African spiny *Solanum* (subgenus *Leptostemonum*, Solanaceae): a thorny phylogenetic tangle

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Although most diverse in the New World tropics, approximately 100 species of *Solanum* (Solanaceae) are native to continental Africa and Madagascar. The majority of these are 'spiny solanums' (subgenus *Leptostemonum*). We present here the first phylogenetic reconstruction of African and Madagascan species of *Solanum* subgenus *Leptostemonum*, with 62 of 76 species native to these areas, plus an additional seven species of largely Asian distribution, using internal transcribed spacer (ITS), *waxy* and *trnT-F* regions. We identify monophyletic groups, many of which correspond to previously recognized units, although the large, traditionally recognized sections of *Oliganthes* and *Melongena* are polyphyletic. These groups are distinguished from each other by their breeding systems, with members of *Oliganthes* being hermaphroditic and *Melongena* andromonoecious. The phylogenetic relationships suggest multiple changes of breeding system between these two states, and observations of plants across their range indicate that there is considerable lability in this character. The African and Malagasy clades are largely geographically coherent, although there is evolutionary interchange between African vegetation types. All of the Madagascan endemics included in the analysis form a coherent group and probably represent an *in situ* radiation. © 2013 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2013, **173**, 176–193.

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INTRODUCTION

Solanum L. (Solanaceae) is one of the largest genera of flowering plants with *c*. 1500 species occurring on all continents, except Antarctica. Major centres of species diversity are the Andean and Atlantic forest regions of South America, but a secondary centre of diversity occurs in East Africa. The genus includes crops of global agricultural importance, such as potato (*S. tuberosum* L.), tomato (*S. lycopersicum* L.) and aubergine/eggplant (*S. melongena* L.), and minor crops of local significance, such as naranjilla (*S. quitoense* Lam.), tree tomato (*S. betaceum* Cav.), pepino (*S. muricatum* Aiton), scarlet and gboma eggplants

(*S. aethiopicum* L. and *S. macrocarpon* L.) and garden huckleberry (*S. scabrum* Mill.). A morphologically variable and taxonomically challenging group (e.g. Ovchinnikova *et al*., 2011), *Solanum* has not been revised in full since Dunal's (1852) treatment for De Candolle's great *Prodromus*. Since that time, work has largely proceeded at a floristic level (see reviews in Knapp, 2002) until, in 2004, an international group began to monograph the genus as part of the Planetary Biodiversity Inventory (National Science Foundation) programme. *Solanum* has become a model group for an internationally collaborative project towards a modern online monograph of a species-rich genus (see http://www.solanaceaesource.org). Revisionary and descriptive work has been accompanied by phylogenetic studies across the genus (e.g. Bohs,

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2004, 2005; Levin, Watson & Bohs, 2005; Levin, Myers & Bohs, 2006; Martine *et al.*, 2006; Bohs *et al.*, 2007; Weese & Bohs, 2007, 2010; Martine, Anderson & Les, 2009; Stern, Agra & Bohs, 2011) to delimit groups and investigate the mechanisms at work in the generation of such extraordinary species richness.

Solanum subgenus *Leptostemonum* Bitter, informally known as the spiny solanums, is the most species rich of the major *Solanum* lineages (*c.* 450 species) and has long been recognized as a distinct group (Dunal, 1852) defined by the possession of stellate trichomes, long tapering anthers and usually prickles. Phylogenetic reconstruction has shown the spiny solanums to be monophyletic (Bohs, 2005; Levin *et al.*, 2006). Like the rest of the genus, the spiny solanums are most diverse in Central and South America and are less common in the Old World, with only 76 native species in Africa and Madagascar (M. S. Vorontsova & S. Knapp, in press), *c.* 20 native species across Asia and *c.* 80–140 species in Australia (Symon, 1981; Bean, 2004). Old World species are often highly similar to New World species, and have sometimes been placed together on the basis of morphological similarity [e.g. section *Torvaria* (Dunal) Bitter; Bitter, 1921]. Phylogenetic analyses with molecular markers (Levin *et al.*, 2006) have shown that the similarity between the Old World and New World species is a result of high levels of parallelism, with only a few exceptions [e.g. *S. lasiocarpum* Dunal of Asia and *S. repandum* Forst.f. of Asia, both members of the otherwise New World section *Lasiocarpa* (Dunal) D'Arcy; Whalen, Costich & Heiser, 1981; Bruneau, Dickson & Knapp, 1985; Bohs, 2004]. All other Old World species analysed to date are members of a monophyletic lineage of spiny solanums.

