitate an informed decision on re-circumscribing a monophyletic *Gnidia*.

A more recent molecular phylogenetic analysis of an expanded sampling of 4-merous taxa with involucre inflorescences consistent with the revised circumscription of *Lasiosiphon* sensu Beaumont & al. (2009) was carried out by Olaniyan & al. (2024) and convincingly supported the revised circumscription of *Lasiosiphon* that had been proposed. *Lasiosiphon* is now well supported as a distinct genus comprising some 80 species from southern and tropical Africa, Arabia, southwest India and Sri Lanka. In its current circumscription, i.e., excluding *Lasiosiphon*, the genus *Gnidia* includes some 70 species that are almost entirely southern African in distribution, with a single species extending north into tropical Africa and a single anomalous species endemic in Madagascar.

In this study, we further explored relationships and generic circumscriptions within the “*Gnidia* group” using plastid (*matK*, *rbcL*, *rps16*, *trnL-F*) and nuclear (ITS) regions, based on an analysis of 169 species representing 27 genera in subfamily Thymelaeoideae and 34 genera in Thymelaeaceae. Our aim was to test the extent of polyphyly remaining in *Gnidia* (excluding *Lasiosiphon*) by broadening the sampling to include 25 additional southern African species selected to reflect the morphological diversity currently recognized in the genus.

The recent molecular classification of the family by Colli-Silva & al. (2025) has refined the higher-level relationships within Thymelaeaceae but the generic treatment by Herber (2003) represents the most comprehensive morphological synthesis of Thymelaeaceae in providing detailed generic circumscriptions and diagnostic characters at the generic level, and we have accordingly followed it in this article.

■ MATERIALS AND METHODS

Taxon sampling, outgroups and loci selection. — The selection of gene regions (ITS, *matK*, *rbcL*, *rps16*, *trnL-F*) used in this study was based on previous studies on Thymelaeaceae (Van der Bank & al., 2002; Beaumont & al., 2009; Motsi & al., 2010; Olaniyan & al., 2024). A total of 273 sequences for 86 taxa that were not included in the previous studies were generated in the present study, including 25 newly sampled species of *Gnidia*. These sequences were

incorporated into the pre-existing datasets. In total, 169 species representing 34 genera of Thymelaeaceae, including all genera of the “*Gnidia* group” sensu Herber (2003) were analysed. Among these were 53 *Gnidia* species from southern Africa, representing all the segregate genera historically recognized in the genus and 76% of the species. Selection of species was guided by published taxonomic treatments of the southern African flora to ensure balanced representation across the morphological spectrum. The genus *Lasiosiphon* has now been firmly established as phylogenetically outside of the rest of *Gnidia* (Olaniyan & al. (2024) and its status and circumscription are no longer an issue.

Dialyceras coriaceum (R.Cap.) J.-F.Leroy and *Rhopalocarpus* sp. from the family Sphaerosepalaceae were selected as outgroups because they were used in previous analyses and are closely related to Thymelaeaceae (Fay & al., 1998). Voucher specimens and GenBank accession numbers are listed in Appendix 1.

DNA extraction, amplification, and sequencing. —

DNA was extracted from herbarium, fresh, or silica-dried material using the 10× cetyltrimethylammonium bromide (CTAB) method of Doyle & Doyle (1987) with the addition of 2% polyvinylpyrrolidone (PVP) to prevent the interaction of polyphenolic compounds with the DNA samples. Polymerase chain reaction (PCR) amplification and sequencing were performed with parameters and amplification primers optimized for each locus based on previous studies: *rbcL* and *trnL-F* regions as in Van der Bank & al. (2002); ITS as in Beaumont & al. (2009); *matK* and *rps16* regions as in Motsi & al. (2010). Geneious v.8.1.9 (<https://www.geneious.com>) was used for the editing and assembly of complementary strands. The sequences were aligned using multiple sequence comparison by log-expectation (MUSCLE v.3.8.31; Edgar, 2004) in the Geneious suite and visually checked for any alignment errors. Sequence alignments are available as suppl. Appendices S1–S3.

Most of the taxa used in this study were obtained from herbarium specimens. Consequently, amplification of all targeted gene regions was not successful for every taxon, likely due to the degraded nature of DNA commonly associated with herbarium material.

Phylogenetic analyses. — Individual datasets, combined plastid datasets, and combined ITS and plastid datasets were analysed using the maximum parsimony (MP) algorithm of PAUP* v.4.0a168 (Swofford, 2003). Tree searches were conducted using a heuristic search with 1000 random sequence additions and 10 trees held at each step, using tree bisection-reconnection (TBR) branch swapping with the MULTrees option enabled. Delayed transformation character optimization (DELTRAN) was used for calculating branch lengths. Branch support was estimated using bootstrap analysis (Felsenstein, 1985) implemented in PAUP* with 1000 replicates, employing TBR branch swapping, with 10 trees held at each step and random sequence addition. Only values of 50% and above are reported. The following scale was used to evaluate bootstrap support (MPB): 50%–74%, weak;

75%–84%, moderate; 85%–100%, strong. The congruence of the individual datasets was assessed by comparing bootstrap percentages. The trees were considered incongruent only when they exhibited “hard” (i.e., with strong bootstrap support) rather than “soft” (i.e., with weak to moderate bootstrap support) incongruence (Seelanan & al., 1997; Wiens, 1998).

Bayesian inference (BI) analyses were carried out on the combined ITS and plastid datasets using MrBayes on XSEDE v.3.2.7 (Ronquist & al., 2012) on the CIPRES Science Gateway (Miller & al., 2010). Before the Bayesian analysis, the following best-fit model of evolution was determined for each matrix: ITS (TIM1+I+Γ), *matK* (TVM+Γ), *rbcL* (TVM+I+Γ), *rps16* (TVM+Γ), and *trnL-F* (TPM1uf+Γ). This was done with jModelTest 2.1.7 v.20141120 (Darriba & al., 2012), which uses log-likelihood scores to estimate the model of DNA evolution that best suits a specific dataset. Four parallel Markov chain Monte Carlo (MCMC) estimations were run for 10,000,000 generations, with trees sampled every 1000 generations. The stationarity was checked using tracer v.1.7 (Rambaut & al., 2018), and all ESS (effective sample size) values were found to be above 200, indicating that the number of generations was sufficient. Suboptimal trees were discarded as the “burn-in” phase. The posterior probability (PP) values were evaluated using the following scale: below 0.95, weak; 0.95–1.0, strong.

Maximum likelihood (ML) analyses were performed on the combined ITS and plastid datasets using RAxML-HPC2 on XSEDE (Stamatakis, 2014) on the CIPRES Science Gateway (Miller & al., 2010). A single consensus tree was generated from 1000 nonparametric bootstrap replicates. Node support values (MLB) of 50%–74% were regarded as weak; 75%–84% as moderate; and 85%–100%, as strong.

A topological constraint analysis was conducted in PAUP* (Swofford, 2003) using the constrained monophyly option. The genus *Lachnaea* was constrained to monophyly to test whether topologically constrained trees, including the three species placed outside of the main clade of *Lachnaea* (*L. alpina* Meisn., *L. filamentosa* Meisn., *L. pomposa* Beyers), differed significantly from the trees that did not include them in the genus. A Templeton-Wilcoxon test (Templeton, 1983; Swofford, 2003) was run to test for a significant difference between the two trees produced under topological constrained and unconstrained parameters.

Taxonomic treatment. — The taxonomic treatment focused solely on the members of the “Gnidia group” sensu Herber (2003). For the species of *Gnidia* we followed Wright (1915) for southern Africa, Peterson (1978) for tropical Africa, and Rogers (2009) as well as Olaniyan & al. (2024) for Madagascar. The remaining generic treatments are based largely on Herber (2003) with additional references cited for each genus.

■ RESULTS

Sequence analyses. — A summary of statistics for all datasets is presented in suppl. Table S1. Among the plastid

regions, *trnL-F* had a higher number (621; 44%) of variable sites than *matK* (296; 38%), *rbcL* (312; 23%) and *rps16* (359; 38%). The number of parsimony-informative characters was higher for *matK* (185; 24%) than for *rbcL* (217; 16%), *rps16* (214; 22%) and *trnL-F* (331; 23%). The ITS region had significantly more variable sites (447; 62%) and a higher number of parsimony-informative sites (385; 53%) than the plastid regions. It also showed more site changes than the plastid regions (5.7 changes per variable site).

Topologies. — A comparison of the clades in the trees from the ITS analysis with those from the combined plastid regions (suppl. Fig. S1) on a node-by-node basis revealed no strongly supported incongruences. Both datasets were therefore combined, as in previous studies (Van der Bank & al., 2002; Beaumont & al., 2009). The BI, ML, and MP analyses of the concatenated dataset produced similar topologies and hence results and combined support values are displayed on the BI phylogenetic tree (Fig. 3).

Thymelaeaceae were strongly supported as monophyletic (PP = 1.00, MLB = 100, MPB = 100). The subfamily Octolepidoideae (= Gonystyloideae) (clade N; Figs. 3C, 4) was strongly supported as monophyletic in all the analyses (PP = 0.98, MLB = 89, MPB = 86), with *Octolepis* placed as sister to the remaining genera in the subfamily. This convincingly resolves the previously uncertain taxonomic placement of *Octolepis*. Subfamily Octolepidoideae was resolved as sister to Thymelaeoideae. The position of the tribe Synandrodaphneae (clade O; Figs. 3C, 4) was unresolved in the analyses. With the exclusion of the tribe Synandrodaphneae (clade O; Figs. 3C, 4), the monophyly of subfamily Thymelaeoideae was strongly supported (PP = 1.00, MLB = 99, MPB = 99). Within the Thymelaeoideae, the two remaining tribes (Aquilarieae, Daphneae) were recovered as monophyletic and the monophyly of Aquilarieae (clade M; PP = 1.00, MLB = 100, MPB = 100; Figs. 3C, 4) and Daphneae (clades A–L; PP = 1.00, MLB = 100, MPB = 98; Figs. 3C, 4) combined was recovered with strong support (PP = 1.00, MLB = 99, MPB = 99; Figs. 3C, 4).

Within the tribe Daphneae, the “Linostoma group” sensu Herber (2003) (clade F and clade L; Fig. 4), the “Daphne group” sensu Herber (2003) (clade G and clade J; Fig. 4), the “Phaleria group” sensu Herber (2003) (clade H and clade K; Fig. 4) and the “Gnidia group” sensu Herber (2003) (clades A–I) were all evidently polyphyletic. This was especially marked in the “Gnidia group”, in which *Dirca* and *Ovidia* (clade G; Fig. 3B) from the “Daphne group”, *Stephanodaphne* (clade F; Fig. 3B) from the “Linostoma group”, and *Peddlea* (clade H; Fig. 3B) from the “Phaleria group” were all embedded within it.

Within the “Gnidia group”, the genera *Passerina* (clade B; PP = 1.00, MLB = 100, MPB = 100; Fig. 3A), *Struthiola* (clade D1; PP = 1.00, MLB = 100, MPB = 100; Fig. 3A), *Pimelea* (clade E1; PP = 1.00, MLB = 100, MPB = 100; Fig. 3B) and *Lasiosiphon* (clade I; PP = 1.00, MLB = 100, MPB = 100; Fig. 3C) were all strongly supported as monophyletic in all three analyses, and *Englerodaphne* (clade E4, Fig. 3B) was

retrieved as monophyletic with moderate MP support and strong BI and ML support (PP = 1.00, MLB = 98, MPB = 81).

Gnidia was evidently polyphyletic and dispersed among four clades (A, C, D, E) within the “*Gnidia* group”. In clade A (Fig. 3A), four species of *Gnidia* (subclade A2) were nested in *Lachnaea*, rendering *Lachnaea* paraphyletic. This relationship was weakly supported in the BI and MP analyses but strongly supported in the ML analysis (PP = 0.93, MLB = 88, MPB = 63). In clade C (Fig. 3A), 24 species of *Gnidia* (subclade C2) were retrieved as a subclade sister to *Drapetes* + *Kelleria* with strong support (PP = 1.00, MLB = 94, MPB = 96). In clade D (Fig. 3B), five species of *Gnidia* (subclades D2 and D3) were grouped with maximum support (PP = 1.00, MLB = 100, MPB = 100) in a subclade with *Struthiola*. Finally, in clade E (Fig. 3B), 20 species of

Gnidia (subclades E2, E3 and E5) were retrieved with maximum support (PP = 1.00, MLB = 100, MPB = 100) in a subclade with *Pimelea* and *Englerodaphne*.

Constraint analysis. — Constraining *Lachnaea* to monophyly resulted in a topology in which the three recovered outlier species (*L. alpina*, *L. filamentosa*, *L. pomposa*) were placed within the main *Lachnaea* clade. The constrained topology differed from the unconstrained optimal tree by two additional steps (tree length = 6089 vs. 6091 steps). Statistical comparison of the two topologies using the Templeton-Wilcoxon test indicated no significant difference (Templeton test: $p = 0.77$; Winning-sites test: $p = 0.88$) (suppl. Table S2). Therefore, enforcing monophyly of *Lachnaea* does not result in a statistically significant decrease in tree optimality under parsimony.

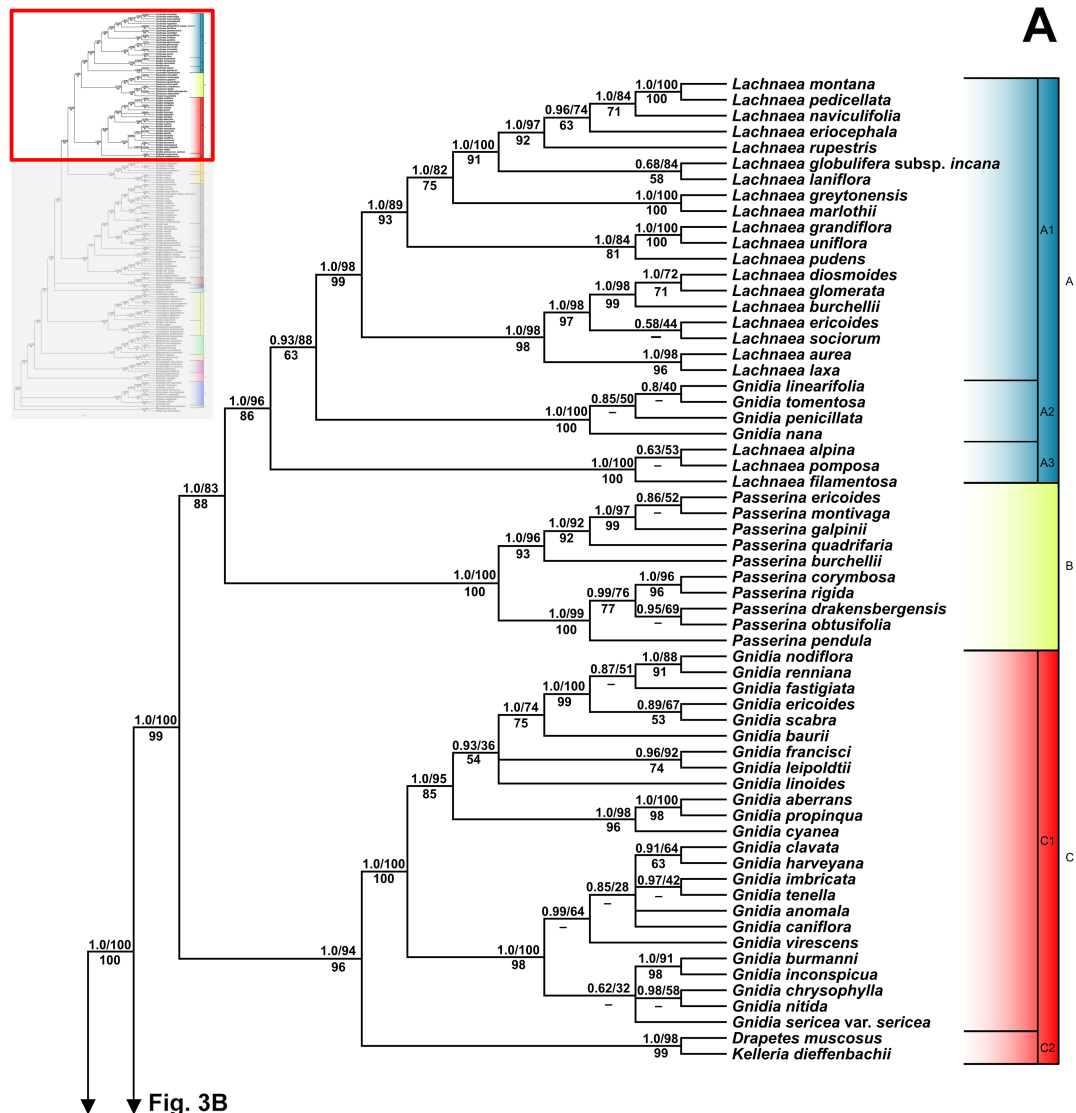


Fig. 3. Cladogram summarizing relationships of major taxonomic groupings within Thymelaeaceae. Bayesian posterior probabilities (PP) and maximum likelihood bootstrap (MLB) values are indicated above the branches, and maximum parsimony bootstrap (MPB) support values are indicated below the branches. The classification system, shown in colour, is that of Herber (2003), with the taxonomic equivalents adopted by Colli-Silva & al. (2025) as follows: Tribe Aquilarieae = Subfamily Aquilarioideae; Subfamily Octolepidoideae = *Octolepis* + Subfamily Gonystyloideae.

DISCUSSION

Relationships within subfamily Thymelaeoideae. —

Herber (2003) subdivided subfamily Thymelaeoideae into the three tribes Aquilarieae, Daphneae, and Synandrodaphneae, corresponding closely to the subfamilies Aquilarioideae, Thymelaeoideae and Synandrodaphnoideae of Domke (1934). The relationship recovered in our analyses is broadly consistent with recent phylogenomic analyses of Malvales based on extensive nuclear datasets (Colli-Silva & al., 2025). In that study, the traditional subfamilial framework of the family, which includes Aquilarioideae, Octolepidoideae + Gonystyloideae and Thymelaeoideae was largely recovered, although the position of *Octolepis* was unstable, and a fourth subfamily Tepuianthoideae was recognized to accommodate the morphologically distinctive genus *Tepuianthus*. Our analysis convincingly places *Octolepis* as sister to the other genera of Octolepidoideae, resolving previous uncertainty about its phylogenetic placement in the family (Colli-Silva & al., 2025). The name Octolepidoideae Gilg (Gilg, 1921) has nomenclatural priority over Gonystyloideae Domke (Domke, 1934).