The Old World spiny solanums have been less well studied than those from the New World (e.g. Nee, 1999), with the Asian taxa not having been revised in their entirety since Dunal (1852). The treatment of *Solanum* for the *Flora of China* (Zhang, Lu & D'Arcy, 1994) did not include the centres of diversity in India and Indochina. African spiny solanums were the subject of the detailed taxonomic system brought together by the German botanists Dammer (1895, 1905, 1906, 1912, 1915) and Bitter (1913, 1917, 1921, 1923), but their classification and names were not applied widely until Polhill's work in Nairobi and London in the 1960s (Vorontsova *et al.*, 2010). Their system, most fully realized in Bitter's series of papers comprising the *Solana Africana* (Bitter, 1913, 1917, 1921, 1923), divided the majority of the African species into two large groups, section *Oliganthes* (Dunal) Bitter and section *Melongena* Dunal, based largely on flower and fruit size, both frequently indicators of the breeding system (see below). Dammer

and Bitter both described many taxa at a large number of ranks, at times seemingly describing every specimen as a new taxon, especially in widespread and variable species, such as *S. campylacanthum* Hochst. ex A.Rich., which has 75 heterotypic synonyms (Vorontsova & Knapp, 2012). In addition, the analysis of their work is made more difficult by the fact that many of the specimens they used (and thus the types for these names) were destroyed in air raids in Berlin during World War II (Vorontsova & Knapp, 2010). These factors have contributed to the previously somewhat chaotic identification of African species, and have impeded an understanding of the phylogenetic relationships in the group. Detailed studies by Lester's research group in Birmingham primarily focused on the relationships and domestication history of cultivated species, such as *S. aethiopicum* and *S. melongena* (e.g. Jaeger, 1985; Lester & Niakan, 1986; Lester & Hasan, 1991; Lester, 1997). No taxonomic treatments of African and Madascan solanums have been formally published outside of regional floras (D'Arcy & Rakotozafy, 1994; Gonçalves, 2005; Friis, 2006a, b; Edmonds, 2012; Vorontsova & Knapp, 2012). Whalen (1984) included the African and Madagascan taxa in his morphologically based phylogenetic scheme which covered all of subgenus *Leptostemonum*. In general, he defined distinct groups of Old World taxa (see Table 1), rather than combining Old World and New World groups. A full taxonomic history of spiny *Solanum* in Africa is given in Jaeger (1985), Vorontsova *et al.* (2010) and Vorontsova & Knapp (2010).

Several morphologically 'obvious' species-level relationships have been consistently recognized in African spiny solanums: heterandrous species with one long filament and almost black seeds (Fig. 1L) have been recognized as section *Monodolichopus* Bitter or the *S. thruppii* C.H.Wright group (Whalen, 1984; including *S. melastomoides* C.H.Wright which Whalen considered to be anomalous); erect species with umbel-like inflorescences and multangulate stem trichomes (Fig. 1G) have been recognized as the *S. giganteum* Jacq. group (Whalen, 1984; series *Giganteiformia* Bitter); taxa with curved stem prickles, straight leaf prickles and thick pericarp (Fig. 1H, I) have been thought to be closely related (section *Ischyracanthum* Bitter; Whalen's *S. arundo* Mattei group); and species from Madagascar with lanceolate entire leaves and lepidote trichomes have been recognized as the *S. bumeliifolium* Dunal group (Whalen, 1984). The majority of African species fall outside these somewhat more recently established groups and have been traditionally classified on the basis of whether or not they are andromonoecious.

Andromonoecy is a specialized breeding system in which the proximal flower(s) in every inflorescence

Table 1. Taxonomic placements and breeding systems of the African and Malagasy species used in this analysis. Species not included in a treatment are marked with a dash. Formal sections for African species used by Jaeger (1985) are a simplification of the elaborate system presented by Bitter (1913–1923); Edmonds (2012) used this system and added species described more recently, but treated only East African taxa. Asian and Australian species have not been included. The breeding systems display continuous variation between hermaphroditic and andromonoecious