Our analyses retrieved Aquilarieae (Clade M) as sister to Daphneae in Thymelaeoideae with maximum support (PP = 1.00, MLB = 100, MPB = 100; Fig. 3C). Herber (2003) identified indehiscent fruits as a probable synapomorphy for Daphneae but Aquilarieae were only diagnosable by a combination of characters, viz. long hypanthium, 2-locular ovary, and dehiscent fruits. We could not fully resolve the relationships of *Synandrodaphneae* (clade O), which were retrieved in a trichotomy with Daphneae + Aquilarieae and subfamily Gonystyloideae. *Synandrodaphne* was not included in the phylogenomic analyses of Colli-Silva & al. (2025) but they placed it in subfamily Thymelaeoideae because some classifications (e.g., Herber, 2003; Stevens, 2024) already included Synandrodaphnoideae within Thymelaeoideae. Tribe Synandrodaphneae sensu Herber (2003) is distinct in Thymelaeaceae in its free sepals and well-developed staminal tube, i.e., the filaments are fused to form a conspicuous lobed tube that encloses the ovary, whereas other taxa have a well-developed hypanthium tube with the stamens inserted individually on the upper part of the tube (Heinig, 1951; Herber, 2003). This distinctive morphology, together with the unstable phylogenetic placement recovered here and in

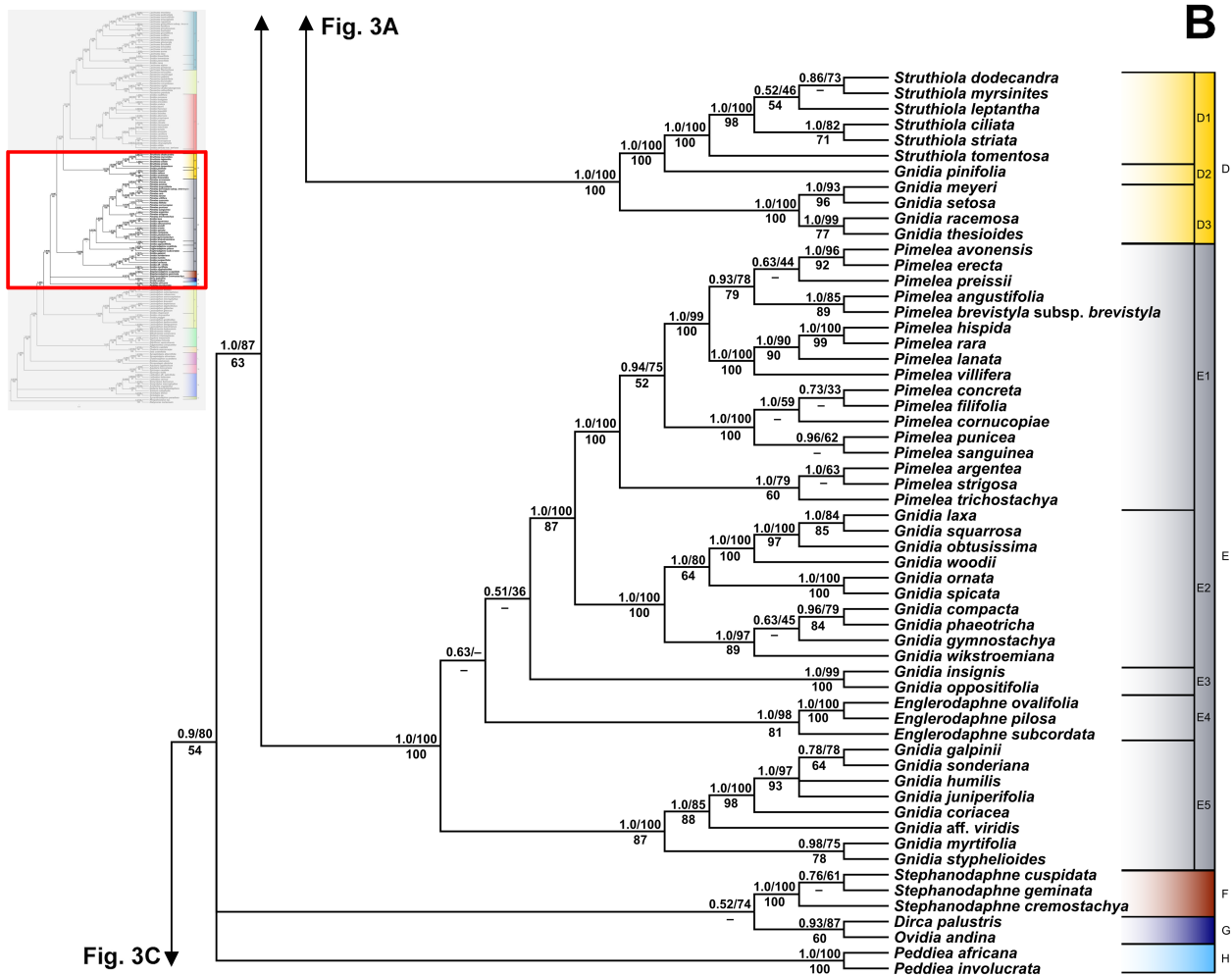


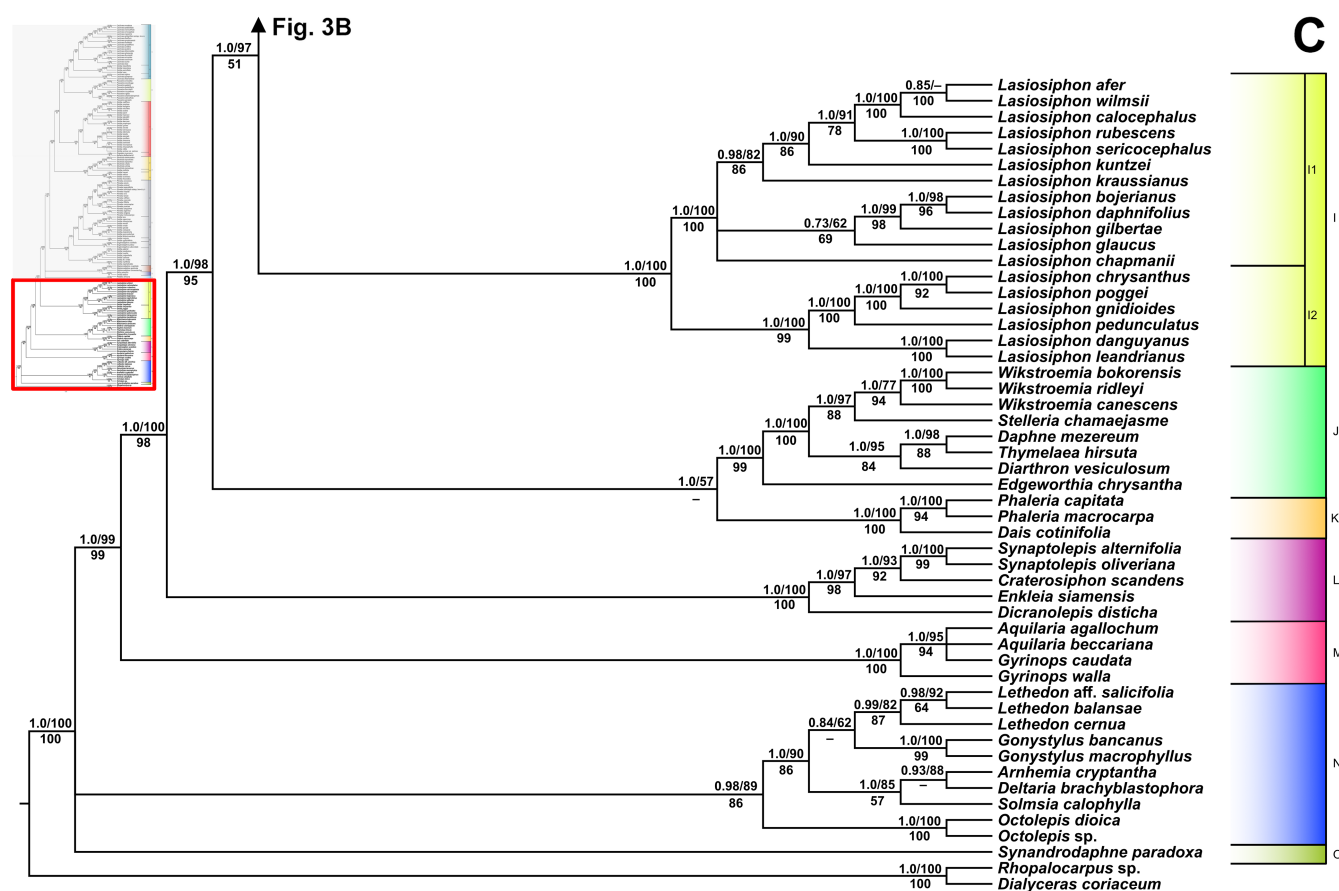
Fig. 3. Continued.

previous studies, suggests that Synandrodaphneae may be more appropriately treated as a separate subfamily when additional data become available.

Relationships within the tribe Daphneae. — Herber (2003) recognized four informal generic groupings in Daphneae, viz. the “Linostoma group”, “Phaleria group”, “Daphne group” and “Gnidia group”, with the admission that these groups have no obvious synapomorphies. In our analyses the “Linostoma group” was retrieved as monophyletic (clade L; PP = 1.00, MPB = 100, MLB = 100; Fig. 3C) with the exclusion of *Stephanodaphne*, which Herber (2003) provisionally appended to the “Linostoma group” but which our analysis found to be embedded in the “Gnidia group” with no resolution. The “Linostoma group” was characterized anatomically by the frequent presence of interxylary phloem, which is never present in the others. The relationships of the Madagascan *Stephanodaphne* were unclear to both Domke (1934), who considered it as having an affinity with the small Asian genus *Edgeworthia* Meisn. (“Daphne group” sensu Herber, 2003) and to Herber (2003), who considered that its affinities lay with the genera in the “Linostoma group”. Our analyses showed a weakly supported relationship between *Stephanodaphne* and the two genera *Dirca* and *Ovidia* in the “Daphne group”.

The “Daphne group” comprises two geographically separated clades (clades G and J). Clade G (*Dirca palustris* and *Ovidia andina*) is represented by American genera and is embedded in the “Gnidia group” although its position within the group is not clear. It can be distinguished morphologically from clade J (Eurasian genera) by having petaloid scales and long filaments versus the lack of petaloid scales and sessile or subsessile anthers among the Eurasian genera. This result supports the supposition by Herber (2003) that these two geographically disjunct groups might represent two natural groups.

The “Phaleria group” comprises two well-supported clades (clades H and K) whose relationships within Thymelaeoideae are not fully resolved. Clade H (the African and Madagascan *Peddiea*) was embedded in the “Gnidia group” without clarity on its exact relationships within the group. In contrast, clade K (the Indo-Malesian and Australasian *Phaleria*) is placed with maximum support (PP = 1.00, MLB = 100, MPB = 100) outside of the “Gnidia group as sister to *Dais cotinifolia* from southern and subtropical Africa. The “Phaleria group” is distinctive in the tribe Daphneae in its 2-locular ovary, all of the other genera having a 1-locular ovary. Our analysis suggests the possibility that the 2-locular condition is independently derived in these two genera.

**Fig. 3. Continued.**

In summary, our results demonstrate that the informal groupings proposed by Herber (2003) comprise a mixture of monophyletic, paraphyletic, and polyphyletic assemblages. These findings highlight the need for a revised, phylogenetically informed classification of Daphneae, based on expanded taxon sampling and additional molecular data, particularly

from nuclear genomes. The recent phylogenomic studies of Colli-Silva & al. (2025) provides an important framework for subfamilial relationships within Thymelaeaceae but their sampling was not designed to resolve relationships at the tribal level and did not include sufficient representation of Daphneae to address the questions examined here.

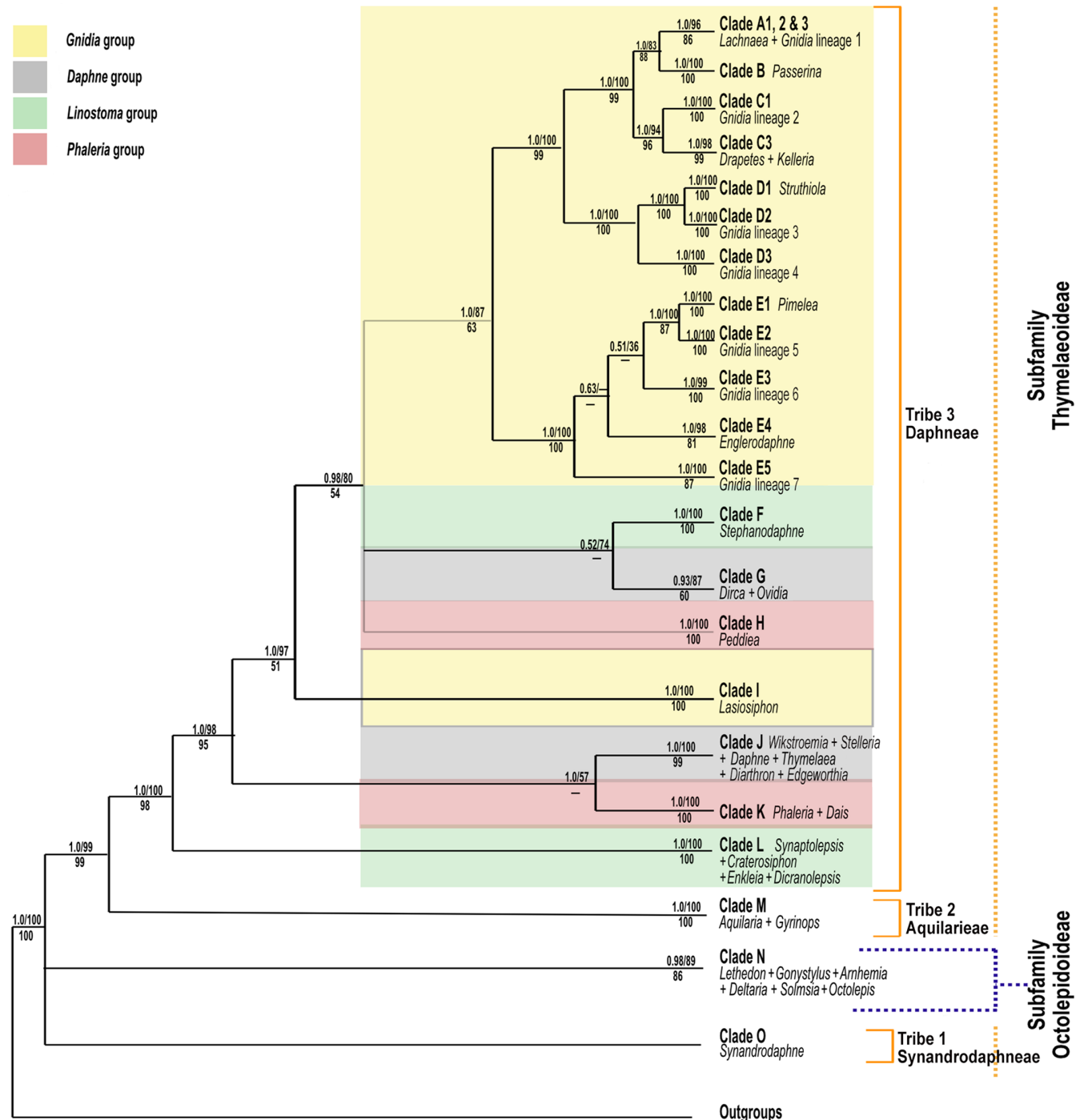


Fig. 4. Cladogram summarizing relationships of major taxonomic groupings within Thymelaeaceae. Bayesian posterior probabilities (PP) and maximum likelihood bootstrap (MLB) values are indicated above the branches, and maximum parsimony bootstrap (MPB) support values are indicated below the branches. The classification system, shown in colour, is that of Herber (2003), with the taxonomic equivalents adopted by Colli-Silva & al. (2025) as follows: Tribe Aquilarieae = Subfamily Aquilarioideae; Subfamily Octolepidoideae = *Octolepis* + Subfamily Gonystyloideae.

Relationships within the “Gnidia group”. — Within the “Gnidia group”, the genera *Passerina* (± 20 spp.), *Struthiola* (± 30 spp.), *Pimelea* (± 110 spp.), *Englerodaphne* (3 spp.), and *Lasiosiphon* (± 80 spp.) were all strongly supported as monophyletic whereas *Gnidia* was confirmed to be polyphyletic, corresponding to the findings of Van der Bank & al. (2002) and Beaumont & al. (2009). Our extended analyses retrieved seven monophyletic lineages in *Gnidia* nested in four supported clades within the “Gnidia group” as follows:

1. “Cape Clade” (clade A and B). — In clade A (*Lachnaea-Craspedostoma* clade), the four species *Gnidia penicillata* Licht. ex Meisn., *G. tomentosa* L., *G. nana* (L.f.) Wikstr. and *G. linearifolia* (Wikstr.) B.Peterson, previously referred to as *Craspedostoma* Domke (Domke, 1934) comprise a clade embedded within the genus *Lachnaea*, thereby rendering *Lachnaea* paraphyletic. However, support for expanding *Lachnaea* to include this lineage is weak in the BI and MP analyses (PP = 0.93 MPB = 63). With such low supports, it remains possible that this topology does not reflect the true relationships among the species and that *Lachnaea* may in fact be monophyletic. To evaluate this alternative hypothesis, a constraint analysis was conducted. The Templeton test, a statistical method used in parsimony analysis to compare competing tree topologies, was applied to test the hypothesis that *Lachnaea* is monophyletic. Constraining all species of *Lachnaea* to monophyly resulted in trees that were only two steps longer than the unconstrained trees, and the difference between the topologies was not statistically significant. The hypothesis that *Lachnaea* is monophyletic cannot be rejected. The current data therefore do not provide strong statistical evidence that *Lachnaea* must be expanded to include the Cape *Gnidia* lineage. Additionally, we are unable to identify any morphological support for including these four taxa in *Lachnaea*, and expanding the circumscription of that genus to include them would render *Lachnaea* undiagnosable. *Lachnaea* is morphologically unique in the “Gnidia group” in having the petaloid scales inserted below the stamens whereas all other genera have the scales inserted above the stamens (Beyers, 2001). Pending additional evidence, it is therefore preferable to retain these four species outside *Lachnaea*, as their inclusion would obscure the clear morphological circumscription of that genus without strong phylogenetic justification.

Passerina (clade B) is strongly supported as monophyletic and is recovered as sister to the *Lachnaea-Craspedostoma* clade (clade A) with strong support in the BI and MP analyses and moderate support in the ML analysis (PP = 1.0, MLB = 83, MPB = 88; Fig. 3A). It is readily distinguishable in the “Gnidia group” by its well-exserted anthers with ex-torse, explosive dehiscence, and a mop-like stigma. These characters are evidently associated with the unique anemophilous pollination system that is characteristic of the genus (Bredenkamp & Van Wyk, 2003). In addition, the genus lacks an articulation of the hypanthium, fragmenting at or above the ovary (Bredenkamp & Van Wyk, 2003), whereas all other genera in the group have a clear articulation above the ovary (Herber, 2003). The strong molecular support for the

monophyly of *Passerina*, together with its distinctive floral morphology and pollination biology, supports the continued recognition of the genus as a well-defined lineage within the “Gnidia group”.

2. “Circumaustral Clade” (clade C). — A maximally supported clade of 24 species of *Gnidia* (subclade C1) is strongly supported (PP = 1.00, MLB = 94, MPB = 96) as sister to a clade comprising the New World *Drapetes muscosus* Lam. and the Australasian *Kelleria dieffenbachii* (Hook.) Endl. (subclade C2; PP = 1.00, MLB = 98, MPB = 99; Fig. 3A). *Drapetes* is a monotypic genus distinguished among the “Gnidia group” by its lateral style and is distinct from *Kelleria* in lacking petaloid scales and in its articulated hypanthium. The flowers of both genera are 4-merous and resemble *Struthiola* in being haplostemonous with four stamens arranged in a single whorl alternating with the sepals (alternisepalous). Three species of *Gnidia* are also recorded as having only a single whorl of stamens, two of which are included in this clade (*G. aberrans* C.H. Wright, *G. propinqua* (Hilliard) B.Peterson) and the third (*G. singularis* Hilliard) not included in our analysis. The stamens in all three of these *Gnidia* species are positioned opposite the sepals (antesepalous) in a single whorl, thus evidently representing the upper whorl of stamens. This is compelling morphological support for an independent reduction in stamen number in these species of *Gnidia* and in *Struthiola* as well as *Drapetes-Kelleria*. Although this clade of *Gnidia* species (subclade C1) is maximally supported in all three analyses, it comprises a morphologically diverse group of species that vary in the number of scales and stamens. However, the strong molecular support nevertheless indicates that these species represent a distinct evolutionary lineage within the “Gnidia group”.

3. “Core Gnidia Clade” (clade D). — A small clade of four species of *Gnidia* (subclade D3) plus the generitype *G. pinifolia* L. (subclade D2) are placed successively as a clade to a monophyletic *Struthiola* (subclade D1) with maximum support (PP = 1.00, MLB = 100, MPB = 100; Fig. 3B). *Struthiola* shares haplostemonous flowers with a single whorl of alternisepalous stamens with the monotypic South American *Drapetes* and the Malesian-Australasian *Kelleria* but the racemose inflorescence, hairy scales and lateral style of the African *Struthiola* immediately distinguishes it from these two genera. These three-character states have also traditionally served to separate *Struthiola* from *Gnidia*, which typically has capitate inflorescences, and diplostemonous flowers with eight stamens and glabrous scales. All of the *Gnidia* species in the *Struthiola* clade also have hairy petaloid scales, providing morphological support for this association. They differ from *Struthiola*, however, in having eight diplostemonous anthers. This clade is entirely African and occurs mainly in temperate southern Africa, suggesting a regional radiation of closely related lineages within the “Gnidia group”. The position of the *Gnidia* species as successive sisters to *Struthiola* further indicates a close evolutionary relationship between these taxa, although clear morphological synapomorphies uniting them remain limited.

4. “Amphiaustral Clade” (clade E). — Twenty species of *Gnidia* in three strongly supported lineages (subclades E2, E3, and E5) were retrieved in a clade that also includes the large Australasian-Malesian genus *Pimelea* (clade E1), which is strongly supported as monophyletic, and the small African *Englerodaphne* (clade E4), which is strongly supported as monophyletic in the BI and ML analyses but only moderately supported in the MP analysis. The relationships among the three *Gnidia* lineages and these two genera are largely unresolved, but this topology is consistent with the earlier recognition of the genus *Englerodaphne* as separate from *Gnidia* (Olaniyan & al., 2020). This small genus of three species (*E. pilosa* Burt Davy, *E. ovalifolia* (Meisn.) E. Phillips, *E. subcordata* (Meisn.) Engl.) is readily distinguished from *Gnidia* by its arborescent habit, broad and thin-textured leaves, and flowers with four, deeply bifurcate, membranous scales. The flowers of *Pimelea* lack petaloid scales, a condition also found in some species of *Gnidia*, but the genus is unique in the “*Gnidia* group” in having only two stamens.

The first of the three *Gnidia* lineages (subclade E2) is strongly supported as sister to *Pimelea* (PP = 1.00, MLB = 100, MPB = 87) and comprises a florally heterogeneous clade that includes several southern African species previously placed in *Arthrosolen* because of their lack of petaloid scales, viz. *G. laxa* (L.f.) Gilg, *G. ornata* (Meisn.) Gilg, *G. spicata* (L.f.) Gilg, *G. compacta* (C.H. Wright) J.H. Ross, *G. phaeotricha* Gilg and *G. gymnostachya* (C.A. Mey.) Gilg, as well as other species of *Gnidia* with eight (*G. squarrosa* (L.) Druce, *G. obtusissima* Meisn., *G. woodii* C.H. Wright) and four (*G. wikstroemiana* Meisn.) petaloid scales. The second lineage of *Gnidia* (subclade E3) includes two species that are morphologically similar in having four anther-like scales (*G. oppositifolia* L., *G. insignis* Compton). The third lineage of *Gnidia* (subclade E5) is also morphologically homogeneous and comprises the species that were segregated from the rest of the genus under the manuscript name “*Epichroxantha*” (Meisner, 1857), characterized by small, canary yellow flowers with a distinctive funnel-shaped hypanthium and four large, membranous petaloid scales.