	Jaeger (1985) and Edmonds (2012)	Whalen (1984)	Andromonoecy
S. aculeastrum Dunal	section *Melongena* Dunal	*Solanum incanum* group	Andromonoecious
S. aethiopicum L.	section *Oliganthes* (Dunal) Bitter	*Solanum anguivi* and relatives	Hermaphroditic
S. agnewiorum Voronts.	section *Oliganthes* (Dunal) Bitter	–	Weakly andromonoecious
S. anguivi Lam.	section *Oliganthes* (Dunal) Bitter	*Solanum anguivi* and relatives	Hermaphroditic
S. anomalum Thonn.	section *Torva* Nees	*Solanum giganteum* group	Hermaphroditic
S. arundo Mattei	section *Ischyracathum* Bitter	*Solanum arundo* group	Weakly andromonoecious
S. bumeliifolium Dunal	section *Croatianum* D'Arcy & Keating	*Solanum bumeliifolium* group	Hermaphroditic
S. burchellii Dunal	section *Oliganthes* (Dunal) Bitter	*Solanum tomentosum* and relatives	Hermaphroditic
S. campylacanthum Hochst. ex A. Rich.	section *Melongena* Dunal	*Solanum incanum* group	Andromonoecious
S. capense L.	section *Oliganthes* (Dunal) Bitter	*Solanum capense* and relatives	Hermaphroditic
S. catombelense Peyr.	section *Oliganthes* (Dunal) Bitter	*Solanum tomentosum* and relatives	Hermaphroditic
S. cerasiferum Dunal	section *Melongena* Dunal	*Solanum incanum* group	Andromonoecious
S. coagulans Forssk.	section *Monodolichopus* Bitter	*Solanum thruppii* group	Hermaphroditic
S. cordatum Forssk.	section *Oliganthes* (Dunal) Bitter	*Solanum gracilipes* and relatives	Hermaphroditic
S. croatii D'Arcy & Keating	section *Croatianum* D'Arcy & Keating	*Solanum bumeliifolium* group	Hermaphroditic
S. cyaneopurpureum De Wild.	section *Oliganthes* (Dunal) Bitter	*Solanum zanzibarense* and relatives	Hermaphroditic
S. dasyphyllum Schumach. & Thonn.	section *Melongena* Dunal	*Solanum incanum* group (distant)	Andromonoecious
S. dennekense Dammer	section *Ischyracathum* Bitter	*Solanum arundo* group	Weakly andromonoecious
S. erythracanthum Dunal	section *Oliganthes* (Dunal) Bitter	*Solanum zanzibarense* and relatives	Hermaphroditic
S. giganteum Jacq.	section *Torva* Nees	*Solanum giganteum* group	Hermaphroditic
S. glabratum Dunal	section *Oliganthes* (Dunal) Bitter	*Solanum capense* and relatives	Hermaphroditic
S. goetzei Dammer	section *Torva* Nees	*Solanum giganteum* group	Hermaphroditic
S. heinianum D'Arcy & Keating	section *Croatianum* D'Arcy & Keating	*Solanum bumeliifolium* group	Hermaphroditic
S. humile Lam.	section *Oliganthes* (Dunal) Bitter	*Solanum capense* and relatives/ miscellaneous species of *Solanum anguivi* group	Hermaphroditic
S. inaequiradians Werderm.	section *Oliganthes* (Dunal) Bitter	*Solanum zanzibarense* and relatives	Hermaphroditic
S. incanum L.	section *Melongena* Dunal	*Solanum incanum* group	Andromonoecious
S. insanum L.	section *Melongena* Dunal	*Solanum incanum* group	Andromonoecious
S. jubae Bitter	section *Somalanum* Bitter	*Solanum jubae* group	Hermaphroditic
S. lamprocarpum Bitter	section *Oliganthes* (Dunal) Bitter	*Solanum zanzibarense* and relatives	Hermaphroditic
S. lichtensteinii Willd.	section *Melongena* Dunal	*Solanum incanum* group	Andromonoecious
S. lidii Sunding	section *Nycterium* (Ventenat) Dunal	*Solanum vespertilio* group	Weakly andromonoecious

Table 1. *Continued*

	Jaeger (1985) and Edmonds (2012)	Whalen (1984)	Andromonoecy
S. linnaeanum Hepper & P.-M.L. Jaeger	section *Melongena* Dunal	*Solanum incanum* group (distant)	Andromonoecious
S. macrocarpon L.	section *Melongena* Dunal	*Solanum incanum* group (distant)	Andromonoecious
S. mahoriense D'Arcy & Rakot.	cf. section *Cryptocarpum* Dunal	–	Andromonoecious
S. malindiense Voronts.	section *Oliganthes* (Dunal) Bitter	–	Weakly andromonoecious
S. mauense Bitter	section *Oliganthes* (Dunal) Bitter	*Solanum anguivi* and relatives	Hermaphroditic
S. melastomoides C.H.Wright	section *Monodolichopus* Bitter	*Solanum thruppii* group	Hermaphroditic
S. melongena L.	section *Melongena* Dunal	*Solanum incanum* group	Andromonoecious
S. myoxotrichum Baker	section *Oliganthes* (Dunal) Bitter	*Solanum zanzibarense* and relatives	Hermaphroditic
S. nigriviolaceum Bitter	section *Melongena* Dunal	*Solanum incanum* group (distant)	Andromonoecious
S. phoxocarpum Voronts.	section *Melongena* Dunal	*Solanum incanum* group	Andromonoecious
S. polhillii Voronts.	section *Oliganthes* (Dunal) Bitter	–	Weakly andromonoecious
S. pyracanthos Lam.	section *Oliganthes* (Dunal) Bitter	Miscellaneous species of *Solanum anguivi* group	Hermaphroditic
S. richardii Dunal	section *Melongena* Dunal	*Solanum incanum* group (distant)	Andromonoecious
S. ruvu Voronts.	section *Oliganthes* (Dunal) Bitter	–	Hermaphroditic
S. schimperianum Hochst. ex A.Rich.	section *Torva* Nees	*Solanum giganteum* group	Hermaphroditic
S. schliebenii Werderm.	section *Torva* Nees	*Solanum giganteum* group	Hermaphroditic
S. schumannianum Dammer	section *Torva* Nees	*Solanum giganteum* group	Hermaphroditic
S. setaceum Dammer	section *Oliganthes* (Dunal) Bitter	*Solanum gracilipes* and relatives	Hermaphroditic
S. somalense Franch.	section *Anisantherum* Bitter	*Solanum jubae* group (tentative)	Hermaphroditic
S. stipitatostellatum Dammer	section *Oliganthes* (Dunal) Bitter	*Solanum zanzibarense* and relatives	Hermaphroditic
S. supinum Dunal	section *Oliganthes* (Dunal) Bitter	*Solanum capense* and relatives	Hermaphroditic
S. tettense Klotzsch	section *Torva* Nees	*Solanum giganteum* group	Hermaphroditic
S. thomsonii C.H.Wright	section *Melongena* Dunal	*Solanum incanum* group	Weakly andromonoecious
S. toliaraea D'Arcy & Rakot.	section *Oliganthes* (Dunal) Bitter	–	Hermaphroditic
S. tomentosum L.	section *Oliganthes* (Dunal) Bitter	*Solanum tomentosum* and relatives	Hermaphroditic
S. umtuma Voront. & S.Knapp	–	–	Andromonoecious
S. usaramense Dammer	section *Oliganthes* (Dunal) Bitter	–	Hermaphroditic
S. vespertilio Aiton	section *Nycterium* (Ventenat) Dunal	*Solanum vespertilio* group	Andromonoecious
S. violaceum Ortega	section *Oliganthes* (Dunal) Bitter	*Solanum anguivi* and relatives	Hermaphroditic
S. zanzibarense Vatke	section *Oliganthes* (Dunal) Bitter	*Solanum zanzibarense* and relatives	Hermaphroditic