Taken together, these results indicate that several morphologically distinct lineages of *Gnidia* are more closely related to *Pimelea* than to *Gnidia* sensu stricto, further highlighting the polyphyletic nature of the traditional circumscription of *Gnidia*.

■ TAXONOMIC IMPLICATIONS

There is increasing consensus among modern taxonomists on the importance of aligning classifications with phylogenies by recognizing only reciprocally monophyletic groups, at least at generic and higher taxonomic levels (e.g., Bergh & al., 2018; Klak & al., 2024). Significant changes in generic circumscriptions are therefore required to render *Gnidia* monophyletic. Applying the principle of monophyly in this case is not straightforward and several options

have previously been proposed to resolve the polyphyly of *Gnidia* (Beaumont & al., 2009; Foster & al., 2016). In this context, Backlund & Bremer (1998) outlined some useful secondary principles—maximizing stability; maximizing phylogenetic information; maximizing support for monophyly; maximizing ease of identification to the primary principle of monophyly, to guide taxonomic decisions when multiple solutions are possible.

We identify three available options for achieving a monophyletic classification of *Gnidia* and evaluate them in light of these secondary principles and their potential conflicts.

Option 1. — As proposed by Beaumont & al. (2009), this option emphasizes maximum taxonomic stability by adopting a very broad circumscription of *Gnidia* to include clades A through E (Fig. 5). In this option, *Drapetes*, *Englerodaphne*, *Kelleria*, *Lachnaea*, *Passerina*, *Pimelea*, and *Struthiola* would all be subsumed within *Gnidia*, with the possible recognition of three hypothetical subgenera: “subg. *Gnidia*” (clades A, B, C, and D), “subg. *Pimelea*” (clades E1, E2, E3, E4), and “subg. *Epichroxantha*” (clade E5).

There are no known shared derived characters supporting this large genus or most of the proposed subgenera, apart from the small “subg. *Epichroxantha*” (Olaniyan, 2021). Several monophyletic and morphologically diagnosable segregates could nevertheless be recognized as sections within the remaining two subgenera, some corresponding to currently recognized genera and others to distinct lineages of *Gnidia*.

Within “subg. *Gnidia*”, “sect. *Lachnaea*” (clade A) can be identified by the presence of white punctulae on one or both sides of the leaves (Beyers, 2001); “sect. *Passerina*” (clade B) by the absence of scales, exserted stamens, and extrorse anthers (Bredenkamp & Van Wyk, 2003); “sect. *Basutica*” (subclade C1) by four or eight scales and a hypanthium that is densely white-silky or woolly; “sect. *Drapetes*” (subclade C2) by four alternisepalous stamens (Heads, 1990); and “sect. *Gnidia*” (clade D) by having four, eight, or twelve scales surrounded by a tuft of hairs.

Within “subg. *Pimelea*”, “sect. *Pimelea*” (subclade E1) can be recognized by the absence of scales and the reduction of stamens to two (Rye & Heads, 1990); “sect. *Thymelina*” (subclade E2) by the general absence of scales or, if four or eight scales are present, by the presence of a prominent midrib beneath the leaves; “sect. *Gnidiopsis*” (subclade E3) by four thickly fleshy anthers with inrolled margins; and “sect. *Englerodaphne*” (subclade E4) by the arborescent habit, mesophyllous leaves, and four deeply bifid (thus apparently eight) membranous scales. “Subgenus *Epichroxantha*” (subclade E5) can be recognized by the bright yellow, funnel-shaped hypanthium and four membranous scales.

A significant advantage of this option is that it is maximally stable, i.e., adding taxa to the phylogenetic tree will not disrupt the generic classification. There are, however, significant disadvantages. Although there is strong support for the proposed monophyletic clade in the BI and ML analyses, there is moderately low support in the bootstrap analysis (clades A–E; PP = 1.00, MLB = 87, MPB = 63), and there is

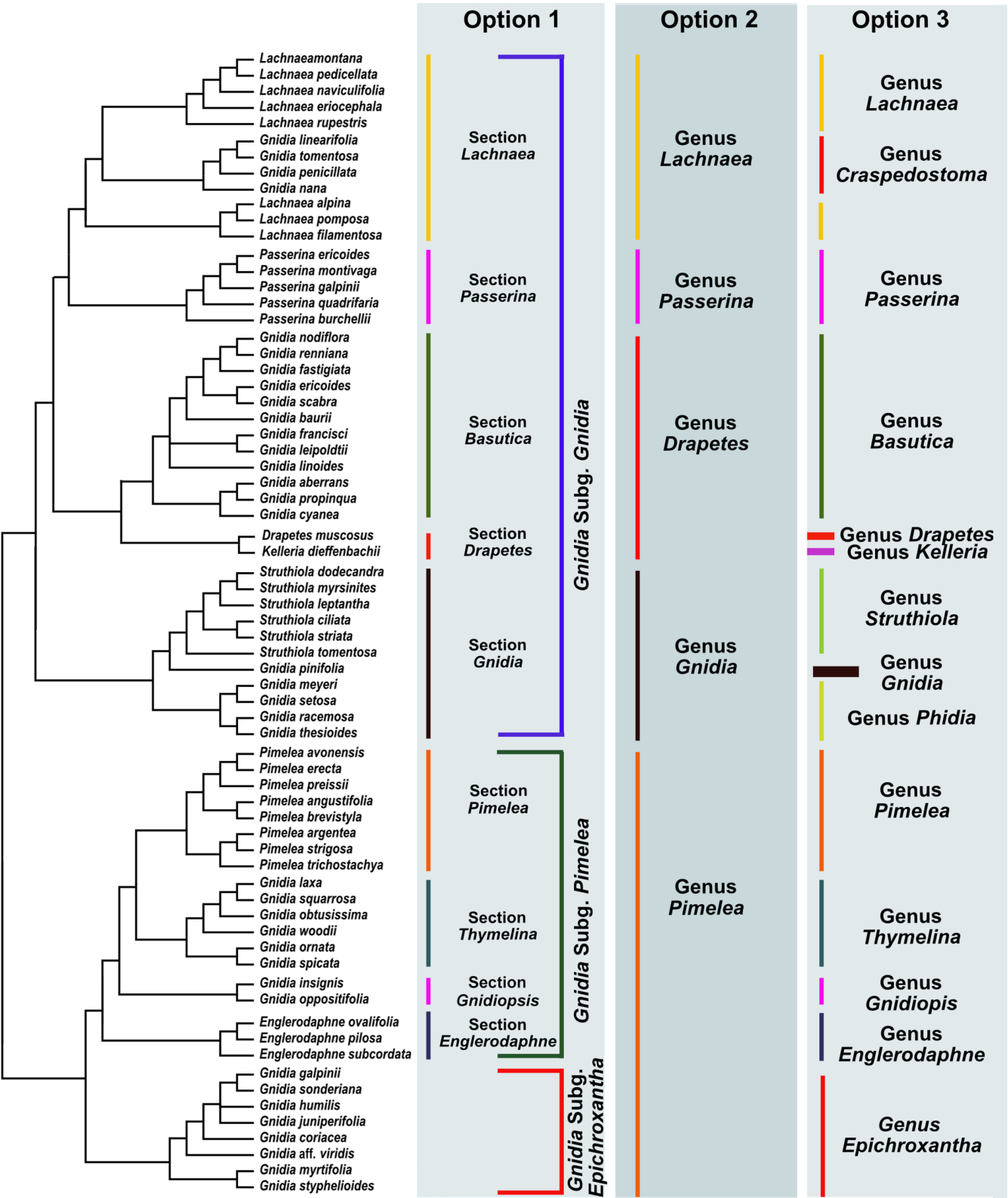


Fig. 5. Summary tree of the three options proposed for a monophyletic circumscription of *Gnidia* and allied genera. The infrageneric names shown in the figure are hypothetical, used for illustrative purposes only, and do not represent validly published names at the ranks indicated.

no synapomorphy to support the clade. Additionally, a large number of nomenclatural changes is required since this clade includes several segregate genera that have not been previously included in *Gnidia* and thus lack combinations in the genus. These include the southern African genera *Lachnaea* (± 40 spp.), *Passerina* (± 20 spp.) and *Struthiola* (± 40 spp.); as well as the large genus *Kelleria* (11 spp.) and *Pimelea* (± 110 spp.) both of which are Australasian-Malesian, and the South American *Drapetes*. All three of these genera have long been accepted and none have been previously included in *Gnidia*. Uniting them with *Gnidia* will require extensive and unprecedented name changes as well as obscuring the biogeographic distinction among the Australasian, African and South American elements.

In short, the advantage of nomenclatural stability in this option is outweighed by the taxonomic and nomenclatural disadvantages and loss of biogeographical predictivity in the resulting classification.

Option 2. — This option explores the possibility of a less extensive and radical re-circumscription of *Gnidia*, with the aim of avoiding the numerous nomenclatural changes and disruption to the large genus *Pimelea*, by incorporating some or all of the *Gnidia* lineages into existing sister genera (Fig. 5). Although there is strong molecular support for the inclusion in *Lachnaea* of the four *Gnidia* species comprising subclade A2 this association has only very weak morphological support, viz., the presence of white punctulae on one or both sides of the leaves, and the genus *Lachnaea* can no longer be recognized by the unique synapomorphy of scales inserted below the anthers.

There is similarly strong molecular support for including subclade C1 together with genus *Kelleria* in *Drapetes* but again there is no evident synapomorphy to support this association. There is also support for combining *Struthiola* with subclades D2 and D3. This clade includes the type of *Gnidia* (*G. pinifolia*), which has nomenclatural priority over *Struthiola*. This association is well supported in all the phylogenetic analyses, and the clade can also be recognized morphologically by hairy petaloid scales, but the resulting taxonomic change would require transferring all species of *Struthiola* to *Gnidia*, thereby substantially altering the circumscription of both genera.

The association of subclades E2, E3 and E5, together with *Englerodaphne* (subclade E4), with *Pimelea* is also strongly supported in all the analyses but lacking in any morphological synapomorphy to support the association. Furthermore, the biogeographical distinction between *Pimelea* and the other members of the group will be lost.

In summary, option 2 is an unhappy compromise that lacks the primary advantages of either option 1 (maximum stability) or option 3 below (maximum information and historical continuity) while still sharing their principal disadvantages, particularly substantial changes to the circumscription of *Gnidia*. As in option 1, this approach would also result in a significant loss of taxonomic and biogeographic predictivity.

Option 3. — The traditionally recognized genera *Drapetes*, *Kelleria*, *Lachnaea*, *Passerina*, *Pimelea*, and *Struthiola* can be retained with their current circumscriptions if the seven lineages of *Gnidia* (subclades A2, C1, D2, D3, E2, E3, and E5) are treated as separate genera (Fig. 5). We argue that the advantages offered by this option outweigh the disadvantages and that this option has previously been implemented in some form by earlier authors (Endlicher, 1847; Meisner, 1857; Bentham & Hooker, 1880; Pearson, 1910; Wright, 1915; Marloth, 1925; Burt-Davy, 1926; Phillips, 1944, 1951; Leandri, 1950; Hutchinson, 1967). The principal disadvantage of this option is some possible instability, although we consider this risk to be minimal as we are confident that our sampling is sufficiently extensive across the morphological and geographical spectrum of *Gnidia* to negate this. We have included representatives from all previously recognized segregate genera of *Gnidia*, and our sampling covers the entire morphological spectrum of the genus, with a focus on the southern African species. All of the endemic tropical African taxa previously included in *Gnidia* share the morphological characters that are diagnostic for *Lasiosiphon* and have been transferred to that genus (Olaniyan & al., 2024). Our thorough sampling of the southern African variation thus makes it highly unlikely that the addition of any additional species to the phylogenetic tree will affect the stability of the proposed classification or nomenclature.

The remaining seven lineages of *Gnidia* are strongly supported as monophyletic units in the molecular analysis. Some of the lineages have uniquely derived characters but others can only be circumscribed by a combination of characters (Table 1). Although these characters may sometimes be difficult to define, the difficulty of identifying clear generic synapomorphies is a well-known feature of the family as a whole (Peterson, 1959; Ding, 1960). Importantly, there is historical precedent for most of these taxonomic changes: the majority of these lineages in *Gnidia* have been recognized previously, either wholly or in part, by earlier authors at various taxonomic ranks, often at the generic level. Generic names are therefore available for most of the segregate groups.

This option also provides the greatest phylogenetic and taxonomic predictivity, as each segregate genus corresponds to a well-supported evolutionary lineage and can be identified by unique synapomorphies or combinations of characters. The lineages are also biogeographically coherent. Similar approaches have also been applied in other taxonomically and biogeographically complicated groups, e.g., *Acacia* L. s.l. (Ebinger & Seigler, 2005; Seigler & al., 2006; Kyalangalilwa & al., 2013; Maslin, 2015) and *Aloe* L. s.l. and their segregates (Grace & al., 2013; Manning & al., 2014).

The seven lineages of *Gnidia*. — **Lineage 1** (subclade A2): There is maximum support for the lineage comprising the four species *Gnidia linearifolia*, *G. tomentosa*, *G. penicillata* and *G. nana*. Along with *G. scabrida* Meisn., these five species are morphologically distinct in *Gnidia* in their scabrous and shining white-punctulate leaves that are ciliate when young, a densely hairy hypanthium, and petaloid scales with

a basal callus (Olaniyan & al., 2023). This lineage was previously recognized by Domke (1934) as the genus *Craspedostoma*, and Peterson (1959) later commented on the peculiarity of these species within *Gnidia*. All members of this group are endemic to fynbos shrublands in the extreme south-western part of the Core Cape Floristic Region (Manning & Goldblatt, 2012). **Lineage 2** (subclade C1): This lineage includes 24 species that are morphologically diverse but maximally supported as monophyletic. Meisner (1857) recognized these species, together with the *Gnidia* species in Lineage 1 (above), as his informally ranked “group two” of *G. sect. Gnidia* (as “*Eugnidia*”) on the basis of their densely woolly or silky hypanthium. It is not surprising, however, that Lineage 1 is retrieved as a clade separate from Lineage 2 since its members are morphologically distinct from all other *Gnidia* species (see above). Lineage 2 is morphologically diagnosable by the combination of a densely hairy, mostly white-silky hypanthium and a capitate stigma (versus the conical stigma of lineage 1). **Lineage 3** (subclade D2): This lineage comprises the single species *G. pinifolia*, the generitype. A significant autapomorphy for this species is the four densely hairy scales, which distinguishes *G. pinifolia* from all other species of *Gnidia*. In this regard, it is significant that earlier authors (Meisner, 1857; Gilg, 1894) have always placed this species in a separate monotypic group in their infrageneric groupings of *Gnidia*. **Lineage 4** (subclade D3): This lineage of four species is maximally supported and these four species (*G. meyeri* Meisn., *G. racemosa* Thunb., *G. setosa* (Thunb.) Wikstr. and *G. thesioides* Meisn.) along with *G. parvula* Wolley-Dod (not included in this analysis) can be recognized morphologically by their eight hairy scales

combined with a diplostemonous androecium (eight stamens in two series). Some of the species in this group (viz. *G. racemosa*, *G. setosa*, and *G. thesioides*) were segregated within *Gnidia* by Endlicher (1847), who recognized *Phidia* as an unranked infrageneric group, and later by Gilg (1894), who treated *Phidia* as *Gnidia* subg. *Phidia*. Meisner (1857) likewise recognized this assemblage, although not under the name *Phidia*, based on their somewhat racemose inflorescences with flowers mostly in the axils of the upper leaves. In this respect, they approach the genus *Struthiola*. **Lineage 5** (subclade E2): This maximally supported lineage of 10 species is retrieved as sister to the *Pimelea* clade. Most members in this lineage lack floral scales (viz. *G. laxa*, *G. ornata*, *G. spicata*, *G. compacta*, *G. phaeotricha*, *G. gymnostachya*, along with *G. fraterna* (N.E.Br.) E.Phillips and *G. variabilis* (C.H.Wright) E.Phillips [not included in the analysis]) but other species in the group have either eight (*G. squarrosa*, *G. obtusissima*, *G. woodii*) or four (*G. wikstroemiana*) scales. The species without scales comprise the remaining 4-merous South African species that were previously included in the genus *Arthrosolen* (now treated as a synonym of *Lasiosiphon*). The number of scales is now known to be variable within both *Lasiosiphon* and *Struthiola*. This lineage is weakly diagnosed by the frequent lack of scales and the dorsifixed anthers but the leaves of all the species in this clade have a prominent midrib beneath. In addition, the inflorescences are mostly congested spikes and only rarely capitate. **Lineage 6** (subclade E3): The two species in this strongly supported lineage, together with *G. orbiculata* C.H.Wright (not included in this analysis), all share four unique, thickly fleshy petaloid scales with inrolled margins (thus resembling anthers) and a densely

Table 1. Diagnostic features of the revised *Gnidia* lineages.

Lineages with clear morphological diagnostic characters		Lineages weakly diagnosed morphologically (primarily supported by molecular data)	
Prospective genus	Morphological diagnostic characters	Prospective genus	Combined morphological characters
<i>Craspedostoma</i>	Scabrous, shining white-punctulate leaves that are ciliate when young	<i>Basutica</i>	Weakly diagnosed by a combination of a densely hairy, mostly white-silky hypanthium and a capitate stigma
<i>Epichroxantha</i>	Four large membranous petaloid scales and a unique funnel-shaped, canary yellow hypanthium	<i>Thymelina</i>	Weakly diagnosed by a prominent midrib beneath the leaves and a tinge of maroon colour on flowers and leaves. It can also be diagnosed by the frequent lack of scales and congested spikes with the exception of <i>G. wikstroemiana</i> with four scales and eight scales in <i>G. squarrosa</i> , <i>G. obtusissima</i> , <i>G. pallida</i> and <i>G. woodii</i> , all five with terminal umbel
<i>Gnidia</i>	Acerose leaves and flowers with four fleshy scales that are densely strigose all over		
<i>Gnidiopsis</i>	Unique thickly fleshy petaloid scales with inrolled margins (thus resembling anthers) and glabrous orbicular leaves		
<i>Phidia</i>	Inflorescence elongating into a spike with flowers having eight scales surrounded with tuft of hairs		

hirsute ovary with no hypogynous disk. **Lineage 7** (subclade E5): This strongly supported lineage of eight species, as well as *G. decurrens* Meisn., *G. flanaganii* C.H.Wright., *G. parviflora* Meisn. and *G. variegata* Gand. (not included in this analysis), is readily diagnosed by four large membranous petaloid scales and a funnel-shaped, canary-yellow hypanthium that is either glabrous or puberulous. It was previously recognized with this circumscription under the manuscript name “*Epichroxantha* Eckl. & Zeyh.” (Meisner, 1857) and has also been recognized as a natural assemblage by other authors (e.g., Wright, 1915).

■ TAXONOMIC TREATMENT

The taxonomic classification described here largely follows the generic framework of the informally ranked “Gnidia group” of Herber (2003). Although our phylogenetic analyses do not fully recover this group as monophyletic, we retain Herber’s circumscription for the purposes of the present treatment. In our studies, for example, *Dais* is placed outside the group, whereas a clade consisting of *Stephanodaphne*, *Dirca*, and *Ovidia* is recovered within the group, but with unresolved relationships. These findings suggest that the traditional concept of the “Gnidia group” (sensu Herber, 2003) does not strictly correspond to a natural lineage. Despite these findings, the available evidence is insufficient to justify a broader re-circumscription of generic boundaries within the tribe Daphneae at this stage.

Our study is primarily concerned with resolving relationships within *Gnidia* and closely allied taxa and it does not include enough taxon sampling in the tribe to support a stable reclassification of the higher-level grouping. Nevertheless, it clearly demonstrates that *Gnidia* in its traditional broad circumscription is polyphyletic. To achieve a classification that reflects monophyletic lineages, we therefore recognise several well-supported clades within this polyphyletic assemblage as distinct genera. The taxonomic changes required to implement this revised classification are listed below.

Key to the genera in the “Gnidia group” (adapted from Herber, 2003)

1. Hypanthium not articulated above ovary.....2
1. Hypanthium distinctly or weakly articulated above ovary.....3
2. Stamens 4, haplostemonous, shortly exerted; anthers introrse; petaloid scales (4)8.....12. **Kelleria**
2. Stamens 8, diplostemonous, well exerted; anthers extrorse; petaloid scales absent.....15. **Passerina**
3. Stamens 1 or 2; flowers bisexual or unisexual; sepals 4; petaloid scales absent; Australasia–Malesia... 8. **Pimelea**
3. Stamens 4 to 10; flowers bisexual; sepals 4 or 5; petaloid scales usually present, rarely absent; Africa, Madagascar or South America4
4. Stamens as many as sepals (4), alternisepalous.....5
4. Stamens twice as many as sepals (8 or 10), diplostemonous6
5. Petaloid scales 4, 8 or 12, surrounded by stiff hairs; inflorescence racemose; stamens shortly exerted; Africa..... 11. **Struthiola**
5. Petaloid scales absent; inflorescence few-flowered terminal umbels; stamens distinctly exerted; South America..... 13. **Drapetes**
6. Inflorescences involucre heads, distinctly pedunculate; involucral bracts coriaceous, foliaceous or brightly coloured and papyraceous; petaloid scales as many as sepals or lacking.....7
6. Inflorescences exinvolucre heads, umbels, spikes, or solitary flowers, mostly sessile or subsessile, rarely short-pedunculate; bracts absent or foliaceous; petaloid scales as many as sepals or twice as many as sepals, rarely lacking.....8
7. Inflorescences terminal or axillary involucre heads; involucral bracts, foliaceous or brightly coloured and papyraceous, deciduous or persistent but not indurated in fruit; flowers 4- or 5-merous, homostylous; lobes deep yellow, orange or red; petaloid scales as many as sepals or lacking; stamens 8 or 10; filaments included or shortly exerted 2. **Lasiosiphon**
7. Inflorescences terminal involucre heads; involucral bracts coriaceous, persistent and becoming indurated in fruit; flowers 5-merous, heterostylous; lobes pink, lilac or mauve, rarely white; petaloid scales lacking; stamens 10; filaments distinctly exerted..... 1. **Dais**
8. Petaloid scales present, inserted below stamens..... 17. **Lachnaea**
8. Petaloid scales absent or present but then inserted above stamens.....9
9. Inflorescences ebracteate; leaves opposite, broad10
9. Inflorescences bracteate; leaves alternate or opposite, narrow11
10. Small trees; leaves membranous; petaloid scales 4 but deeply bifid to base, thus apparently 8; southern and tropical continental Africa 5. **Englerodaphne**
10. Shrubs; leaves coriaceous; petaloid scales absent; Madagascar 3. **Zacharia**
11. Hypanthium densely white-silky or woolly; petaloid scales present.....12
11. Hypanthium glabrous, sparsely silky or puberulous; petaloid scales present or absent13
12. Leaves white-punctulate, glabrous, margins ciliate when young; stigma conical 16. **Craspedostoma**
12. Leaves not white-punctulate, white-woolly on one or both sides or rarely glabrous, without ciliate margins; stigma capitate 14. **Basutica**
13. Petaloid scales surrounded by tuft of silky hairs or covered with or dense white-woolly hairs.....14
13. Petaloid scales glabrous15
14. Inflorescence a terminal cluster elongating into a spike; leaves flattened; petaloid scales 8, surrounded by a tuft of silky hairs.....9. **Phidia**

14. Inflorescences many-flowered capitate heads; leaves acerose; petaloid scales 4, covered with dense white woolly hairs 10. *Gnidia*
15. Petaloid scales 4, large and membranous; hypanthium funnel-shaped; flowers bright canary yellow 4. *Epichroxantha*
15. Petaloid scales 4 to 8 or lacking, oblong and fleshy; hypanthium cylindrical; flowers pale yellow 16
16. Petaloid scales 4, thickly fleshy with inrolled margins (anther-like) 6. *Gnidiopsis*
16. Petaloid scales usually absent, rarely 4 or 8 and then coriaceous and entire 7. *Thymelina*

1. *Dais* Royen ex L., Sp. Pl., ed. 2: 565. 1762.

Description. – Small trees or shrubs. *Leaves* opposite or rarely alternate, ± obovate, usually clustered at the end of branches. *Inflorescences* terminal, capitate, involucre; involucre of 2–6(–12) suborbicular bracts, persistent, coriaceous after anthesis. *Flowers* hermaphroditic, 5-merous, heterostylous, pink; hypanthium cylindrical, weakly articulated, basal portion persistent; shorter than floral tube, lobes spreading. *Petaloid scales* lacking. *Androecium* diplostemonous, stamens 10 in 2 whorls. *Hypogynous disc* cup-shaped, occasionally lobed. *Ovary* 1-locular, ± pubescent; style longer than ovary. *Fruit* dry, enclosed in persistent base of hypanthium. (Herber, 2003; Leandri, 1950).

Diagnostic characters. – *Dais* is readily distinguished by a unique combination of involucre, long-pedunculate inflorescences with coriaceous bracts that become thick and hard in fruit, enclosing the fruit cluster in a cupule-like structure, and heterostylous, pink, 5-merous flowers lacking petaloid scales.

Distribution. – Two species., *Dais cotinifolia* L. and *D. glaucescens* Decne., Madagascar, tropical and Southern Africa.

2. *Lasiosiphon* Fresen. in Flora 21(2): 602–603. 1838 ≡ *Gnidia* sect. *Lasiosiphon* (Fresen.) Staner in Bull. Jard. Bot. État Bruxelles 13(4): 355. 1935 – Type: *Lasiosiphon glaucus* Fresen.

= *Arthrosolen* C.A.Mey. in Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Petersbourg 1: 356, 359. 1843 ≡ *Gnidia* [unranked] *Arthrosolen* (C.A.Mey.) Engl. in Engler & Drude, Veg. Erde 9(3,2): 633. 1921 ≡ *Gnidia* subg. *Arthrosolen* (C.A.Mey.) Staner in Bull. Jard. Bot. État Bruxelles 13(4): 363. 1935 – Type (designated by Phillips, Gen. S. Afr. Fl. Pl., ed. 2: 528. 1951): *Arthrosolen polycephalus* (E.Mey. ex Meisn.) C.A.Mey. (= *Passerina polycephala* E.Mey. ex Meisn.).

= *Arthrosolen* [unranked] *Cephalodaphne* C.A.Mey. in Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Petersbourg 1: 359. 1843 ≡ *Arthrosolen* sect. *Cephalodaphne* (C.A. Mey.) Tiegh. in Bull. Soc. Bot. France 40: 75. 1893 – Type: not designated. [Species included: *A. anthylloides* (L.f.) C.A.Mey., *A. calocephalus* (Meisn.) C.A.Mey., *A. polycephalus* (E.Mey. ex Meisn.) C.A.Mey.]

= *Gnidia* sect. *Involucratae* Gilg in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 227. 1894 – Type (designated by Olaniyan & al. in Pl. Syst. Evol. 310: 38. 2024): *Gnidia involucrata* Steud. ex A.Rich (≡ *Lasiosiphon involucratum* (Steud. ex A.Rich) Olaniyan), **syn. nov.**

= *Atemnosiphon* Leandri in Notul. Syst. (Paris) 13: 44. 1947 – Type (designated by Olaniyan & al. in Pl. Syst. Evol. 310: 39. 2024): *Atemnosiphon coriaceus* (Leandri) Leandri (≡ *Lasiosiphon coriaceus* Leandri), **syn. nov.**

Description. – Shrubs or small trees. *Leaves* alternate to opposite, sometimes decussate, sessile, glabrous, or persistently densely silky on one or both sides. *Inflorescences* terminal or axillary involucre heads, usually distinctly peduncled or subsessile, few-flowered to multi-flowered; involucre of coloured membranous or foliaceous bracts, sometimes deciduous. *Flowers* hermaphroditic, sessile or pedicellate and then pedicel with long erect hairs, 4-merous or 5-merous, bright yellow to orange or red (rarely white); hypanthium cylindrical, usually articulated above ovary or rarely unarticulated, with basal portion persistent, glabrous or densely long-villous. *Petaloid scales* as many as the calyx lobes but sometimes reduced or absent. *Androecium* diplostemonous with eight or ten stamens in two whorls, upper whorl shortly exerted; anthers basifixed. *Hypogynous disc* present or absent. *Ovary* 1-locular; glabrous or apically pubescent; 1-locular; style lateral, longer than ovary; stigma capitate, papillate, included. *Fruit* an achene, indehiscent, enclosed in the persistent base of the hypanthium. (Wright, 1915; Herber, 2003).

Diagnostic characters. – *Lasiosiphon* is distinguished from other genera in the “*Gnidia* group” by its pedunculate, involucre heads of 4- or 5-merous bright yellow to red flowers, often with the pedicel or the lower part of the hypanthium set with long erect hairs, and modified, ± enlarged inflorescence bracts that are often membranous and petaloid.

Distribution. – ±78 species; mainly southern Africa, Tropical Africa and adjacent Madagascar, Southwest India, Arabia, and Sri Lanka.

3. *Zacharia* Olaniyan & Boatwr., **gen. nov.** – Type: *Zacharia neglecta* (Z.S.Rogers) Olaniyan & Boatwr. (≡ *Gnidia neglecta* Z.S.Rogers).

Description. – Shrubs. *Leaves* opposite, decussate, broad, coriaceous, somewhat glaucous, base cordate, secondary venation forming discrete brochidodromous loops. *Inflorescences* terminal, capitate, pedunculate, ebracteate. *Flowers* 4-merous; hypanthium cylindrical, articulated above ovary, persistent, glabrous. *Petaloid scales* absent. *Androecium* diplostemonous with 8 stamens in two whorls, upper whorl shortly exerted; anthers basifixed. *Hypogynous disc* present. *Ovary* 1-locular, glabrous or apically sparsely pubescent; style lateral, longer than ovary; stigma capitate, papillate, included. (Rogers, 2009).

Diagnostic characters. – This genus is distinguished by a unique combination of characters, viz. opposite leaves with broad, coriaceous blade and cordate base, and flowers in pedunculate inflorescences without bracts (i.e., subtended at

the base of the peduncle by two diminutive foliage leaves) with a glabrous hypanthium.

Distribution. – Monotypic; Madagascar.

Etymology. – The new genus is named for Dr Zachary Scott Rogers (1976–) of the New Mexico State University and Missouri Botanical Gardens for his contributions to the taxonomy of the Thymelaeaceae.

Note. – This monotypic genus is described to accommodate a poorly understood taxon from Madagascar currently known only from the type collection (Rogers, 2009). Boatwright & al. (2017) expressed reservations about including this taxon in *Lasiosiphon* when they transferred the other Malagasy species of *Gnidia* to that genus on account of its anomalous combination of characters. We accordingly elect to accommodate this taxon in a separate genus, the status and relationships of which need to be clarified when more material becomes available.

***Zacharia neglecta* (Z.S.Rogers) Olaniyan & Boatwr., comb. nov.** ≡ *Gnidia neglecta* Z.S.Rogers in Ann. Missouri Bot. Gard. 96(2): 356–358, fig. 11, 17 [map]. 2009 – Holotype: Madagascar, “Toamasina: Andevorante [Andevoranto], Moramanga”, 3 Oct 1912, *Afzelius s.n.* (P barcode P00380393!; isotype: S No. S11-21072!).

4. ***Epichroxantha* Eckl. & Zeyh. ex Olaniyan & Magee, gen. nov.** – Type: *Epichroxantha juniperifolia* (Lam.) Olaniyan (≡ *Gnidia juniperifolia* Lam.).

- “*Epichroxantha* Eckl. & Zeyh. ex Meisn.” in Candolle, Prodr. 14(2): 580. 1857, nom. nud. pro syn. *Gnidia*.
- “*Epichroxantha* Tiegh.” in Bull. Soc. Bot. France 40: 76. 1893, nom. nud.

Nomenclatural note. – Although Van Tieghem (1893) considered the possibility of recognizing *Epichroxantha* at generic rank, he ultimately rejected accepting it as a distinct genus, and instead explicitly included the relevant species in his new genus *Gnidiopsis* on the basis of shared periderm characters, which he regarded as diagnostic for that genus. The name “*Epichroxantha*” was therefore not validly published by him (Turland & al., 2025: ICN, Art. 35.1).

Description. – Shrubs or undershrubs, erect or much-branched, glabrous or slightly pubescent. *Leaves* opposite, decussate, sessile, glabrous or rarely pubescent, flat or slightly keeled. *Inflorescence* terminal, solitary, geminate, or few-flowered umbel; inflorescence leaves foliaceous, sometimes slightly bigger than the foliage leaves. *Flowers* bisexual, 4-merous, sessile, canary yellow; hypanthium funnel-shaped, articulated above ovary with basal portion persistent, glabrous or puberulous. *Petaloid scales* 4, large and membranous. *Androecium* diplostemonous, stamens 8 in two whorls, upper whorl reaching rim of hypanthium, lower whorl included anthers basifixed. *Hypogynous disc* absent or rarely present. *Ovary* 1-locular, penicillate; style lateral; stigma capitate, papillate, included. *Fruit* an achene, enclosed in persistent base of hypanthium.

Diagnostic characters. – Distinguished from other genera in the “*Gnidia* group” by its canary-yellow flowers with funnel-shaped, glabrous or puberulous hypanthium and four large, membranous petaloid scales.

Distribution. – 11 species; South Africa.

***Epichroxantha coriacea* (Meisn.) Olaniyan, comb. nov.** ≡ *Gnidia coriacea* Meisn. in Linnaea 14(5): 454–455. 1841 (“1840”) – Holotype: South Africa, Eastern Cape “Zuurebergen” [Zuurberg], *Drège* 7363 (NY barcode 1287770!; isotype: P barcode P00541065!).

***Epichroxantha decurrens* (Meisn.) Olaniyan, comb. nov.** ≡ *Gnidia decurrens* Meisn. in Linnaea 14(5): 451–452. 1841 (“1840”) – Syntypes: South Africa, Western Cape, “Montem Tabularem et Leonis”, without date, *Drège s.n.* (HAL barcode HAL0111674!); South Africa, Western Cape, “Monte Tabulari”, without date, *Drège s.n.* (HBG barcode HBG512571!); South Africa, Western Cape, “catractam ad Montem Diaboli”, without date, *Drège s.n.* (TUB barcode TUB002862!).

***Epichroxantha flanaganii* (C.H.Wright) Olaniyan, comb. nov.** ≡ *Gnidia flanaganii* C.H.Wright in Thiselton-Dyer, Fl. Cap. [Harvey] 5(2): 53–54. 1915 (“*flanaganii*”) – Syntypes: South Africa, Eastern Cape, “near Keimouth” [Kei River mouth], Sep 1914, *Flanagan* 621 (K barcode K000322578!); South Africa, Eastern Cape, “Kentani”, 10 May 1905, *Pegler* 32 (P barcode P00648789!); South Africa Eastern Cape, “between Umkwani and Omsakabo”, *Tyson* 2636 (not located).

***Epichroxantha galpinii* (C.H.Wright) Olaniyan, comb. nov.** ≡ *Gnidia galpinii* C.H.Wright in Thiselton-Dyer, Fl. Cap. [Harvey] 5(2): 55. 1915 (“*galpini*”). – Syntype: South Africa, Western Cape, “Garcias Pass”, 30 Sep 1897, *Galpin* 4519 (K barcode K000322576!).

***Epichroxantha humilis* (Meisn.) Olaniyan, comb. nov.** ≡ *Gnidia humilis* Meisn. in Candolle, Prodr. 14(2): 586. 1857 – Holotype: South Africa, Western Cape, “montis Tabularis”, *Ecklon & Zehyer* 89 [Herb. Sonder] (S No. S09-16159!; isotype: MO barcode MO-313075 [No. 5692793!]).

***Epichroxantha juniperifolia* (Lam.) Olaniyan, comb. nov.** ≡ *Gnidia juniperifolia* Lam., Encycl. 2(2): 765. 1788 ≡ *Gnidia pinifolia* L.f., Suppl. Pl.: 225. 1782, nom. illeg. non L. 1753 – Holotype: South Africa, “Cap bonae Spei”, *Sparrmann s.n.* (LINN No. 502.15!).

***Epichroxantha myrtifolia* (C.H.Wright) Olaniyan, comb. nov.** ≡ *Gnidia myrtifolia* C.H.Wright in Thiselton-Dyer, Fl. Cap. [Harvey] 5(2): 51. 1915 – Syntypes: South Africa, Eastern Cape, “East London, near Cove Rock”, without date, *Galpin* 3177 (not located);

South Africa, Eastern Cape, “near Kwenquea River mouth”, 23 Dec 1900, *Galpin 5803* (GRA barcode GRA0027035!).

Epichroxantha parviflora (Meisn.) Olaniyan, **comb. nov.** ≡ *Gnidia parviflora* Meisn. in *Linnaea* 14(5): 453. 1841 (“1840”) – Holotype: South Africa, Western Cape, “Piquetberg” [Piketberg], without date, *Drège s.n.* (NY barcode 01287780!; isotype: P barcode P00541049!).

Epichroxantha viridis (P.J.Bergius) Olaniyan, **comb. nov.** ≡ *Gnidia viridis* P.J.Bergius, *Descr. Pl. Cap.*: 125–126. Sep 1767 – Original material: South Africa, “Promontorii Bonae Spei”, [illustration] “Thymelaea aethiopica passerinae foliis” in Breyne, *Exot. Pl. Cent.*: 10, t. 6 [“ad Cap. VI”]. [1674–]1678.

= *Gnidia simplex* L., *Mant. Pl.*: 67. 17–31 Oct 1767 – Lectotype (designated by Rogers in *Taxon* 55: 486. 2006): *Herb. Linnaeus* No. 502.3 (LINN!). Epitype (designated by Rogers in *Taxon* 55: 486. 2006): South Africa, Western Cape Province, “Houw Hoek”, 24 Nov 1896, *F.R.R. Schlechter 9388* (MO barcode MO-439647 [No. 5473554]!; isotype: US n.v.).

= *Gnidia subulata* Lam., *Encycl.* 2(2): 765. 1788, nom. illeg. superfl. – Holotype: South Africa, Western Cape, “Cap de Bonne-Esperance”, without date, *Sonnerat s.n.* (P 2D-barcode P00381732!).

Note. – Wright (1915) treated *Gnidia viridis* P.J.Bergius 1767 and *G. simplex* L. 1767 as conspecific under the later name *G. subulata* Lam. 1788. This is an illegitimate superfluous name as Lamarck (1788) cited both *G. simplex* L. and *G. viridis* P.J.Bergius as synonyms of his *G. subulata* (Turland & al., 2025: ICN Art. 52.1 and 52.2). If these species are considered conspecific, then *G. viridis* P.J.Bergius Sep 1767 is the earliest available name as having been published one month earlier than *G. simplex* L. Oct 1767.

Epichroxantha sonderiana (Meisn.) Olaniyan, **comb. nov.** ≡ *Gnidia sonderiana* Meisn. in *Candolle, Prodr.* 14(2): 587. 1857 – Holotype: South Africa, Western Cape, “Babylonsche Toorn” [Babylonstoring], without date, *Ecklon & Zeyher 82* [*Herb. Sonder*] (S No. S10-25324!; isotypes: MO barcode MO-313085 [No. 5414527]!, NY barcode 1287786!, SAM barcode SAM0043794-0!).

Epichroxantha styphelioides (Meisn.) Olaniyan, **comb. nov.** ≡ *Gnidia styphelioides* Meisn. in *Linnaea* 14(5): 453–454. 1841 (“1840”) – Holotype: South Africa, Eastern Cape “Zuurebergen” [Zuurberg], *Drège s.n.* (NY barcode 01288007!).

5. *Englerodaphne* Gilg in *Bot. Jahrb. Syst.* 19: 274. 1894 – Type: *Englerodaphne subcordata* (Meisn.) Engl. (≡ *Gnidia subcordata* Meisn.).

Description. – Shrubs or small trees. *Leaves* opposite-distichous, elliptic to suborbicular, subsessile or

shortly petiolate, broad and membranous. *Inflorescences* a terminal congested spike or umbel, ebracteate, sessile, or pedunculate. *Flowers* bisexual, 4-merous, sessile; hypanthium cylindrical, abscising above the ovary, lower part persistent. *Petaloid scales* 4, divided to near the base and appearing as eight segments, membranous, glabrous. *Androeceum* diplostemonous, stamens 8 in two whorls, upper whorl shortly exerted; anthers dorsifixed. *Hypogynous disc* lacking. *Ovary* 1-locular, densely pilose; style lateral; stigma capitate, shortly papillate, included. *Fruit* an achene, densely pilose. (Olaniyan & al., 2020).

Diagnostic characters. – *Englerodaphne* is distinguished by its arborescent habit and ebracteate umbels or spikes of 4-merous flowers with four membranous scales that are divided to near the base, and densely pilose ovary.

Distribution. – Three species; southern and tropical East Africa.

6. *Gnidiopsis* Tiegh. in *Bull. Soc. Bot. France* 40: 75. 1893, **emend.** Olaniyan & J.C.Manning – **Type (designated here):** *Gnidiopsis oppositifolia* (L.) Olaniyan (≡ *Gnidia oppositifolia* L.).

Description. – Much-branched, densely leafy shrubs with virgate branches. *Leaves* opposite, decussate, sessile, ovate or orbicular, glabrous. *Inflorescences* a terminal few- or many-flowered involucre umbel; involucre foliaceous. *Flowers* bisexual, 4-merous, sessile, pale yellow; hypanthium cylindrical, articulated above ovary with basal portion persistent, pubescent, 16–20mm long. *Petaloid scales* 4, shortly stalked, fleshy with inflexed margin. *Androeceum* diplostemonous, stamens 8 in two whorls, included. *Hypogynous disc* lacking. *Ovary* 1-locular, densely hirsute; stigma capitate with short papillae, included. *Fruit* an achene, enclosed in persistent base of hypanthium.

Diagnostic characters. – *Gnidiopsis* is distinguished from other genera in the group by its glabrous, ± orbicular leaves, and long-tubed flowers with four fleshy petaloid scales with inflexed margins, resembling an anther, and the densely hirsute ovary.