has styles that protrude beyond the anthers and go on to develop fruits, and the distal flowers have partly developed styles and do not develop fruits. It has been hypothesized to be a resource conservation mecha-nism limiting fruit production (Whalen & Costich, 1986; Anderson & Symon, 1989; Miller & Diggle, 2003). In the African spiny solanums, species that are not andromonoecious tend to be plants with small

Figure 1. See caption on next page.

Figure 1. Representative species showing morphological diversity of *Solanum* subgenus *Leptostemonum* in Africa. A, *Solanum nigriviolaceum*, Kenya, Mt. Kenya National Park, 14.v.2009, *Vorontsova et al. 57*. B, *Solanum dasyphyllum*, Tanzania, Morogoro District, Tegetero, 13.iii.2010, *Vorontsova et al. 151*. C, *Solanum anguivi*, Kenya, top of Ngong Hills, 19.v.2009, *Vorontsova et al. 100*. D, *Solanum anguivi*, Tanzania, Mbeya, Mporoto Ridge Forest Reserve, 29.iii.2010, *Tepe et al. 2792*. E, *Solanum mauense*, Kenya, Londiani, Molo–Mau Summit junction, 11.v.2009, *Vorontsova et al. 20*. F, *Solanum somalense*, Kenya, Marsabit, Gobchoba crater, 25.iv.2010, *Vorontsova et al. 207*. G, *Solanum tettense*, Kenya, Namanga Hill, 18.v.2009, *Vorontsova et al. 82*. H, *Solanum dennekense*, Kenya, Marsabit, 24.iv.2010, *Vorontsova et al. 204*. I, *Solanum arundo*, Kenya, Lukenya, 17.v.2009, *Vorontsova et al. 80*. J and K, *Solanum aculeastrum*, Kenya, Londiani, Molo–Mau Summit junction, 11.v.2009, *Vorontsova et al. 19*. L, *Solanum coagulans*, Kenya, Lukenya, 17.v.2009, *Vorontsova et al. 81*. Photograph F by Paweł Ficinski; all other photographs by M.S. Vorontsova.

flowers and numerous small red juicy berries (section *Oliganthes sensu* Bitter; Bitter, 1923, e.g. Fig. 1C, D, E), in contrast with andromonoecious species with larger flowers and single yellow fruits, usually with a leathery pericarp (section *Melongena sensu* Bitter; Bitter, 1923, e.g. Fig. 1A, B, J, K). The many African species exhibiting weak andromonoecy with two to four larger proximal long-styled flowers and intermediate-sized yellow to orange fruits have been included in both groups, depending on overall morphological similarity: e.g. *S. stipitatostellatum* Bitter, with curved prickles, a climbing habit and moderately small fruits, has usually been included in section *Oliganthes*, and *S. cerasiferum* Dunal, with an overall similarity to *S. campylacanthum* and intermediate sized fruits, has usually been included in section *Melongena*. The reproductive biology of *S. lidii* Sunding and *S. vespertilio* Aiton has been treated by Anderson (1979) and Anderson & Symon (1989). The breeding systems of the African and Malagasy species analysed here are listed in Table 1.