Distribution. – Three species; South Africa, endemic to the Core Cape Floristic Region.

Nomenclatural note. – Van Tieghem (1893) distinguished his new genus *Gnidiopsis* from allied genera (*Lasiosiphon*, *Lachnaea*, *Cryptadenia* and others) by the peculiar formation of the periderm (bark). This serves as a validating diagnosis for the genus (Turland & al., 2025: ICN Art. 38.1 and 38.2). Van Tieghem (1893) cited the generic names “*Calysericos* Eckl. & Zeyh. ex Meisn.” 1857 and “*Epichroxantha* Eckl. & Zeyh. ex Meisn.” 1857 as partial synonyms of *Gnidiopsis* but neither were validly published at the time and this therefore does not render his new genus illegitimate (Turland & al., 2025: ICN Art. 52.1). Van Tieghem (1893) listed 17 species of *Gnidia* as belonging in his new genus *Gnidiopsis* but did not directly associate the specific epithets with the generic name *Gnidiopsis* apart from *G. insularis* Gardner and *G. monticola* Miq. [sphalm. *G. monticolor*] (both now in

Lasiosiphon). Under the *International Code of Nomenclature for algae, fungi, and plants*, the valid publication of a genus does not automatically establish new combinations for included species unless the names are explicitly or implicitly combined (Turland & al., 2025: ICN Art. 41.1). On this basis, only the combinations *Gnidiopsis insularis* (Gardner) Tiegh. and *G. monticola* (Miq.) Tiegh. were validly published.

Among the 17 species that Van Tieghem (1893) included in the genus *Gnidiopsis*, all except *G. oppositifolia* are placed in clades for which a published or proposed generic name exists. We therefore designate *G. oppositifolia* as the type of *Gnidiopsis* to avoid having to describe a new genus for the clade to which that species belongs. Our circumscription of the genus is very different from that of Van Tieghem (1893).

Gnidiopsis insignis (Compton) Olaniyan, **comb. nov.** ≡ *Gnidia insignis* Compton in J. S. African Bot. 15: 111–112. 1949 – Holotype: South Africa, Western Cape, “Molenaar’s Berg”, 5 Oct 1947, *Compton 20114* (NBG barcode NBG0053476-0!; isotypes: NBG barcode NBG0053475-2!, PRE barcode PRE0297720-0!).

Gnidiopsis oppositifolia (L.) Olaniyan, **comb. nov.** ≡ *Gnidia oppositifolia* L., Sp. Pl.: 358. 1753 – Lectotype (designated by Rogers in Taxon 55: 486. 2006): “Habitat in Aethiopia”, without collector or date, Herb. Linnaeus No. 502.8, second specimen from left (LINN!).

Gnidiopsis orbiculata (C.H.Wright.) Olaniyan, **comb. nov.** ≡ *Gnidia orbiculata* C.H.Wright in Thiselton-Dyer, Fl. Cap. [Harvey] 5(2): 47. 1915 – Holotype: South Africa, Eastern Cape, “Apies River, in Long Kloof”, 13 Mar 1814, *Burchell 4945* (K barcode K000322527!; isotypes: GH barcode 00443753!, K barcode K000322529!).

Other original material. – South Africa, without locality or date, *Thom 162* (K barcode K000322528!).

Note. – The specimen K000322527 is annotated with the word “Type!” and we therefore accept it as the holotype.

7. ***Thymelina*** Hoffmanns., Verz. Pfl.-Kult.: 198. 1824 – Type: *Thymelina simplex* Hoffmanns. (= *T. squarrosa* (L.) Olaniyan).

= *Arthrosolen* [unranked] *Arthrosolenia* C.A.Mey. in Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Petersbourg 1: 359. 1843 ≡ *Arthrosolen* sect. *Arthrosolenia* (C.A.Mey.) Tiegh. in Bull. Soc. Bot. France 40: 75. 1893 – Type: *Arthrosolen spicatus* (L.f.) C.A.Mey. (≡ *Passerina spicata* L.f.), **syn. nov.**

= *Arthrosolen* [unranked] *Gymnurus* C.A.Mey. in Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Petersbourg 1: 359. 1843 ≡ *Arthrosolen* sect. *Gymnurus* (C.A.Mey.) Tiegh. in Bull. Soc. Bot. France 40: 75. 1893 – Type: *Arthrosolen gymnostachys* (Meisn.) C.A.Mey. (≡ *Passerina gymnostachya* Meisn.), **syn. nov.**

= *Arthrosolen* [unranked] *Rhytidosperma* C.A.Mey. in Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Petersbourg 1: 359. 1843 ≡ *Rhytidosolen* Tiegh. in Bull. Soc. Bot. France 40: 75. 1893 – Type: *Rhytidosolen laxus* (L.f.) Tiegh. (≡ *Passerina laxa* L.f.), **syn. nov.**

Description. – Shrubs or undershrubs. *Leaves* opposite or alternate, glabrous or sparingly pilose, midrib prominent beneath. *Inflorescences* a gradually elongating terminal ebracteate spike or terminal umbel with leafy bracts, rarely a spiciform raceme inflorescence with bracteoles. *Flowers* bisexual, 4-merous, sessile, greenish-yellow or white, usually tinged or flushed maroon; hypanthium cylindrical, rarely urceolate, articulated above ovary with basal portion persistent, pilose or glabrous. *Petaloid scales* usually lacking, rarely 4 or 8, glabrous. *Androecium* diplostemonous, stamens 8 in two whorls, included; anthers dorsifixed. *Hypogynous disc* lacking. *Ovary* 1-locular, apically pilose; style lateral, longer than the ovary, stigma capitate, shortly papillate, included. *Fruit* an achene, enclosed in persistent base of hypanthium.

Diagnostic characters. – The flowers in *Thymelina* are 4-merous and mostly without scales but sometimes with four (*Gnidia wikstroemiana*) or eight (*G. obtusissima*, *G. pallida*, *G. squarrosa*, *G. woodii*) scales. The tinge or flush of maroon colour on the flowers and leaves distinguishes them from other genera. *Thymelina* resembles some *Lasiosiphon* species in the absence of petaloid scales but differs in its ex-involucrate, often spicate inflorescence.

Distribution. – 13 species; southern Africa

Nomenclatural note. – Hoffmannsegg (1824) established the genus *Thymelina* for the single species *T. simplex*, which he distinguished from *Gnidia* s.l. by having eight discrete petaloid scales inserted in pairs at the base of the sepal lobes, versus four entire or deeply bifid scales in *Gnidia*. His diagnosis is accompanied by two figures of detached flowers (Hoffmannsegg, 1824: fig. 2a, b), the most informative of which depicts an entire flower that has been opened out. The hypanthium tube is ±3 times longer than the lobes with 8 discrete, small obovate scales inserted in pairs in the sinuses and less than half as long as the lobes. He cited no specimen but the summary table (Hoffmannsegg, 1824: 117) includes the information that the taxon originated from the Cape of Good Hope and that it required cultivation in a glasshouse (“Orange-rie”). It also includes the annotation “n.” indicating that the name is Hoffmannsegg’s own. This removes any possibility that it was intended as a combination based on *G. simplex* L. 1767, a name that is currently applied to a taxon with four scales (Rogers & Spencer, 2006) and therefore inconsistent with the protologue of *Thymelina*. It is therefore clear that *T. simplex* and *G. simplex* apply to different taxa. The name *T. simplex* Hoffmanns. was treated by Wright (1915) as a synonym of *G. polystachya* P.J.Bergius (= *G. squarrosa* (L.) Druce), an interpretation consistent with Hoffmannsegg’s illustration, particularly in the presence of eight discrete petaloid scales inserted in pairs in the sepal sinuses. In addition, *G. squarrosa* was already well established in cultivation in Europe by the end of the eighteenth century (Andrews, 1799).

This interpretation of the identity of *T. simplex* makes *Thymelina* Hoffmanns. the earliest available generic name for this clade, and to fix this application of the name *T. simplex* we designate as epitype the very fine coloured illustration of *G. squarrosa* that was published by Andrews (1799).

Thymelina compacta (C.H.Wright) Olaniyan, **comb. nov.** = *Arthrosolen compactus* C.H.Wright in Thiselton-Dyer, Fl. Cap. [Harvey] 5(2): 583. 1925 = *Gnidia compacta* (C.H.Wright) J.H.Ross in Bothalia 10(3): 435. 1971 – Holotype: South Africa, KwaZulu-Natal, “Niginya”, *Wylie sub Wood 10531* (K barcode K000324237!).

Thymelina fraterna (N.E.Br.) Olaniyan, **comb. nov.** = *Arthrosolen fraternus* N.E.Br. in Bull. Misc. Inform. Kew 1901: 132. 1901 = *Gnidia fraterna* (N.E.Br.) E.Phillips in J. S. African Bot. 10: 63. 1944 – Holotype: South Africa, Eastern Cape, “mountains near Queenstown”, 1 Jan 1894, *Galpin 1771* (K barcode K000324235!; isotype: GRA barcode GRA0027038!).

Thymelina gymnostachya (Meisn.) Olaniyan, **comb. nov.** = *Passerina gymnostachya* Meisn. in Linnaea 14(5): 397. 1841 (“1840”) = *Arthrosolen gymnostachys* (Meisn.) C.A.Mey. in Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Petersbourg 1: 359. 1843 = *Gnidia gymnostachya* (Meisn.) Gilg in Engler & Prantl., Nat. Pflanzenfam. 3 (6a): 228. 1894 – Syntypes: South Africa, Eastern Cape, “Mooyplaats”, Dec without year, *Drège s.n.* (HAL barcode HAL0111339!, K barcodes K000324232!, K000324324!, NY barcode 386307!, P barcode P00541061!, S. Nos. S09-16154! & S09-16155!, TUB barcode TUB002885!).

Thymelina hirsuta (L.) Olaniyan, **comb. nov.** = *Lobelia hirsuta* L., Sp. Pl.: 932–933. 1753 = *Gnidia hirsuta* (L.) Thulin in Taxon 35(4): 724. 1986 – Lectotype (designated by Thulin in Taxon 35: 724. 1986): South Africa, “Habitat in Aethiopia”, [illustration] “*Rapuntium foliis subrotundis, hirtis, flore ex alis solitario*” in Burman, Rar. Afric. Pl.: t. 40, fig. 2. 1738. = *Arthrosolen ornatus* Meisn. in Candolle, Prodr. 4(2): 559. 1857 = *Gnidia ornata* (Meisn.) Gilg in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 228. 1894 – Syntype: South Africa, Western Cape, Kleinriviersberg, Aug without year, *Zeyher 3755* (GRA barcode GRA0027041!, P barcode P00541072!, S No. S11-24219!).

Thymelina laxa (L.f.) Olaniyan, **comb. nov.** = *Passerina laxa* L.f., Suppl. Pl.: 226. 1782 = *Arthrosolen laxus* (L.f.) C.A.Mey. in Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Petersbourg 1: 359. 1843 = *Rhytidosolen laxus* (L.f.) Tiegh. in Bull. Soc. Bot. France 40: 75. 1893 = *Gnidia laxa* (L.f.) Gilg in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 226. 1894 – Lectotype (designated by Rogers in Taxon 55: 818. 2006): South Africa, “Cap. bonae spei”,

without date, *Thunberg s.n.* (UPS-THUNB No. 9584 n.v.; isoelectotype: LD barcode 1507539!).

Thymelina obtusissima (Meisn.) Olaniyan, **comb. nov.** = *Gnidia obtusissima* Meisn. in Linnaea 14(5): 432–433. 1841 (“1840”) – Holotype?: South Africa, Northern Cape, Kamiesberg, “Roodeberg” [Rooiberg], Nov without year, *Drège 7359* (P barcode P00541051!; isotype?: NY barcode 1287779!).

Thymelina pallida (Meisn.) Olaniyan, **comb. nov.** = *Gnidia pallida* Meisn. in Linnaea 14(5): 442–443. 1841 (“1840”) – Holotype: South Africa, Eastern Cape, “Omtendo” [Umtentu], May, without year, *Drège 4667* (NY barcode 1287791!; isotype: P barcode P00541050!).

Thymelina phaeotricha (Gilg) Olaniyan, **comb. nov.** = *Gnidia phaeotricha* Gilg in Kuntze, Revis. Gen. Pl. 3(3): 281. 1898 = *Arthrosolen phaeotrichus* (Gilg) C.H.Wright in Thiselton-Dyer, Fl. Cap. [Harvey] 5(2): 8. 1915 – Holotype: South Africa, KwaZulu-Natal, “Van Reenen’s Pass”, 20 Mar 1894, *Kuntze s.n.* (NY barcode 1288017!; isotypes: K barcodes K000324228! & K000324229!, US barcode 00117186!).

Thymelina spicata (L.f.) Olaniyan, **comb. nov.** = *Passerina spicata* L.f., Suppl. Pl.: 226. 1782 = *Arthrosolen spicatus* (L.f.) C.A.Mey. in Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Petersbourg 1: 359. 1843 = *Gnidia spicata* (L.f.) Gilg in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 228. 1894 – Lectotype (designated by Rogers in Taxon 55: 486. 2006): South Africa, “Cap. Bonae Spei”, *Thunberg s.n.* (UPS-THUNB No. 9590 n.v.; isoelectotypes: LD barcode 1247245!, SBT barcodes SBT12561! & SBT12562!).

Thymelina squarrosa (L.) Olaniyan, **comb. nov.** = *Daphne squarrosa* L., Sp. Pl.: 358. 1753 = *Gnidia squarrosa* (L.) Druce in Rep. Bot. Exch. Club Soc. Brit. Isles 3(5): 418. 1914 (“1913”) – Lectotype (designated by Rogers in Taxon 55(2): 485. 2006): South Africa, “Habitat in Aethiopia” without collector or date, [illustration] “*Thymelaea capitata, lanuginosa, foliis creberrimis, minimis, aculeatis*” in Burman, Rar. Afric. Pl.: t. 49, fig. 1. 1739. Epitype (designated by Rogers in Taxon 55: 485. 2006): South Africa, Western Cape “Cape Peninsula, Cape Point”, 20 Nov 1938, *Wall s.n.* (MO barcode MO-325038 [No. 5653217]!).

= *Thymelina simplex* Hoffmanns., Verz. Pfl.-Kult.: 198, fig. 2. 1824 – **Lectotype (designated here)**: South Africa, “Pr. B. Spei”, without collector, cultivated in Dresden and Rammenau, [illustration in] Hoffmanns-egg, Verz. Pfl.-Kult.: fig. 2. 1824. **Epitype (designated here)**: South Africa, “Cape”, without collector, cultivated by R. James of Grosvenor Place, London, [illustration] “*Gnidia simplex*” in Andrews, Bot. Repos. 1: t. 70. 1799.

= *Gnidia variegata* Gand. in Bull. Soc. Bot. France 60: 417. 1913 – Holotype: South Africa, Eastern Cape, “Port Elizabeth” [Gqeberha], *Laidley E.S.C.A. Herb.* 488 (LY barcode LY0855782!), **syn. nov.**

Note. – Wright (1915) was unable to examine the type of *Gnidia variegata* and suggested a relationship with *G. subulata*, here treated as a synonym of *G. viridis* in the genus *Epichroxantha*. We have located the type, and it is clearly conspecific with *G. squarrosa*. Our identification is supported by an earlier determination slip that was appended to the specimen by Thymelaeaceae expert Bo Petersen in 1967.

Thymelina variabilis (C.H.Wright) Olaniyan, **comb. nov.** ≡ *Arthrosolen variabilis* C.H.Wright in Thiselton-Dyer, Fl. Cap. [Harvey] 5(2): 8. 1915 ≡ *Gnidia variabilis* (C.H.Wright) Engl. in Engler & Drude, Veg. Erde 9 (3,2): 630. 1921 – Syntypes: South Africa, Free State, “Witzies Hoek” [Witsieshoek], Dec 1893, *Bolus* 8243 (K barcode K000832591!); South Africa, Mpumalanga, “near Ermelo”, 19 Jan 1904, *Burt Davy* 960 (K barcode K000832590!); South Africa, Mpumalanga, “Lydenburg”, Nov 1894, *Wilms* 1287 (K barcode K000832587!); South Africa, Mpumalanga, “Lydenburg”, Dec 1895, *Wilms* 1288 (K barcode K000832589!, P barcodes P00648762!, P00648763!); South Africa, Eastern Cape “near Kokstad”, Dec 1883, *Tyson* 1214 (K barcode K000832586!); South Africa, KwaZulu-Natal, “Weenen County”, 17 Dec 1890, *Wood* 4550 (K barcode K000832585!); South Africa, KwaZulu-Natal, “near Newcastle”, 17 Jan 1898, *Wood* 7200 (K barcode K000832592!); South Africa, KwaZulu-Natal, “near Charlestown”, 5 Dec 1892, *Wood* 4802 (K barcode K000832593!); South Africa, KwaZulu-Natal, “Zulu-land”, without date, *Gerrard* 284 (BM barcode BM001009965!, K barcode K000832588!).

Thymelina wikstroemiana (Meisn.) Olaniyan, **comb. nov.** ≡ *Gnidia wikstroemiana* Meisn. in Linnaea 14(5): 434–435. 1841 (“1840”) – Isotype?: South Africa, Eastern Cape, “Compasberg prope Paadekraal”, without date, *Drège* 7369 (K barcode K000322554!).

Thymelina woodii (C.H.Wright) Olaniyan, **comb. nov.** ≡ *Gnidia woodii* C.H.Wright in Thiselton-Dyer, Fl. Cap. [Harvey] 5(2): 60–61. 1915 – Syntypes: South Africa, Eastern Cape, “near Fort Donald”, *Tyson* 1639 (not located); South Africa, KwaZulu-Natal, “Inanda”, *Wood* 153 (not located); South Africa, KwaZulu-Natal, “Inanda”, 1883–1890, *Wood* 755 (BM barcode BM000910836!, GRA barcode GRA0027034!, K barcodes K000322552!, K000322553!, NU barcode NU0015516-0!); South Africa, KwaZulu-Natal, “near Pinewood”, *Wood s.n.* (not located); South Africa, KwaZulu-Natal, “Ingoty”, *Wood s.n.* (not located); South Africa, KwaZulu-Natal, “Zululand”, 25 Mar 1903, *Wylie sub Wood* 9014 (K barcode K000322551!).

8. ***Pimelea*** Banks ex Gaertn., Fruct. Sem. Pl. 1: 186. 1788, nom. cons. – Type: *Pimelea laevigata* Gaertn.

= *Thecanthes* Wikstr. in Kongl. Vetensk. Acad. Handl. 1818: 271. 1818 – Type: *Thecanthes punicea* (R.Br.) Wikstr. (≡ *Pimelea punicea* R.Br.).

Description. – Shrubs, undershrubs, or herbs. *Leaves* opposite-decussate or rarely alternate, petiolate or sessile. *Inflorescence* usually terminal head-like or a condensed raceme, rarely an axillary cluster; involucre absent to many bracts, occasionally ± united. *Flowers* bisexual or rarely unisexual, 4-merous, sessile or subsessile; hypanthium cylindrical or rarely funnel-shaped, basal portion persistent or hypanthium completely persistent, rarely caducous. *Petaloid scales* absent. *Androecium* hemistemonous, stamens 2 or very rarely 1, often exserted; anthers dorsifixed or basifixed, introrse or rarely extrorse. *Hypogynous disc* cupular or of distinct scales, sometimes rudimentary or absent. *Ovary* 1-locular; style subterminal and excentric; stigma papillose or brush-like, often exserted. *Fruit* a drupe, enclosed in persistent base of hypanthium. (Rye & Heads, 1990; Herber, 2003)

Diagnostic characters. – *Pimelea* is unique in the group in the reduction of the stamens to two or very rarely one.

Distribution. – ±110 species; mainly Australia, Lord Howe Island, New Zealand, and the Chatham Islands with a few species extending into Malesia.

9. ***Phidia*** (Endl.) Olaniyan & J.C.Manning, **stat. nov.** ≡ *Gnidia* [unranked] *Phidia* Endl., Gen. Pl. suppl. 4(2): 64. 1847 ≡ *Gnidia* subg. *Phidia* (Endl.) Gilg in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 228. 1894 – Type: *Phidia racemosa* (Thunb.) Olaniyan (≡ *Gnidia racemosa* Thunb.).

Description. – Shrubs or subshrubs. *Leaves* alternate, ovate to lanceolate, sessile or subsessile, glabrous, *Inflorescences* a terminal cluster elongating into a spike. *Flowers* bisexual, 4-merous, sessile, greenish-yellow; hypanthium cylindrical, articulated above ovary with basal portion persistent, glabrous. *Petaloid scales* 8 covered with a tuft of hairs. *Androecium* diplostemonous, stamens 8 in two whorls, upper whorl shortly exserted; anthers basifixed. *Hypogynous disc* present. *Ovary* 1-locular, glabrous; style lateral; stigma capitate, shortly papillate, included. *Fruit* an achene, enclosed in persistent base of hypanthium.

Diagnostic characters. – *Phidia* is readily distinguished from other genera in the group by the 4-merous flowers with eight hairy scales. Hairy scales are characteristic of *Struthiola* and *Gnidia* s.str. but *Phidia* has eight scales vs four in *Gnidia* s.str. and diplostemonous flowers with eight stamens vs haplostemonous flowers with four stamens in *Struthiola*.

Distribution. – Five species; South Africa.

Phidia meyeri (Meisn.) Olaniyan, **comb. nov.** ≡ *Gnidia meyeri* Meisn. in Linnaea 14(5): 443–444. 1841 (“1840”) – Holotype: South Africa, Northern Cape, Kamiesberg, “Kasparskloof” [Zwischen Uitkomst und Geelbeksraal], Aug without year, *Drège* 2974 (NY barcode

1287795!; isotypes: HAL barcode HAL0111684!, HBG barcode HBG512583!, HEID barcode HEID702631!, K barcodes K000322517!, K000322518!, MO barcode MO-313076 [No. 5692792]!, P barcode P00541055!, TUB barcode TUB002873!).

Phidia parvula (Wolley-Dod) Olaniyan, **comb. nov.** $\equiv$ *Gnidia parvula* Wolley-Dod in J. Bot. 39(468): 401–402. 1901 – Holotype: South Africa, Western Cape, Cape Peninsula, “Lions Mount by the Signal Station”, 21 Sep 1897, *Wolley-Dod* 2928 (K barcode K000322602!; isotype: PRE barcode PRE0297722-0!).

Phidia racemosa (Thunb.) Olaniyan, **comb. nov.** $\equiv$ *Gnidia racemosa* Thunb., Prodr. Pl. Cap. 1: 76. 1794 – Holotype: South Africa, without locality or date, *Thunberg s.n.* (UPS-THUNB No. 9556 n.v.; isotypes: LD barcode 1240813!, M barcode M-0145910!, S No. S11-22243!, W No. W0009021!).

Phidia setosa (Thunb.) Olaniyan, **comb. nov.** $\equiv$ *Passerina setosa* Thunb., Prodr. Pl. Cap. 1: 75. 1794 $\equiv$ *Gnidia setosa* (Thunb.) Wikstr. in Kongl. Vetensk. Acad. Handl. 1818: 315. 1818 – Holotype: South Africa, Western Cape, “e Cap. b. spei”, without date, *Thunberg s.n.* (UPS-THUNB No 9589 n.v.; isotype: SBT barcode SBT12541!).

Phidia thesioides (Meisn.) Olaniyan, **comb. nov.** $\equiv$ *Gnidia thesioides* Meisn. in Linnaea 14(5): 457–458. 1841 (“1840”) $\equiv$ *Gnidia thesioides* var. *laxa* Meisn. in Candolle, Prodr. 14(2): 590. 1857, nom. illeg. superfl. – Holotype: South Africa, Eastern Cape, “Zuurebergen bei Bontjesrivier”, Nov without year, *Drège* 7353 (not located).

10. ***Gnidia*** L., Sp. Pl.: 358. 1753 – Type: *Gnidia pinifolia* L. = *Dessenia* Adans., Fam. Pl. 2: 285. 1763, nom. illeg. superfl., non L. 1753 – Type: Not designated.
 - = *Canalia* F.W.Schmidt, Neue Selt. Pfl.: 30. 1793 – Type: *Canalia daphnoides* F.W.Schmidt (= *Gnidia pinifolia* L.).
 - = *Gnidia* sect. *Exinvolucratae* Gilg in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 226. 1894 – Type: not designated.
 - = *Gnidia* sect. *Pergnidia* Engl. in Engler & Drude, Veg. Erde 9(3,2): 631. 1921, nom. illeg. superfl. – Type: *Gnidia pinifolia* L.
 - = *Gnidia* subg. *Pergnidia* Staner in Bull. Jard. Bot. l'Éat. Brux. 13(4): 344. 1935, nom. illeg. superfl. – Type: *Gnidia pinifolia* L.
 - “*Struthia* Royen ex L.”, Opera Var.: 222. 1758, nom. nud.
- Description.** – Shrub. *Leaves* alternate, acrose, pungent-acuminate, glabrous. *Inflorescence* terminal many-flowered head; involucre leaves rather wider than cauline leaves. *Flowers* bisexual, 4-merous, sessile, white, sweetly scented at night; hypanthium cylindrical, articulated above ovary, basal portion persistent, sparsely pubescent with short erect hairs. *Petaloid scales* 4, densely strigose all over. *Androecium*

diplostemonous, stamens 8 in two whorls, antesealous ones shortly exserted; anthers dorsifixed. *Hypogynous disc* cupular. *Ovary* 1-locular, shortly stipitate, glabrous; style lateral, stigma capitate, papillate, included. *Fruit* an achene, enclosed in persistent base of hypanthium.

Diagnostic characters. – *Gnidia* s.str. is distinguished from other genera in the “*Gnidia* group” by its acrose leaves and 4-merous flowers with four fleshy scales that are densely strigose all over.

Distribution. – Monotypic; South Africa in the Core Cape Floristic Region.

11. ***Struthiola*** L., Mant. Pl.: 4. 1767, nom. cons. – Type: *Struthiola virgata* L.

Description. – Shrubs or shrublets. *Leaves* opposite-decussate, whorled or more rarely alternate, often slightly involute, sessile or subsessile. *Inflorescences* racemose. *Flowers* bisexual, 4-merous; bracteoles present; hypanthium cylindrical, articulated above ovary, basal portion persistent. *Petaloid scales* 4, 8, or 12, surrounded by stiff erect hairs. *Androecium* haplostemonous, stamens 4 in one whorl, alternisealous, $\pm$ included; anthers $\pm$ sessile, basifixed. *Hypogynous disc* small, cupular or lobed, rarely absent. *Ovary* 1-locular, usually glabrous; style lateral, stigma capitate, shortly papillate, included. *Fruit* an achene, enclosed in persistent base of hypanthium. (Wright, 1915; Herber, 2003)

Diagnostic characters. – *Struthiola* is distinguished by its spicate inflorescence of 4-merous flowers with four alternisealous stamens and 4, 8, or 12 petaloid scales each surrounded by a tuft of stiff hairs.

Distribution. – ± 40 species; mainly South Africa but also tropical Africa.

12. ***Kelleria*** Endl., Gen. Pl. suppl. 4: 61. 1848 – Type: *Kelleria dieffenbachii* (Hook.) Endl. ($\equiv$ *Drapetes dieffenbachii* Hook.).

Description. – Perennial shrublets or subshrubs, occasionally forming loose mats. *Leaves* alternate, sessile, occasionally involute, usually ericoid. *Inflorescences* a terminal, capitate, enclosed by leafy bracts. *Flowers* hermaphrodite or unisexual, sessile or shortly pedicellate; pedicel densely hirsute; hypanthium cylindrical, not articulated, caducous; sepals 4, spreading. *Petaloid scales* 8 or occasionally 4, minute. *Androecium* haplostemonous, stamens 4, alternisealous, shortly exserted; male flowers with pistillode. *Hypogynous disc* absent; female flowers with staminodia. *Ovary* 1-locular, sessile, glabrous or apically puberulous; style lateral, stigma capitate with short papillae. *Fruit* an achene. (Heads, 1990; Herber, 2003)

Diagnostic characters. – *Kelleria* is distinct in its capitate inflorescence of haplostemonous flowers with four stamens and unarticulated hypanthium.

Distribution. – 11 species; New Zealand, Australia and Malaysia.

13. ***Drapetes*** Banks ex Lam. in J. Hist. Nat. 1: 188. 1792 – Type: *Drapetes muscosus* Lam.

Description. – Perennial subshrub, forming a moss-like mat. *Leaves* opposite-decussate, sessile. *Inflorescence* terminal, umbellate, few-flowered, involucre of leafy bracts; peduncle elongated in fruit. *Flowers* bisexual, 4-merous; hypanthium tubular, articulated above ovary, basal portion persistent. *Petaloid scales* absent. *Androecium* haplostemonous, stamens 4, alternisepalous; anthers exerted, basifixed, introrse. *Hypogynous disc* absent. *Ovary* 1-locular, sessile, apically pubescent; style terminal. *Fruit* an achene. (Heads, 1990; Herber, 2003)

Diagnostic characters. – *Drapetes* is distinct in its moss-like habit and 4-merous flowers lacking petaloid scales and with haplostemonous androecium.

Distribution. – Monotypic; Patagonia and Falkland Islands.

14. ***Basutica*** E.Phillips in J. S. African Bot. 10: 64. 1944 – Type: *Basutica aberrans* (C.H.Wright) E.Phillips (≡ *Gnidia aberrans* C.H.Wright).

= *Nectandra* P.J.Bergius, Descr. Pl. Cap.: 131. 1767, nom. rej. – Type: *Nectandra sericea* (L.) P.J.Bergius (≡ *Passerina sericea* L.).

= *Pseudognidia* E.Phillips in J. S. African Bot. 10: 63. 1944 – Type: *Pseudognidia anomala* (Meisn.) E.Phillips (≡ *Gnidia anomala* Meisn.), **syn. nov.**

Description. – Shrubs or subshrubs, single- or multi-stemmed. *Leaves* alternate or opposite, decussate or distichous, ovate to linear-subulate, sessile, glabrous or persistently densely silky on one or both surfaces. *Inflorescences* terminal or axillary umbel, 1- or few-flowered; involucre foliaceous. *Flowers* bisexual, 4-merous, sessile, pale yellow or blue; hypanthium cylindrical, articulated above ovary with basal portion persistent, densely hairy, mostly white silky or woolly. *Petaloid scales* 4 or 8, minute, glabrous or alternating with tuft of short hairs. *Androecium* dispostemonous or rarely haplostemonous, stamens (4)8 in two whorls, subsessile, upper whorl shortly exerted, sometimes reduced to staminodes or completely absent, lower whorl included in upper part of calyx-tube slightly below upper whorl; anthers basifixed. *Hypogynous disc* present. *Ovary* 1-locular, glabrous or puberulous, sometimes only apically; style lateral; stigma capitate, shortly papillate, included. *Fruit* an achene, enclosed in persistent base of hypanthium.

Diagnostic characters. – *Basutica* is mainly distinguished from other genera in the “*Gnidia* group” by its densely hairy hypanthium, mostly white woolly or silky. The minute scales are either 4 or 8, and glabrous or alternating with tufts of hairs. The flowers are either pale yellow or pale blue. Minute scales are also found in some species of *Lasiosiphon* but that genus is readily distinguished from *Basutica* by the pedunculate inflorescence of bright yellow, orange or red flowers with mostly papyraceous or petaloid, colourful involucral bracts and densely hairy pedicels.

Distribution. – 31 species; mainly southern Africa with one species (*Gnidia fastigiata*) extending into tropical East Africa.

Basutica aberrans (C.H.Wright) E.Phillips in J. S. African Bot. 10: 64. 1944 ≡ *Gnidia aberrans* C.H.Wright in Thiselton-Dyer, Fl. Cap. [Harvey] 5(2): 584. 1925 – Holotype: South Africa, KwaZulu-Natal, “Giant’s Castle Pass”, 23 Oct 1907, *Wylie sub Wood 10611* (K barcode K000322565!; isotype: K barcode K000322564!).

Basutica anomala (Meisn.) Olaniyan, **comb. nov.** ≡ *Gnidia anomala* Meisn. in Linnaea 14(5): 435–436. 1841 (“1840”) ≡ *Pseudognidia anomala* (Meisn.) E.Phillips in J. S. African Bot. 10: 64. 1944 – Type: South Africa, western Cape, “[Sir] Lowry’s Pass”, without date, *Drège 7348a* (not located).

Basutica baurii (C.H.Wright) Olaniyan, **comb. nov.** ≡ *Gnidia baurii* C.H.Wright in Thiselton-Dyer, Fl. Cap. [Harvey] 5(2): 61. 1915 – Holotype: South Africa, Eastern Cape, “Tembuland, Bazeia Mountain”, Nov without year, *Baur 732* (K barcode K000322569!; isotype: NU barcode NU0015515-0!).

Basutica burmanni (Eckl. & Zeyh. ex Meisn.) Olaniyan, **comb. nov.** ≡ *Gnidia burmanni* Eckl. & Zeyh. ex Meisn. in Candolle, Prodr. 14(2): 583. 1857 – Syntypes: South Africa, Western Cape, Cape Peninsula, “montis Leonis”, *Ecklon [& Zeyher] 85* (LD barcode 1501899!); South Africa, without locality, *Zeyher s.n.* (Herb. Sieber 63) (JE barcode JE00003402!).

Basutica caniflora (Meisn.) Olaniyan, **comb. nov.** ≡ *Gnidia caniflora* Meisn. in Linnaea 14(5): 440. 1841 (“1840”) – Holotype?: South Africa, Western Cape, “Giftberg”, without date, *Drège 7357* (NY? n.v.; isotype?: P barcode P00541069!).

Basutica cayleyi (C.H.Wright) Olaniyan, **comb. nov.** ≡ *Gnidia cayleyi* C.H.Wright in Thiselton-Dyer, Fl. Cap. [Harvey] 5(2): 57. 1915 – Holotype: South Africa, “C.B.S.”, *Cayley s.n.* (K barcode K000322519!).

Basutica chrysophylla (Meisn.) Olaniyan, **comb. nov.** ≡ *Gnidia chrysophylla* Meisn. in Candolle, Prodr. 14(2): 584. 1857 – Holotype: South Africa, Western Cape, “Kars-rivier”, 4 Oct 1826, *Ecklon 86* (NY barcode 1288008!).

Basutica clavata (Schinz) Olaniyan, **comb. nov.** ≡ *Gnidia clavata* Schinz in Vierteljahrsschr. Naturf. Ges. Zürich 66: 232–233. 1921 – Syntypes: South Africa, Western Cape, “Olifant Rivier Bergen”, 31 Aug 1894, *Schlechter 5101* (GH barcode 00443742!, K barcode K000322573!, P barcode P00648790!, S Nos. S09-16150!, S09-16151!).

Basutica cyanea (Burch.) Olaniyan, **comb. nov.** ≡ *Gnidia cyanea* Burch., Trav. S. Africa 1: 255, 257. 1822 – Holotype: South Africa, Northern Cape, “Roggeveld”, 6 Aug

1811, *Burchell 1316* (K barcode K000322570!; isotypes: GH barcode 00443743!, NY barcode 1288018!).

Basutica ericoides (C.H.Wright) Olaniyan, **comb. nov.** ≡ *Gnidia ericoides* C.H.Wright in Thiselton-Dyer, Fl. Cap. [Harvey] 5(2): 58. 1915 – Holotype: South Africa, Western Cape, “Tygerfontein”, 26 Sep 1897, *Galpin 4523* (K barcode K000332579!).

Basutica fastigiata (Rendle) Olaniyan, **comb. nov.** ≡ *Gnidia fastigiata* Rendle in Trans. Linn. Soc. London, Bot. 4 (1): 41. 1894 – Holotype: Malawi, “Milanji”, Nov 1891, *Whyte s.n.* (K barcode K0003225971!; isotype: BM barcode BM000910851!).

Basutica francisci (Bolos) Olaniyan, **comb. nov.** ≡ *Gnidia francisci* Bolus in Trans. S. African Philos. Soc. 16: 399. 1906 – Holotype: South Africa, Western Cape, “Zwartberg Pass”, Dec 1904, *Bolus 11631* (BOL barcode BOL0306072!; isotype: K barcode K000322577!).

Basutica geminiflora (E.Mey. ex Meisn.) Olaniyan, **comb. nov.** ≡ *Gnidia geminiflora* E.Mey. ex Meisn. in Linnaea 14(5): 441–442. 1841 (“1840”) – Syntypes: South Africa, Northern Cape, “Mierenkasteel et Zwartdoornrivier”, *Drège s.n.* (HAL barcode HAL0111676!, HBG barcode HBG512574!, K barcodes K000322587!, K000322588!, MO barcode MO-313236 [No. 5692790]!, NY barcode 1287722!, P barcode P00541062!).

Basutica harveyana (Meisn.) Olaniyan, **comb. nov.** ≡ *Gnidia harveyana* Meisn. in Linnaea 14(5): 437. 1841 (“1840”) – Type: South Africa, “Africa Capensi”, without locality and date, *Drège s.n.* (not located).

Basutica imbricata (L.f.) Olaniyan, **comb. nov.** ≡ *Gnidia imbricata* L.f., Suppl. Pl.: 225. 1782 – Lectotype (designated by Rogers in Taxon 55(2): 486. 2006): South Africa, “Cap. b. spei.”, without date, *Thunberg s.n.* (UPS-THUNB No. 9552 n.v.; isoelectotype: SBT barcode SBT12536!).

Basutica inconspicua (Meisn.) Olaniyan, **comb. nov.** ≡ *Gnidia inconspicua* Meisn. in Linnaea 14(5): 433–434. 1841 (“1840”) – Holotype: South Africa, “Africa Capensi”, without date, *Drège 7349* (NY barcode 1287799!; isotype: P barcode P00541060!).

= *Passerina inconspicua* Meisn. in Linnaea 14(5): 397–398. 1841 (“1840”) ≡ *Arthrosolen inconspicuus* (Meisn.) Meisn. in Candolle, Prodr. 14(2): 560. 1857 – Holotype: South Africa, without locality or date, *Drège 7372* (NY barcode 1288005!; isotype: P barcode P00113303!).

Basutica leipoldtii (C.H.Wright) Olaniyan, **comb. nov.** ≡ *Gnidia leipoldtii* C.H.Wright in Thiselton-Dyer, Fl. Cap.

[Harvey] 5(2): 64. 1915 – **Lectotype (designated here):** South Africa, Northern Cape, “Nieuwoudtville, Willems River, and Bokkeveldt Mountains”, without date, *Leipoldt 882* (BOL barcode BOL136952!; isoelectotypes: K barcodes K000322520!, K000322521!, NBG barcode NBG0100229-0!, PRE barcodes PRE0617456-0!, PRE0587578-0!).

Basutica linoides (Thunb.) Olaniyan, **comb. nov.** ≡ *Passerina linoides* Thunb., Prodr. Pl. Cap. 1: 75. 1794 ≡ *Gnidia linoides* (Thunb.) Wikstr., Kongl. Vetensk. Acad. Handl. 1818: 316. 1818 ≡ *Craspedostoma linoides* (Thunb.) Domke in Biblioth. Bot. 27(111): 95. 1934 – Syntypes: South Africa, without locality and date, *Thunberg s.n.* (S Nos. S09-16241!, S09-16242!, UPS-THUNB Nos. 9585 n.v. & 9586 n.v.).

Basutica nitida (Bolos ex C.H.Wright) Olaniyan, **comb. nov.** ≡ *Gnidia nitida* Bolus ex C.H.Wright in Thiselton-Dyer, Fl. Cap. [Harvey] 5(2): 64. 1915 – Holotype: South Africa, Northern Cape, “near Ookiep” 1 Sep 1883, *Bolus 689* (BOL barcode BOL136953!; isotypes: GH barcode 00443752!, GRA barcode GRA0027031!, K barcode K000322524!, P barcode P00648772!, PRE barcode PRE0297721-0!).

Basutica nodiflora (Meisn.) Olaniyan, **comb. nov.** ≡ *Gnidia nodiflora* Meisn. in Linnaea 14(5): 458–459. 1841 (“1840”) – Syntype: South Africa, Western Cape, “Hoogekraalsrivier” 19 Sep 1831, *Drège s.n.* (HAL barcode HAL0111688!, K barcode K0003225231!, MO barcode MO-313070 [No. 5692788]!, P barcode P00541054!, S No. S-11-24270!).

Basutica propinqua Hilliard in Notes Roy. Bot. Gard. Edinburgh 31(1): 31–32. 1971 ≡ *Gnidia propinqua* (Hilliard) B.Peterson in Bothalia 14(1): 82. 1982 – Holotype: Lesotho, “entrance to Bushman’s River Pass”, 5 Dec 1987, *Wright 333* (NU barcode NU15536!; E barcode E00193578!, K barcode K000324177!).

Basutica renniana (Hilliard & B.L.Burt) Olaniyan, **comb. nov.** ≡ *Gnidia renniana* Hilliard & B.L.Burt in Notes Roy. Bot. Gard. Edinburgh 43(2): 218–219. 1986 – Holotype: South Africa, KwaZulu-Natal, Polela District, “Sunset & Glengariff farms”, 10 Oct 1984, *Rennie 1433* (NU barcode NU0015517-0!); isotypes: E barcode E00193581!, K barcode K000324176!, PRE barcode PRE0587579-0!).

Basutica scabra (Thunb.) Olaniyan, **comb. nov.** ≡ *Gnidia scabra* Thunb., Prodr. Pl. Cap. 1: 76. 1794 – Holotype: South Africa, without locality and date, *Thunberg s.n.* (UPS-THUNB No. 9557 n.v.; isotype: SBT barcode SBT12540!).

Basutica sericea (L.). Olaniyan, **comb. nov.** $\equiv$ *Passerina sericea* L., Cent. Pl. II: 15. 1756 $\equiv$ *Lachnaea sericea* (L.) Crantz, Inst. Rei Herb. 1: 129. 1766 $\equiv$ *Nectandra sericea* (L.) P.J.Bergius, Descr. Pl. Cap.: 131. 1767 $\equiv$ *Gnidia sericea* (L.) L., Syst. Nat., ed. 12, 2: 272. 1767 – Lectotype (designated by Rogers in Taxon 55: 487. 2006): South Africa, “*Passerina (sericea)* foliis ovatis tomentosis, caule hirsuto, floribus coronatis ...”, Herb. Burman (G n.v.).