The African spiny solanums have been underrepresented in molecular phylogenetic studies, with few sequences published before the study of Levin *et al.* (2006). They sampled 25 of 76 species of spiny solanums from Africa and Madagascar, but most of these formed a polytomy in the Old World clade. Weese & Bohs (2010) studied the evolution of *S. melongena* and its immediate relatives, also including 25 species from Africa and Madagascar, but with insufficient sampling across wild taxa to make any inferences about the monophyly of species groups. We present the first study focusing on the evolutionary history of spiny solanums in continental Africa and Madagascar, sampling 62 of the 76 native species. Additional species are sampled from Arabia, India, China and South-East Asia in order to begin an examination of the area relationships in Old World spiny solanums. This work complements the morphological reassessment and taxonomic treatment of species in Africa and Madagascar (M. S. Vorontsova & S. Knapp, in press). African and Malagasy clades are identified and described. Australian species are outside the scope of this analysis, but are the subject

of a study by Bohs (unpubl. data), Anderson (e.g. Anderson & Symon, 1989) and Martine (e.g. Martine *et al.*, 2009). We assess the occurrence of andromonoecy in a phylogenetic context and examine the emerging geographical structure of the Old World clade with reference to African and Madagascan lineages.

MATERIAL AND METHODS

PLANT MATERIAL

We sampled 128 accessions of 93 *Solanum* spp. in the combined analysis. Sequences for seven more taxa were obtained for internal transcribed spacer (ITS) (not presented). Sampling was focused on spiny solanums from Africa and Madagascar, but also included species from Australia and Asia, in order to test whether the African species formed a monophyletic group or whether biotic interchange between Old World regions was occurring. Following Levin *et al.* (2006), ten New World species from three clades of subgenus *Leptostemonum* were used as outgroup taxa and the tree was rooted using *S. betaceum* Cav., a distantly related, non-spiny species from the *Pachyphylla* clade (see Weese & Bohs, 2007). Samples of leaf material from herbarium specimens (BM, K, L, P, MO and WAG) were used for many of the species (see Appendix), and freshly field collected material was used for taxa from Kenya and Tanzania, the two countries with the highest species-level diversity of subgenus *Leptostemonum* in Africa. For widespread or problematic species, multiple accessions were included in the analysis from across the species range. All taxa, with voucher information and GenBank accession numbers, are listed in the Appendix.

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

Total genomic DNA was extracted from fresh, silica gel-dried or herbarium material using the DNeasy plant mini extraction kit (Qiagen, Inc., Valencia, CA, USA). PCR amplification for each gene region followed standard procedures described by Taberlet *et al.* (1991), Bohs & Olmstead (2001) and Bohs (2004)

Table 2. Descriptive statistics for each dataset analysed. Strongly supported nodes for parsimony indicate those with ≥ 90% bootstrap support (BS); Bayesian strongly supported nodes are those with ≥ 0.95 posterior probability (PP)

Data partition	Aligned sequence length	No. potentially parsimony informative characters	No. most parsimonious trees	Tree length	CI	RI	No. strongly supported nodes Parsimony	Model selected	No. strongly supported nodes Bayesian
ITS	697	215	379	1004	0.460	0.742	18	TIM + I + G	39
waxy	1820	258	280567	856	0.752	0.826	21	GTR + I + G	57
trnT-F	2462	180	215848	622	0.841	0.890	8	TVM + I + G	40
Combined	4979	629	272	2490	0.633	0.763	38	GTR + I + G	79

CI, consistency index; ITS, internal transcribed spacer; RI, retention index.

for the *trnT-L* and *trnL-F* intergenic spacer regions, Levin *et al*. (2005) for *waxy* and Levin *et al*. (2006) for ITS. The ITS region was amplified as a single fragment using the primers ITSleu1 (Bohs & Olmstead, 2001) and ITS4 (White *et al*., 1990), employing the polymerase chain reaction (PCR) conditions described in Bohs & Olmstead (2001). Because many of the extracts were obtained from herbarium material with lower quality DNA, we were unable to amplify most accessions for *trnT-F* and *waxy* as single fragments. Overlapping fragments for *trnT-F* were amplified using primers a with d, and c with f (Taberlet *et al*., 1991), and the PCR conditions following Bohs & Olmstead (2001). Primers waxyF with 1171R, and 1058F with 2R, were used to amplify *waxy* with PCR conditions following Levin *et al*. (2005). The *waxy* gene occasionally proved recalcitrant to amplify as two overlapping fragments, and it was therefore necessary to amplify it in four overlapping fragments using primers waxyF with Ex4R, Ex4F with 1171R, 1058F with 3′N, and 3F with 2R, as described by Stern, Weese & Bohs (2010).

PCR products were cleaned using the Promega Wizard SV PCR Clean-Up System (Promega Corporation, Madison, WI, USA). The University of Utah DNA Sequencing Core Facility performed sequencing on an ABI automated sequencer. Sequences were edited in Sequencher (Gene Codes Corporation, Ann Arbor, MI, USA) and all new sequences were submitted to GenBank. Missing data comprised 0.00062% of the combined data matrix (286 of 462 031 total bases). Sequence alignments for all gene regions were straightforward and were performed visually using Se-Al (Rambaut, 1996).