Basutica singularis (Hilliard) Olaniyan, **comb. nov.** $\equiv$ *Gnidia singularis* Hilliard in Notes Roy. Bot. Gard. Edinburgh 45(2): 196–197. 1989 – Holotype: Lesotho, “Sani Pass Top”, Feb 1985, Manning 554 (E barcode E00193580!; isotypes: K barcode K000322550!, NU barcode NU0015535-0!).

Basutica strigillosa (Meisn.) Olaniyan, **comb. nov.** $\equiv$ *Gnidia strigillosa* Meisn. in Linnaea 14(5): 459–460. 1841 (“1840”) – Holotype: South Africa, Eastern Cape, “Blesbokvlakte”, Drège s.n. (NY barcode 1287802!; isotype: TUB barcode TUB002881!).

Basutica tenella (Meisn.) Olaniyan, **comb. nov.** $\equiv$ *Gnidia tenella* Meisn. in London J. Bot. 2: 554 [as ‘454’, printing error]. 1843 – Holotype: South Africa, Western Cape, “Constantiaberg”, Sep 1838, Krauss 776 (NY barcode 1287775!; isotypes: MO barcode MO-313083 [No. 5414528]!, P barcode P00541043!, TUB barcode TUB002884!).

Basutica virescens (Wikstr.) Olaniyan, **comb. nov.** $\equiv$ *Gnidia virescens* Wikstr. in Kongl. Vetensk. Acad. Handl. 1818: 317. 1818 – Holotype: South Africa, “*Passerina anthylloides* α ad. Promont. b. spei”, without date, Thunberg s.n. (UPS-THUNB No. 9565 n.v.).
 $\equiv$ *Gnidia denudata* Lindl. in Bot. Reg. 9: t. 757. 1823 $\equiv$ *Gnidia imbricata* var. *denudata* (Lindl.) Ker Gawl. in Bot. Reg. 9: t. 2. 1823 – Holotype: Without locality and date, cultivated at Mr. Colvill’s Nursery, Chelsea, Lindley s.n. (CGE barcode 00060!).

Note. – *Gnidia virescens* Wikstr. was treated by Meisner (1857) as possibly conspecific with *G. denudata* Lindl. but was later regarded by Wright (1915) as a synonym of *Lasiosiphon anthylloides* (L.f.) Meisn. This confusion likely stems from the fact that Thunberg has two sheets under the name *Passerina anthylloides* in his herbarium: the first, labelled α (UPS-THUNB No. 9565) is the type of *G. virescens* as designated by Wikström (1818), and the second, labelled β (UPS-THUNB No. 9566) is true *P. anthylloides* L.f. In his description of *G. virescens*, Wikström (1818) noted its superficial similarity to *P. anthylloides* but distinguished it from that species by, *inter alia*, its fewer-flowered heads of less villous, tetramerous flowers with small petaloid scales less than half as long as the lobes versus the many-flowered heads of villous, pentamerous flowers with large petaloid scales of the latter. These diagnostic features of *G. virescens* are

perfectly consonant with *G. denudata* and confirm Meisner’s suspicion that the two are conspecific, with *G. virescens* having nomenclatural priority.

Poorly known species

The types of the following species could not be located, and they have not been recollected since their original description. We have therefore followed the descriptions provided by Wright (1915) to assign these species to the genus *Basutica*.

Basutica multiflora (Bartl. ex Meisn.) Olaniyan, **comb. nov.** $\equiv$ *Gnidia multiflora* Bartl. ex Meisn. in Linnaea 14(5): 462–463. 1841 (“1840”) – Type: South Africa, without locality or collector (B, not located).

Basutica sparsiflora (Bartl. ex Meisn.) Olaniyan, **comb. nov.** $\equiv$ *Gnidia sparsiflora* Bartl. ex Meisn. in Linnaea 14(5): 462. 1841 (“1840”) – Type: South Africa, Western Cape, “Autniqua” [Outeniqua Mtns], without date or collector (B, not located).

Basutica stellatifolia (Gand.) Olaniyan, **comb. nov.** $\equiv$ *Gnidia stellatifolia* Gand. in Bull. Soc. Bot. France 60: 417. 1913 – Type: South Africa, KwaZulu-Natal, “Pinetown”, Wood 6489 (not located).

15. ***Passerina*** L., Sp. Pl.: 559. 1753 – Type: *Passerina filiformis* L.
 $\equiv$ *Chymococca* Meisn. in Candolle, Prodr. 14(2): 565. 1857 – Type: *Chymococca empetroides* Meisn. (= *Passerina ericoides* L.).

Description. – Shrubs or small trees. *Leaves* opposite-decussate, sessile, usually involute and inversely ericoid. *Inflorescences* spicate, usually proliferating; bracts $\pm$ foliose, winged. *Flowers* bisexual, 4-merous, sessile, or subsessile; hypanthium funnel-shaped or cylindrical, not articulated, persistent, rarely caducous; sepals flexed in flower. *Petaloid scales* absent. *Androecium* diplostemonous, stamens $8 \pm$ in one whorl; anthers exerted, extrorse. *Hypogynous disc* absent. *Ovary* 1-locular, subsessile, glabrous; style lateral; stigma $\pm$ globose, mop-like or penicillate, reaching beyond hypanthium rim. *Fruit* an achene or rarely a 1-seeded berry. (Bredenkamp & Van Wyk, 2003; Herber, 2003)

Diagnostic characters. – *Passerina* is distinguished from other genera in the group by its inversely ericoid leaves and spicate inflorescences of flowers with $\pm$ one whorl of 8, distinctly exerted stamens with extrorse anthers.

Distribution. – ± 20 species; mainly South Africa with a few species extending into adjacent southern Tropical Africa.

16. ***Craspedostoma*** Domke in Biblioth. Bot. 27(111): 135. 1934 – Type: *Craspedostoma cephalotes* (Lichtenst. ex Meisn.) Domke (= *Craspedostoma linearifolium* (Wikstr.) Olaniyan).
 $\equiv$ *Struthiolopsis* E.Phillips in J. S. African Bot. 10: 64–65. 1944 – Type: *Struthiolopsis pulvinata* (Bolos) E.Phillips

(= *Gnidia pulvinata* Bolus; = *Craspedostoma nanum* (L.f.) Olaniyan), **syn. nov.**

Description. – Shrubs or undershrubs, young branches pubescent or pilose. *Leaves* alternate, coriaceous, ovate to lanceolate, sessile, minutely tuberculate, glabrous, rarely penicillate or margins ciliate, adaxial surface shining. *Inflorescence* terminal umbel, 2- to 6-flowered, sessile; involucre foliaceous. *Flowers* bisexual, 4-merous, sessile, lilac to dull purple or bluish; hypanthium slender, cylindrical, articulated and circumscissile above ovary, densely adpressed pubescent above, glabrous below; basal portion persistent. *Petaloid scales* 4 or rarely 8, either slightly emarginate and sparsely hairy or partite into segments interspersed with hairs. *Androecium* diplostemonous, stamens 8 in two whorls, subsessile, upper row sometimes reduced to staminodes, if present then shortly exerted, lower whorl included; anthers dorsifixed. *Ovary* 1-locular, glabrous except for a few short erect hairs at apex; style lateral; stigma conical, included. *Hypogynous disc* present. *Fruit* an achene, enclosed in persistent base of hypanthium.

Diagnostic characters. – *Craspedostoma* is distinguished from other genera in the “*Gnidia* group” by its lilac to dull purple or bluish flowers with conical stigma. It is also distinct in its linear-lanceolate leaves that are often glabrous or with ciliate margins, and glossy with scabrous or minutely tuberculate lower surface.

Distribution. – 5 species; South Africa in the Core Cape Floristic Region.

Craspedostoma linearifolium (Wikstr.) Olaniyan, **comb. nov.** = *Passerina linearifolia* Wikstr. in Kongl. Vetensk. Acad. Handl. 1818: 343. 1818 = *Gnidia linearifolia* (Wikstr.) B.Peterson in Bot. Not. 112: 470. 1959 – Holotype: South Africa, Western Cape “Cap. b. spei” [Cape of Good Hope], without date, *Thunberg s.n.* (SBT barcode SBT12527!; isotype: S No. S-G-004578!).

Craspedostoma nanum (L.f.) Olaniyan, **comb. nov.** = *Struthiola nana* L.f., Suppl. Pl.: 128. 1782 = *Gnidia nana* (L.f.) Wikstr. in Kongl. Vetensk. Acad. Handl. 1818: 316. 1818 – Lectotype (designated by Peterson in Bot. Not. 112: 467. 1959): South Africa, Western Cape, without date and locality, *Thunberg s.n.* (UPS-THUNB No. 3733 n.v.; isoelectotype: S No. S5-9776!).

Craspedostoma penicillatum (Licht. ex Meisn.) Domke in Biblioth. Bot. 27(111): 146. 1934 (‘*penicillata*’) = *Gnidia penicillata* Licht. ex Meisn. in Linnaea 14(5): 448–449. 1841 (“1840”) – Lectotype (designated by Olaniyan & al. in S. African J. Bot. 163: 369. 2023): South Africa, Western Cape, “Lowryspas” [Sir Lowry’s Pass], Dec without year, *Drege s.n.* (P barcode P00541047!; isoelectotypes: HAL barcode HAL0111542!, HBG barcode HBG512591!, HEID barcode HEID702627!, MO barcode MO313235 [No. 5692787]!, PRE

barcode PRE0300740!, S No. S-11-24348!, TUB barcode TUB002879!; possible isoelectotype: B-W 07576 -01 0!).

Craspedostoma scabridum (Meisn.) Olaniyan, **comb. nov.** = *Gnidia scabrida* Meisn. in Linnaea 14(5): 446–447. 1841 (“1840”) – Lectotype (designated by Olaniyan & al. in S. African J. Bot. 163: 369. 2023): South Africa, Western Cape, “in dumetis montanis prope” 28 Aug 1831, *Drege 7356* (P barcode P00541096!).

Craspedostoma tomentosum (L.) Olaniyan, **comb. nov.** = *Gnidia tomentosa* L., Sp. Pl.: 358. 1753 – Neotype (designated by Rogers in Taxon 55: 486. 2006): South Africa, Western Cape, “Cape Peninsula, Kalk Bay Mountain”, 2 Jun 1974, *Goldblatt 2024* (MO barcode MO-439646 [No. 2243060]!).

17. ***Lachnaea*** L., Sp. Pl.: 560. 1753 – Type (designated by Domke in Biblioth. Bot. 27(111): 137. 1934): *Lachnaea eriocephala* L.

= *Cryptadenia* Meisn. in Linnaea 14: 404–405. 1841 (“1840”) – Type (designated by Domke in Biblioth. Bot. 27(111): 137. 1934): *Cryptadenia grandiflora* (L.f.) Meisn. (= *Passerina grandiflora* L.f.).

– “*Calysericos* Eckl. & Zeyh. ex Meisn.” in Candolle, Prodr. 14(2): 573. 1857, nom. nud.

Description. – Shrubs or shrublets single-stemmed or multi-stemmed. *Leaves* alternate or opposite-decussate, glabrous or occasionally penicillate or margins ciliate, sessile. *Inflorescences* terminal or axillary capitulum or determinate umbel or 1-flowered; involucre foliaceous. *Flowers* bisexual, 4-merous, often zygomorphic, sessile or pedicellate; hypanthium cylindrical, campanulate or funnel-shaped, articulated above ovary, lower part persistent. *Petaloid scales* 8, inserted below stamens. *Androecium* diplostemonous, stamens 8 in two whorls, antesealous ones sometimes longer, occasionally adnate to sepal bases. *Hypogynous disc* absent. *Ovary* 1-locular, sessile, usually glabrous; style lateral, rarely pubescent; stigma penicillate, capitate, or conical. *Fruit* an achene, enclosed in persistent base of hypanthium. (Beyers, 2001; Herber, 2003)

Diagnostic characters. – *Lachnaea* is distinguished by its eight petaloid scales that are inserted below the antesealous stamens. All other genera in the group with petaloid scales have these inserted above or at the same level as the upper whorl of stamens.

Distribution. – ±20 species; mainly South Africa with two species extending into Mozambique and Zimbabwe.

■ AUTHOR CONTRIBUTIONS

ODO: Laboratory performance of the research, data analyses, and writing of the first draft of the manuscript. JSB: Conceptualization of the research, interpretation of the result, taxonomic and nomenclatural

treatment, field and herbarium collections, reviewing and editing of the manuscript. ARM: Conceptualization of the research, interpretation of the result, taxonomic and nomenclatural treatment, herbarium collections, reviewing and editing of the manuscript. JCM: Field and herbarium collections, supervision of herbarium work, taxonomic and nomenclatural treatment, reviewing and editing of the manuscript. MVDB: Funding of the project, supervision of the laboratory work, data analyses, reviewing and editing of the manuscript.

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Appendix 1. Voucher information and GenBank accession numbers (*trnL-F*, *rbcL*, *rps16*, *matK*, ITS) for taxa used in this study. DNA sequences obtained from GenBank are indicated by ¹Van der Bank & al. (2002), ²Rautenbach (2006), ³Beaumont & al. (2009), ⁴Motsi & al. (2010), ⁵Farah & al. (2018), ⁶Maurin & al. (2013), ⁷Van Niekerk (2005), ⁸Robinson (2004), ⁹Hollingsworth & al. (2009), ¹⁰Charles-Dominique & al. (2016), ¹¹Fay & al. (1998), ¹²Oguri & al. (2017), ¹³Galicia-Herbada (2006) and ¹⁴Olaniyan & al. (2024). “*” represents the sequences generated in this study, while “–” represents the regions that were not sequenced.

Aquilaria agallochum Roxb. ex Finl., India, Lee & Mohamed JAI0001 (UPM), MF443412⁵, –, –, MF443398⁵, MH134137⁵. *Aquilaria beccariana* Tiegh., Malaysia, Chase 1380 (K), AJ308643¹, Y15149¹, –, –, *Arnhemia cryptantha* Airy Shaw, Australia, Lazarides 7870 (K), AJ308678¹, AJ297236¹, –, –, *Craetorsiphon scandens* Engl. & Gilg, Western Africa, Lock 84/84 (K), AJ297235¹, –, –, *Dais cotinifolia* L., South Africa, OM 1708 (JRAU), OK647912*, OK412929*, OK504560*, –, OK647863*. *Daphne mezereum* L., Europe, Chase 6357 (K), AJ308645¹, AJ297233¹, –, –, AJ744931¹. *Deltaria brachyblastophora* Steenis, New Caledonia, McPherson 4965 (K), AM404304², AM398174², –, –, *Diarthron vesiculosum* (Fisch. & C.A.Mey. ex Kar. & Kir.) C.A.Mey., Türkiye, Merton 3960 (K), AJ308646¹, AM398181¹, –, –, *Dicranolepis disticha* Planch., Cameroon, Gereau & al. 5626 (MO), AM404352², AM398182², –, –, *Dirca palustris* L., United States of America, Horn 12584 (NBVC), AJ308647¹, U26322¹, –, –, *Drapetes muscosus* Lam., –, Kubitzki & Feuerey 99-34 (HBG), AJ308648¹, AJ297237¹, –, –, AM159529¹. *Edgeworthia chrysantha* Lindl., –, Chase 6338 (K), AJ308649¹, AJ297920¹, –, –, AJ744932¹. *Englerodaphne ovalifolia* (Meisn.) E.P. Phillips, South Africa, Abbott 9108 (JRAU), OK647913*, OK412930*, OK504560*, JX517508⁶, OK647864*. *Englerodaphne pilosa* Burtt Davy, South Africa, OM 1893 (JRAU), OK647914*, OK412931*, OK504561*, JX572552*, OK647865*. *Englerodaphne subcordata* (Meisn.) Engl., South Africa, Ward-Hilhorst 524 (PRE), OK647915*, OK412932*, OK504562*, OK403282*, OK647866*. *Enkleia siamensis* (Kurz) Nevling, –, Von Beusekam 4060 (K), AJ308664¹, AJ297921¹, –, –, *Gnidia aberrans* C.H. Wright, South Africa, Koekemoer M1595 (PRE), OP437538¹⁴, OK412957*, OP437524¹⁴, OK403285*, OK647867*. *Gnidia anomala* Meisn., South Africa, Duncan G.D. 511 (NBG), OK647916*, OK412958*, OK504563*, –, OK647868*. *Gnidia baurii* C.H. Wright, South Africa, Goldblatt & Manning 14237 (NBG), OK647917*, OK412961*, –, –, OK647869*. *Gnidia burmanni* Eckl. & Zeyh. ex Meisn., South Africa, Odette Curtis 468 (NBG), OP437539¹⁴, OK412952*, OP437525¹⁴, OK403288*, OK647870*. *Gnidia caniflora* Meisn., South Africa, Helme 4196 (NBG), –, OK412951*, –, –, OK647871*. *Gnidia chrysophylla* Meisn., South Africa, TCM 56 (NBG), OP437542*, OP437513*, –, –, OP437502*, –, *Gnidia clavata* Schinz, South Africa, Helme 4600 (NBG), OK647918*, OK412959*, OK504564*, OK403292*, OK647872*. *Gnidia compacta* (C.H. Wright) J.H. Ross, South Africa, Manning 3639 (NBG), OK647919*, OK412940*, OK504565*, OK403274*, OK647873*. *Gnidia coriacea* Meisn., South Africa, Mark Johns s.n. (Kogelberg Reserve Field Herbarium), AM404227², AM162516², OK504566*, OK403276*, AM159512². *Gnidia cyanea* Burch., South Africa, Manning 3749 (NBG), OK647920*, OK412954*, OK504567*, OK403284*, OK647874*. *Gnidia ericoides* C.H. Wright, South Africa, J.P.H. Acocks 23088 (PRE), OP437543¹⁴, OP437515¹⁴, OP437528¹⁴, –, –, *Gnidia fastigiata* Rendle, South Africa, Manning 3663 (NBG), OK647921*, OK412950*, OK504568*, OK403287*, OK647875*. *Gnidia francisci* Bolus, South Africa, Helme N.A. 3901 (NBG), –, OP437514*, OP437529*, OP437503*, –, *Gnidia galpinii* C.H. Wright, South Africa, Mark Johns s.n. (Kogelberg Reserve Field Herbarium), AM404230², AM396994², OK504569*, OK403279*, AM159516². *Gnidia gymnostachya* Gilg, South Africa, Angela Beaumont s.n. (NU), OK647922*, OK412939*, OK504570*, OK403273*, OK647876*. *Gnidia harveyana* Meisn., South Africa, TCM 62 (NBG), OP437544*, OP437516*, OP437530*, OP437504*, –, *Gnidia humilis* Meisn., South Africa, Mark Johns s.n. (Kogelberg Reserve Field Herbarium), AM404236², AM162510², OK504571*, OK403280*, AM159517². *Gnidia imbricata* L.f., South Africa, W.J. Hanekom 2349 (PRE), OP437545¹⁴, OP437517¹⁴, OP437531¹⁴, OP437505¹⁴, OP456325¹⁴. *Gnidia inconspicua* Meisn., South Africa, Nicholson & Roets 456 (NBG), OK647923*, OK412953*, OK504572*, OK403289*, OK647877*. *Gnidia insignis* Compton, South Africa, Helme 4109 (NBG), OK647924*, OK412933*, –, –, OK647878*. *Gnidia juniperifolia* Lam., South Africa, Manning 3700 (NBG), OK647925*, OK412936*, OK504573*, OK403281*, OK647879*. *Gnidia laxa* Gilg, South Africa, Strohbach 3 (NBG), OK647926*, OK412943*, OK504574*, OK403269*, OK647880*. *Gnidia leipoldtii* C.H. Wright, South Africa, Pretorius, W.A.J. 420 (PRE), OP437546*, OP437518*, OP437532*, OP437506*, OP456326*. *Gnidia linearifolia* (Wikstr.) B. Peterson, South Africa, Runnals 560 (NBG), OK647927*, OK412965*, OK504575*, OK403305*, OK647881*. *Gnidia linoides* Wikstr., South Africa, Oliver 9 (NBG), OK647928*, OK412960*, –, –, OK647882*. *Gnidia meyeri* Meisn., South Africa, Manning 3750 (NBG), OK647929*, OK412924*, –, –, OK403256*, OK647883*. *Gnidia myrtifolia* C.H. Wright, South Africa, Helme 3199 (NBG), –, OK412970*, –, –, OK647884*. *Gnidia nana* (L.f.) Wikstr., South Africa, Beyers 263 (NBG), OK647930*, OK412968*, OK504576*, OK403306*, OK647885*. *Gnidia nitida* Bolus ex C.H. Wright, South Africa, Helme N.A. 7884 (NBG), –, OP437519*, OP437533*, OP437507*, –, *Gnidia nodiflora* Meisn., South Africa, Rogers, Applequist & Dold 1031 (NBG), OK647932*, OK412962*, OK504578*, –, OK647887*. *Gnidia obtusissima* Meisn., South Africa, Helme 2009 (NBG), OK647933*, OK412945*, OK504579*, OK403270*, OK647888*. *Gnidia*

Appendix 1. Continued.