PARSIMONY ANALYSES

Parsimony analyses were performed on each dataset separately and on the combined dataset using PAUP*4.0b10 (Swofford, 2002). All characters were weighted equally in analyses that implemented tree bisection–reconnection (TBR) branch swapping, with 1000 heuristic random addition replicates, each limited to 1 000 000 swaps per replicate. Gaps were treated as missing data. Bootstrapping (bootstrap support, BS; Felsenstein, 1985) was used to evaluate branch support, with 1000 random addition replicates and TBR branch swapping limited to 1 000 000 swaps per replicate. Datasets were further analysed using TNT (Goloboff, Farris & Nixon, 2008) to search for shorter trees than obtained in standard PAUP analyses. One thousand heuristic partition homogeneity replicates were completed, each with ten random addition sequence replicates, TBR branch swapping, MulTrees off and gaps treated as missing data.

BAYESIAN ANALYSES

Prior to Bayesian analyses, a general model of nucleotide evolution was selected for the separate and combined datasets using the Akaike information criterion (AIC) identified in Modeltest 3.7 (Posada & Crandall, 1998). MrBayes 3.1 (Huelsenbeck & Ronquist, 2001) was used to analyse each of the separate and combined datasets. For each marker, five million generations were run using eight Markov chains, each initiated from a random tree and sampled every 1000 generations. Each of the analyses reached a standard deviation below 0.01 between the chains. All parameters from each analysis were visualized graphically and the samples obtained prior to achieving a stationary state were discarded as burn-in.

RESULTS

PHYLOGENETIC ANALYSES

The parsimony strict consensus and Bayesian majority rule consensus trees of all datasets differed only in the degree of resolution, with Bayesian tree topologies

Figure 2. 50% majority rule tree from the Bayesian analysis of the combined dataset including internal transcribed spacer (ITS), *waxy* and *trnT-F* regions. The first number on each branch indicates bootstrap support (BS) values > 50% and the second number indicates posterior probabilities (PPs) from the Bayesian analysis. Only branches with > 0.80 PP are shown. Branches with > 90% BS and > 0.95PP are marked in bold. Broken lines represent branches that collapse in the parsimony strict consensus tree. Species vouchered from cultivated plants are marked with a star. Wild accessions from continental Africa and Madagascar are marked in colour to indicate the vegetation type in which each species occurs, and a legend is included. The recognized clades are marked with a full line on the right-hand side of the figure and named. The *Anguivi* grade is marked with a broken line. The tree is continued in Figure 3.

more resolved than parsimony trees (Table 2). Clades with low posterior probabilities (PPs), typically those below PP = 0.90, but, occasionally, those with up to PP = 1.0, in Bayesian analyses were often collapsed in parsimony strict consensus trees. Descriptive statistics for individual and combined datasets are provided (Table 2). More nodes were strongly supported by combining the data than were obtained in any of the separate analyses.

In parsimony analyses, each DNA sequence region consistently identified the same major, well-supported clades comprising identical species groups, but relationships among these were often not strongly supported (BS < 90%) or were unresolved, and thus cannot be considered to be conflicting under Wiens' (1998) criteria. The 50% majority rule trees from the Bayesian analysis of the combined dataset are presented in Figures 2 and 3. A summary of the clades recognized is presented in Figure 4 to aid interpretation.

PHYLOGENETIC RELATIONSHIPS

In our analyses, the Old World spiny solanums emerge as a monophyletic group (BS = 83%; PP = 1.0), confirming the results of Bohs (2005) and Levin *et al*. (2006). Within the Old World spiny solanums, a few clear strongly supported monophyletic groups stand out: we recognize these as clades (groups with PP > 0.95 and BS > 90%), whereas other less strongly supported groups we refer to here as grades (Figs 2–4).

The Asian and Australian species included in our analyses are part of a polytomy including African taxa; most Australian species are monophyletic (BS = 90%, PP > 0.95) and these relationships are the subject of current studies (Martine *et al*., 2009; L. Bohs, unpubl. data). Several other Asian species (e.g. *S. pubescens* Willd., see Fig. 3) resolve in largely African clades.

In this large early-diverging grade, several well-supported clades (see definition above) are recovered. The *Aculeastrum* and *Coagulans* clades are sister to one another (PP = 1.0, BS = 80%). The sister relationship of *S. arundo* and *S. dennekense* Dammer is strongly supported (Fig. 2). The species traditionally recognized as the *S. giganteum* group (of Whalen,

1984) form a strongly supported group (*Giganteum* clade in Figs 2 and 4); in this group, there is a strong sister relationship between *S. schliebenii* Werderm. and *S. schumannianum* Dammer.

Part of this early-diverging polytomy, which has only moderate support (PP = 1.0, BS = 73%), includes all of the spiny solanums endemic to Madagascar. In this group, *S. erythracanthum* Dunal and *S. myoxotrichum* Baker are strongly supported as sister species.