oppositifolia L., South Africa, Manning 3707 (NBG), OK647934*, OK412935*, OK504580*, OK403283*, OK647889*. *Gnidia ornata* Meisn. (Gilg), South Africa, Mucina 141006/22 (NBG), OK647935*, OK412941*, OK504581*, OK403271*, OK647890*. *Gnidia penicillata* Licht. ex Meisn., South Africa, Olaniyan 003 (NBG), OK647937*, OK412966*, OK504583*, OK403307*, OK647892*. *Gnidia phaeotricha* Gilg, South Africa, Balkwill 10316 (MO), –, AM162517², –, FJ572798², AM159520². *Gnidia pinifolia* L., South Africa, Manning 3852 (NBG), OK647938*, OK412927*, OK504584*, OK403258*, OK647893*. *Gnidia propinqua* (Hilliard) B.Peterson, South Africa, Morris C. 299 (PRE), OP437548*, OK412956*, OP437537*, OK403286*, –, *Gnidia racemosa* Thunb., South Africa, Beaumont s.n. (NU), AJ308665¹, AJ295268¹, –, –, AM159522². *Gnidia renniana* Hilliard & B.L.Burt, South Africa, Beaumont s.n. (NU), AM404233², AM162519², –, –, AM396522². *Gnidia scabra* Thunb., South Africa, Schmid 116979 (NBG), OK647939*, OK412963*, OK504585*, –, –, *Gnidia sericea* L. var. *sericea*, South Africa, Rogers 1074 (NBG), OK647940*, OK412955*, OK504586*, OK403290*, OK647894*. *Gnidia setosa* (Thunb.) Wikstr., South Africa, Euston-Brown 4/1 (NBG), –, OK412923*, –, –, OK647895*. *Gnidia sonderiana* Meisn., South Africa, Helme 3835 (NBG), OK647941*, OK412938*, OK504587*, OK403278*, OK647896*. *Gnidia spicata* (L.f.) Gilg, South Africa, Husted LBH 564 (NBG), OK647942*, OK412942*, –, OK403272*, OK647897*. *Gnidia squarrosa* (L.) Druce, South Africa, Mark John s.n. (Kogelberg Reserve Field Herbarium), OK647943*, OK412946*, OK504588*, OK403268*, OK647898*. *Gnidia styphelioides* Meisn., South Africa, OM 201 (JRAU), OK647944*, OK412937*, OK504589*, OK403277*, OK647899*. *Gnidia tenella* Meisn., South Africa, JSB766 (NBG), OK647945*, OK412934*, OK504590*, OK403291*, OK647900*. *Gnidia thesioides* Meisn., South Africa, Rogers, Applequist & Bold 1036 (NBG), –, OP437521*, –, OP437508*, –, *Gnidia tomentosa* L., South Africa, I. Oliver 5 (NBG), OK647946*, OK412967*, –, OK403308*, OK647901*. *Gnidia virescens* Wikstr., South Africa, Beaumont s.n. (NU), AJ308670*, AJ295266¹, –, FJ572795⁴, AM159514⁴. *Gnidia* aff. *viridis* P.J.Bergius, South Africa, Beaumont s.n. (NU), AJ308652¹, AM162508¹, –, –, AM159509¹. *Gnidia wikstroemiana* Meisn., South Africa, Beaumont & Smith SRF9 (NU), AM404299², AM162524², FJ572888⁴, OK403275*, OK647902*. *Gnidia woodii* C.H.Wright, South Africa, Bester S.P. 8363 (PRE), –, OK412944*, OK504591*, OP437509*, OP456324*. *Gonystylus bancanus* (Miq.) Kurz, Malaysia, Lee FBL01031 (UPM), MF443427⁵, KU244237⁵, –, –, MH134152⁵. *Gonystylus macrophyllus* (Miq.) Airy Shaw, –, Chase 1382 (K), AJ308653¹, Y115150¹, –, –, *Gyrinops caudata* (Gilg) Domke, Indonesia, Turjaman MTJ0002 (UPM), –, MF443410⁵, –, –, KM7779119⁵. *Gyrinops walla* Gaertn., –, Chase 10511 (K), AM404303², AM398173², –, –, *Kelleria dieffenbachii* (Hook.) Endl., –, Flowers G. H6 (CBG), FJ572707⁴, –, –, FJ572793⁴, FJ572746⁴. *Lachnaea alpina* Meisn., South Africa, Beyers 258 (NBG), AJ697829⁸, AJ697771⁸, AJ697636⁸, OK403303*, AJ745754⁸. *Lachnaea aurea* Eckl. & Zeyh. ex Meisn., South Africa, Aggenbush s.n. (NBG), AJ697828⁸, AJ697781⁸, OK504592*, OK403325*, AJ745737⁸. *Lachnaea burchellii* Meisn., South Africa, Oliver & Oliver 11862 (NBG), OK647948*, AJ697799⁸, AJ697613⁸, OK403323*, AJ745743⁸. *Lachnaea diosmoides* Meisn., South Africa, Beyers 181 (NBG), AJ697813⁸, AJ697800⁸, AJ697620⁸, –, AJ745745⁸. *Lachnaea ericoides* Meisn., South Africa, McDonald 1842 (NBG), AJ308673¹, AJ297220¹, AJ697634⁸, OK403322*, AJ745727⁸. *Lachnaea eriocephala* L., South Africa, Beyers 54 (NBG), AJ697834⁸, AJ697780⁸, AJ697625⁸, OK403318*, AJ745728⁸. *Lachnaea filamentosa* Meisn., South Africa, Beyers 245 (NBG), AJ697833⁸, AJ697801⁸, AJ697635⁸, OK403296*, AJ745755⁸. *Lachnaea globulifera* subsp. *incana* Beyers, South Africa, Hanekom 2939 (NBG), AJ697810⁸, AJ697774⁸, OK504595, OK403313*, AJ745723⁸. *Lachnaea glomerata* Fourc., South Africa, Beyers 192 (NBG), AJ697832⁸, AJ697765⁸, AJ697616⁸, OK403324*, AJ745736⁸. *Lachnaea grandiflora* (L.f.) Baill., South Africa, Manning 3701 (NBG), OK647949*, OK412964*, OK504597*, OK403320*, OK647903*. *Lachnaea greytonensis* Beyers, South Africa, Hansford 21 (NBG), AJ697827⁸, AJ697775⁸, AJ697622⁸, OK403311*, AJ745732⁸. *Lachnaea laniflora* (C.H.Wright) Bond, South Africa, Oliver 10679 (NBG), AJ697831⁸, AJ697802⁸, AJ697633⁸, OK403317*, AJ745739⁸. *Lachnaea laxa* (C.H.Wright) Beyers, South Africa, Oliver & Oliver 1177 (NBG), AJ697821⁸, AJ697769⁸, OK504598*, OK403326*, AJ745733⁸. *Lachnaea marlothii* Schltr., South Africa, Oliver & Oliver 11304 (NBG), AJ697823⁸, AJ697776⁸, OK504598*, OK403312*, AJ745726⁸. *Lachnaea montana* Beyers, South Africa, Oliver & Oliver 11308 (NBG), AJ697824⁸, AJ697770⁸, OK504600*, OK403314*, AJ745725⁸. *Lachnaea naviculifolia* Compton, South Africa, Beyers 221 (NBG), AJ697825⁸, AJ697777⁸, OK504601*, OK403316*, AJ745734⁸. *Lachnaea pedicellata* Beyers, South Africa, Beyers 260 (NBG), AM404354⁸, AJ697778⁸, OK504602*, OK403315*, AJ697826⁸. *Lachnaea pomposa* Beyers, South Africa, Oliver 10767 (NBG), AJ697835⁸, AJ697797⁸, AJ697626⁸, OK403304*, AJ745753⁸. *Lachnaea pudens* Beyers, South Africa, Otto 10730 (NBG), AJ697830⁸, AJ697766⁸, AJ697619⁸, OK403328*, AJ745735⁸. *Lachnaea rupestris* Beyers, South Africa, Oliver 11262 (NBG), AJ697807⁸, AJ697779⁸, –, OK403319*, AJ745731⁸. *Lachnaea sociorum* Beyers, South Africa, Beyers 176 (NBG), AJ697808⁸, AJ697795⁸, AJ697621⁸, OK403309*, AJ745741⁸. *Lachnaea uniflora* L., South Africa, Beyers 136 (NBG), AJ697809⁸, AJ697790⁸, AJ697617⁸, OK403321*, AJ745751⁸. *Lasiosiphon afer* Meisn., South Africa, Burrows & Burrows 7754 (BNRH), OP437549¹⁴, AM398170², OK504604*, OK403263*, OK647905*. *Lasiosiphon bojerianus* Decne., Madagascar, Rogers & al. 183 (MO), AM404224², AM162507², –, –, AM159511². *Lasiosiphon calocephalus* (Meisn.) Domke, South Africa, Reid 885 (PRE), AM404225², OK412921¹, OK504605*, OK403262*, AM396521². *Lasiosiphon chapmanii* (B.Peterson) Olaniyan, Mozambique, J.D. & E.G. Chapman 9240 (PRE), OP437540¹⁴, OP437511¹⁴, OP437526¹⁴, –, –, *Lasiosiphon chrysanthus* (Solms ex Schweinf.) Olaniyan, South Africa, Bester S.P. 8976 (PRE), OP437541¹⁴, OP437512¹⁴, OP437527¹⁴, OP437501¹⁴, OP456322¹⁴. *Lasiosiphon dalgues* (Leandri) Boatwr. & J.C.Manning, Madagascar, Rogers & al. 76 (MO), AM404226², AM162515², –, –, AM159513². *Lasiosiphon daphnifolius* (L.f.) Boatwr. & J.C.Manning, Madagascar, Rogers & al. 109 (MO), AM404228², AM162514², –, –, AM159515². *Lasiosiphon gilbertae* (Drake) Boatwr. & J.C.Manning, Madagascar, Randrianasolo 529 (MO), AJ745154¹, AJ745180¹, –, –, AJ744927¹. *Lasiosiphon glaucus* Fresen., Kenya, J. Adamson 6156 (K), AM404232², AM162511², –, –, *Lasiosiphon gnidioides* (Baker) Boatwr. & J.C.Manning, Madagascar, Rogers & al. 126 (MO), –, AM162506², –, –, AM159510². *Lasiosiphon kraussianus* (Meisn.) Burt Davy, South Africa, Beaumont s.n. (NU), AJ308674¹, AJ295267¹, OK504606*, OK403264*, AM159518¹. *Lasiosiphon kuntzei* (Gilg) Kolokoto & Magee, South Africa, Raimondo D. DR394 (PRE), OP437550¹⁴, OP437522¹⁴, OP437534¹⁴, OP437510¹⁴, OP456321¹⁴. *Lasiosiphon leandrianus* Boatwr. & J.C.Manning, Madagascar, Rogers & al. 108 (MO), AJ745153¹, AJ745179¹, –, –, AJ744926¹. *Lasiosiphon pedunculatus* (Beyers) J.C.Manning & Boatwr., South Africa, Helme N.A. 8320 (NBG), OP437551¹⁴, OP437523¹⁴, OP437535¹⁴, –, OP456323¹⁴. *Lasiosiphon poggei* (Gilg) Olaniyan, Tropical Africa, F. Crawford FC383 (PRE), OP437547¹⁴, OP437520¹⁴, OP437536¹⁴, –, –, *Lasiosiphon rubescens* (B.Peterson) J.C.Manning & Magee, South Africa, OM 0677 (JRAU), –, OK412969*, OK504607*, OK403266*, OK647906*. *Lasiosiphon sericeocephalus* (Meisn.) J.C.Manning & Boatwr., South Africa, Dehning & Dehning 108 (NU), OK647951*, OK412920*, OK504608*, OK403267*, AM159523². *Lasiosiphon wilmsii* C.H.Wright, South Africa, Hartley 1079 (J), OK647952*, OK412922*, OK504609*, OK403265*, OK647907*. *Lethedon balansae* (Baill.) Kosterm., New Caledonia, McPherson & Munzinger 610 (MO), AM404307², AM398176², –, –, *Lethedon* aff. *salicifolia* (Labill.) Aymonin, New Caledonia, McPherson & Munzinger 18055 (MO), AM404306², AM398175², –, –, *Ocotelepis dioica* Capuron, Madagascar, Rogers & al. 46 (MO), AM404350², AM398178², –, –, *Ocotelepis* Oliv. sp., Madagascar, Rogers & al. 165 (MO), AM404349², AM398180², –, –, *Ovidia andina* (Poepp. & Endl.) Meisn., –, Kubitzki & Feuerer 99-42 (HBG), AJ308675¹, AJ297222¹, –, –, AM159530¹. *Passerina burchellii* Thoday, South Africa, Bredenkamp 1546 (PRE), AM404356², AM162526², –, AM159159⁷, AM158925⁷. *Passerina corymbosa* Eckl. ex C.H.Wright, South Africa, OM 3106 (JRAU), –, JX572831⁶, –, OK403300*, OK647908*. *Passerina drakensbergensis* Hilliard & B.L.Burt, South Africa, Bredenkamp 1020 (PRE), AM404358², AM162528², AM159160⁷, –, AM158926⁷. *Passerina ericoides* L., South Africa, Bredenkamp 962 (PRE), AM404359², AM162529², AM159161⁷, –, AM158927⁷. *Passerina galpinii* C.H.Wright, South Africa, Meyer 686 (PRE), AM404360², AM162530⁷, AM159163⁷, –, AM158928⁷. *Passerina montivaga* Bredenk. & A.E.van Wyk, South Africa, van Wyk 2586 (PRE), AM404351², AM162531⁷, AM159164⁷, –, AM158930⁷. *Passerina obtusifolia* Thoday, South Africa, Meyer 1505 (PRE), AM404367², AM162532⁷, AM159166⁷, OK403301*, AM158931⁷. *Passerina quadrifaria* Bredenk. & A.E.van Wyk, South Africa, Bredenkamp 1551 (PRE), AM406676², AM162535⁷, AM159168⁷, –, AM158934⁷. *Passerina rigida* Wikstr., South Africa, P. van Wyk 2517 (PRE), AM404363², AM162541⁷, AM159169⁷, –, AM158935⁷. *Peddiea africana* Harv., South Africa, OM 2469 (JRAU), OK647953*, OK412947*, –, JX518167⁶, OK647909*. *Peddiea involucrata* Baker, Madagascar, Rogers & al. 121 (MO), AJ745151¹, AJ745176¹, –, –, AJ744920¹. *Phaleria capitata* Jack, –, Chase 1383 (K), AJ308661¹, AJ297228¹, –, –, *Phaleria macrocarpa* (Scheff.) Boerl., Indonesia, Lee FBL04006

Appendix 1. Continued.

(UPM), MH134159⁵, MH134157⁵, MH134155⁵, MH134153⁵. *Pimelea angustifolia* R.Br., Indonesia, *M. & J. Steward* 79 (PERTH), FJ572688⁴, FJ572820⁴, FJ572862⁴, FJ572768⁴, FJ572726⁴. *Pimelea argentea* R.Br., Australia, *Hislop & M. Griffiths WW 111.39* (PERTH), AM406675⁴, AM167530⁴, FJ572850⁴, FJ572756⁴, AM162490⁴. *Pimelea avonensis* Rye, Australia, *B. Smith & M. Griffiths WW 116.10* (PERTH), FJ572697⁴, FJ572829⁴, FJ572873⁴, FJ572779⁴, FJ572735⁴. *Pimelea brevistyla* Rye subsp. *brevistyla*, Australia, *B. Nyanatusia 130* (PERTH), FJ572698⁴, FJ572830⁴, FJ572874⁴, FJ572780⁴, FJ572736⁴. *Pimelea concreta* F. Muell., Australia, *I.D. Cowie 8563* (MEL), FJ572708⁴, FJ572839⁴, FJ572884⁴, FJ572790⁴, FJ572743⁴. *Pimelea cornucopiae* Vahl, Australia, *P.I. Forster 23116* (MEL), FJ572706⁴, FJ572840⁴, FJ572885⁴, FJ572791⁴, FJ572744⁴. *Pimelea erecta* Rye, Australia, *C.F. Craig 5994* (PERTH), FJ572683⁴, FJ572815⁴, FJ572857⁴, FJ572763⁴, FJ572721⁴. *Pimelea filifolia* (Rye) C.S.P. Foster & Henwood, Australia, *I.D. Cowie 8702* (MEL), FJ572709⁴, FJ572841⁴, FJ572886⁴, FJ572792⁴, FJ572745⁴. *Pimelea hispida* R.Br., Australia, *J. Smith 6* (PERTH), AM406679⁴, FJ572812⁴, FJ572854⁴, FJ572760⁴, FJ572718⁴. *Pimelea lanata* R.Br., Australia, *P. Foreman & J. Kelly KO 332* (PERTH), FJ572701⁴, FJ572833⁴, FJ572783⁴, FJ572739⁴. *Pimelea preissii* Meisn., Australia, *B.G. Ward & R.J. Cranfield 18582* (PERTH), FJ572687⁴, FJ572819⁴, FJ572861⁴, FJ572767⁴, FJ572725⁴. *Pimelea punicea* R.Br., Australia, *T. Hansdasyde TH488* (PERTH), FJ572815⁴, FJ572857⁴, FJ572763⁴, FJ572721⁴. *Pimelea rara* Rye, Australia, *F. & J. Hort 2510* (PERTH), AM407412⁴, AM167538⁴, FJ572872⁴, FJ572778⁴, AM162498⁴. *Pimelea sanguinea* F. Muell., Australia, *A.A. Mitchell 3945* (PERTH), AM406685⁴, FJ572838⁴, FJ572883⁴, FJ572789⁴, AM162503⁴. *Pimelea strigosa* Gand., Australia, *Coveny RG14395* (PERTH), FJ572679⁴, FJ572810⁴, FJ572852⁴, FJ572758⁴, FJ572716⁴. *Pimelea trichostachya* Lindl., Australia, *K.F. Kenneally 12623 & D.J. Edinger 3822* (PERTH), AM406682⁴, AM167537⁴, FJ572849⁴, FJ572755⁴, AM162501⁴. *Pimelea villifera* Meisn., Australia, *F. & B. Hort 2110* (PERTH), FJ572682⁴, FJ572814⁴, FJ572856⁴, FJ572762⁴, FJ572720⁴. *Solmsia calophylla* Baill., New Caledonia, *Guillaumin s.n.* (K), AJ308656¹, AJ295261¹, —, —, —. *Stellera chamaejasme* L., —, *Chase 5530* (K), AJ308657¹, AJ295262¹, —, —, —. *Stephanodaphne cremostachya* Baill., Madagascar, *Toliaris 13.01.1990* (K), AJ308658¹, AJ295263¹, —, GQ248204⁹, AM159532¹. *Stephanodaphne cuspidata* (Leandri) Leandri, Madagascar, *Roger & al. 68* (MO), AM406683², AM398185², —, —, AM159533². *Stephanodaphne geminata* H. Perrier, Madagascar, *Roger & al. 127* (MO), AJ745152¹, AJ745177¹, —, —, AJ744924¹. *Struthiola tomentosa* Andrews, South Africa, *Mark Johns s.n.* (Kogelberg Reserve Field Herbarium), OK647955⁴, AM162540², OK504612³, OK403259³, OK647911³. *Struthiola ciliata* (L.) Lam., South Africa, *Chase 6445* (K), AJ308637¹, AJ297241¹, AJ697645⁸, FJ572803⁴, AJ745756⁸. *Struthiola dodecandra* (L.) Druce, South Africa, *Chase 6354* (K), AJ308638¹, AJ297242¹, AJ697647⁸, FJ572804⁴, —. *Struthiola leptantha* Bolus, South Africa, *Beyers 265* (NBG), AJ308639¹, AJ297243¹, AJ697646⁸, —, AJ745757⁸. *Struthiola myrsinites* Lam., South Africa, *OM 3121* (JRAU), OK647954⁴, OK412928³, OK504610³, OK403260³, OK647910³. *Struthiola striata* Lam., South Africa, *Mark Johns s.n.* (Kogelberg Reserve Field Herbarium), AM404302², AM398172², OK504611³, OK403261³, AM396990². *Synandrodaphne paradoxa* Gilg, Congo, *Sisowski 46609* (K), AJ308676¹, AJ297240¹, —, —, —. *Synaptolepis alternifolia* Oliv., Mozambique, *Vollesen 4043* (K), OK647956⁴, JX573013⁶, OK504613³, JX518008⁶, —. *Synaptolepis oliveriana* Gilg, South Africa, *OM 3691* (JRAU), OK647957³, KU568025¹⁰, OK504614³, KX146249¹⁰, —. *Thymelaea hirsuta* (L.) Endl., —, *Chase 1883* (K), AJ308640¹, Y15151¹¹, —, —, AJ744930¹. *Wikstroemia bokorensis* E. Oguri & Tagane, Cambodia, *Toyama & al. HT 1604* (MAK), LC164915¹², LC164867¹², LC165002¹², —, LC164891¹². *Wikstroemia canescens* Meisn., Nepal, *E 82170* (—), AM406686², AM398186², —, —, AJ549496¹³. *Wikstroemia ridleyi* Gamble, Malaysia, *Lee & Mohamed FBLO5001* (UPM), MH134160⁵, MH134158⁵, —, MH134156⁵, MH134154⁵. — **Outgroup:** *Dialyceras coriaceum* (R. Cap.) J.-F. Leroy, Madagascar, *Schatz & al. 3848* (MO), —, AJ297232¹, —, —, —. *Rhopalocarpus* Bojer sp., —, *Chase 906* (K), AJ308642¹, Y15148¹, —, —, —.