A strongly supported monophyletic group contains the climbing clade (*Solanum richardii* Dunal, *S. zanzibarense* Vatke and *S. stipitatostellatum*) and the eggplant clade, in addition to the bulk of the African species analysed here, which form the *Anguivi* grade. Relationships among the component taxa are less clear.

The composition of the eggplant clade is similar to that recovered by Weese & Bohs (2010), but also includes *S. agnewiorum* Voronts. and *S. umtuma* Voronts. & S.Knapp, and reflects the more resolved nomenclature (Vorontsova & Knapp, 2012) of the African eggplant relatives. Within the clade, the three South African species (*S. umtuma*, *S. lichtensteinii* Willd. and *S. linnaeanum* Hepper & P.M.L.Jaeger) form a strongly supported monophyletic group (Fig. 2).

The bulk of the African species are found here in the grouping we refer to as the *Anguivi* grade (see Fig. 2), within which a few sister taxon relationships are recovered: *S. setaceum* Dammer and *S. cyanopurpureum* De Wild. are sister species, the Canary Island endemics *S. lidii* and *S. vespertilio* are sister taxa (as found by Anderson *et al*., 2006), *S. macrocarpon* is sister to its wild progenitor *S. dasyphyllum* Schumach. & Thonn., and *S. aethiopicum* is similarly sister to its wild progenitor *S. anguivi* Lam. The Asian *S. violaceum* Ortega, long confused with *S. anguivi*, is a member of this grade.

Table 1 provides a summary of the African species treated here, their breeding systems and their placement in the classifications of Jaeger (1985), Edmonds (2012) and Whalen (1984).

DISCUSSION

Although many groups identified in this analysis of *Solanum* subgenus *Leptostemonum* in Africa and
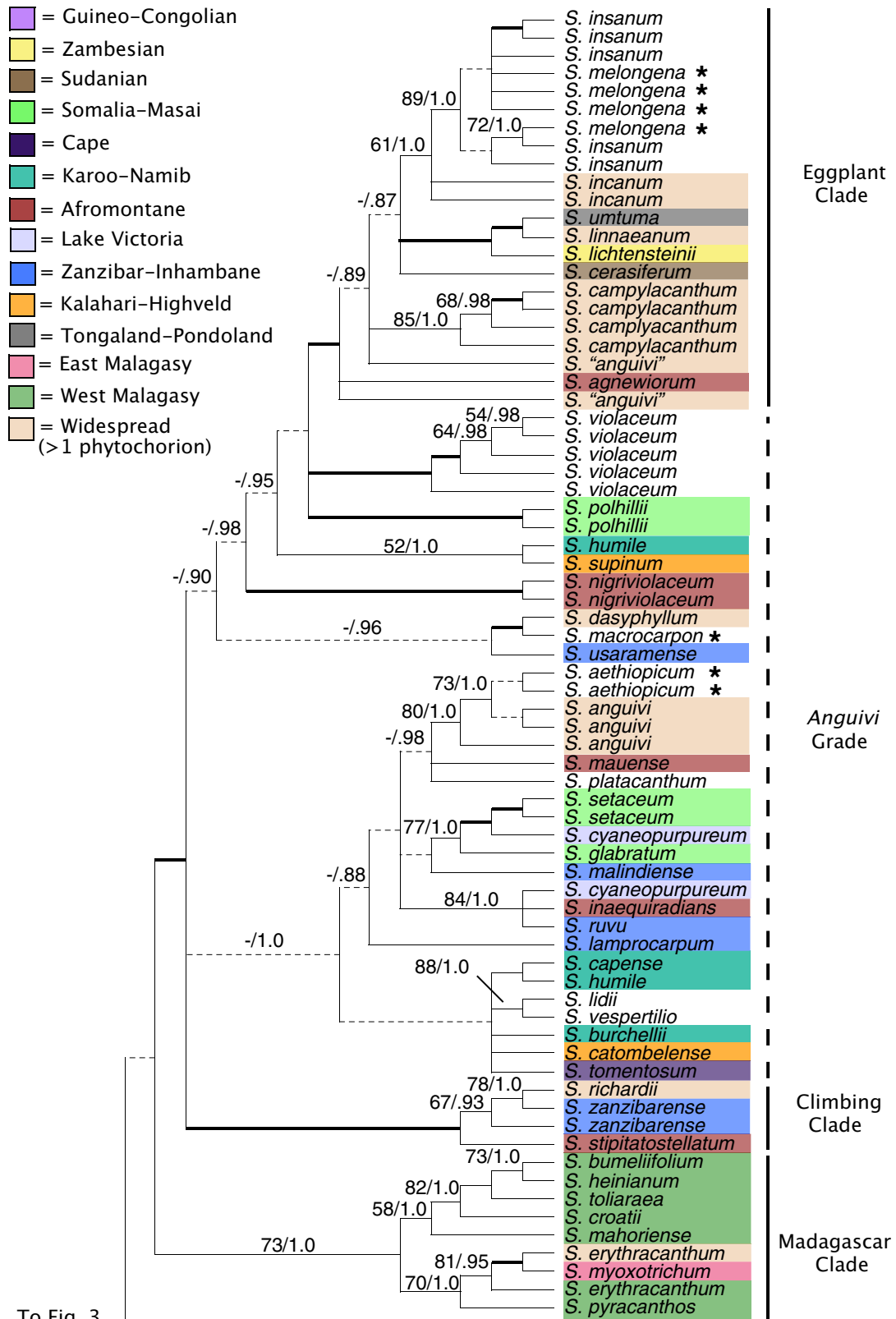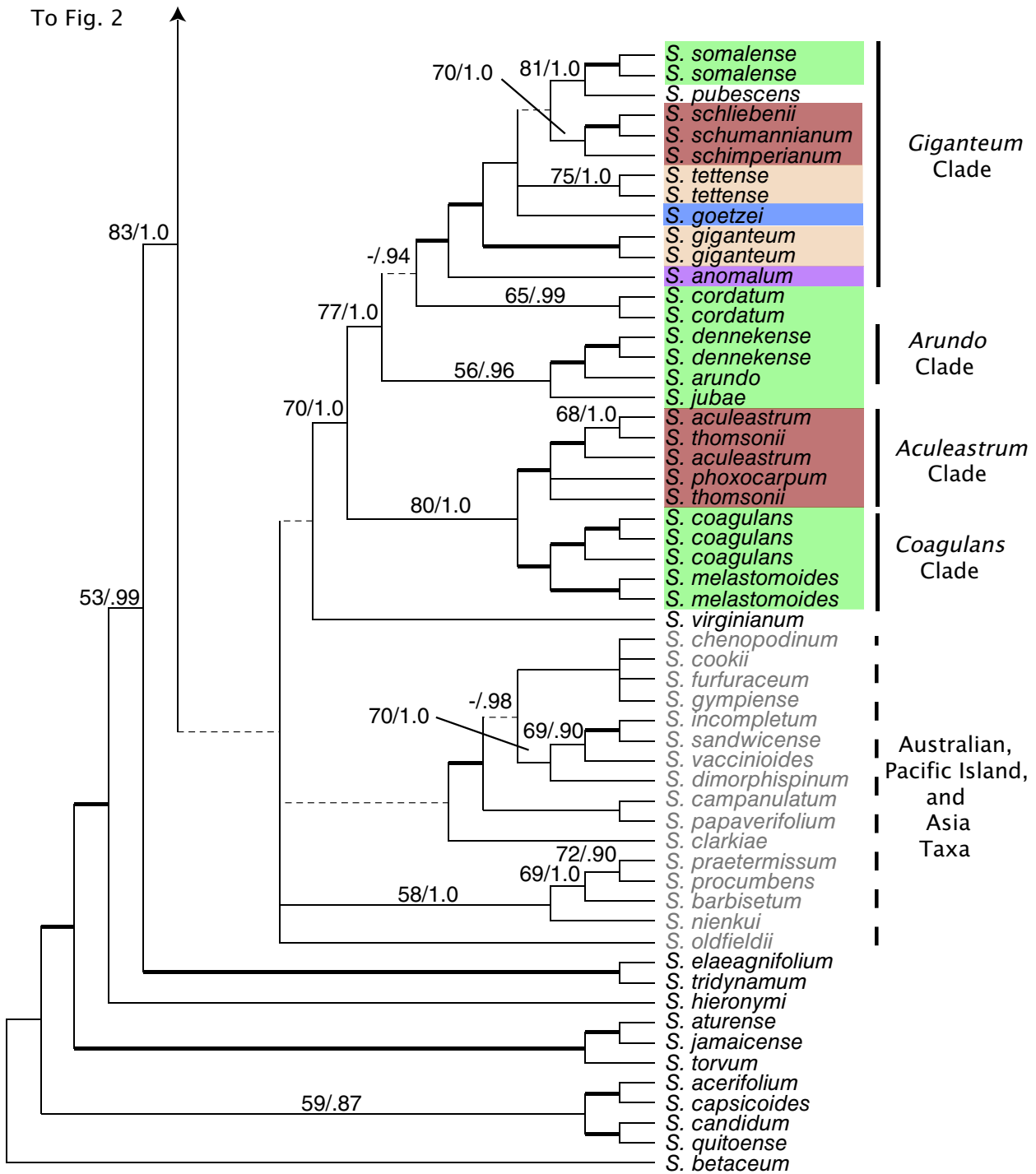
Figure 2. See caption on previous page.

Figure 3. Figure 2 continued. 50% majority rule tree from the Bayesian analysis of the combined dataset including internal transcribed spacer (ITS), *waxy* and *trnT-F* regions. The first number on each branch indicates bootstrap values over 50% and the second number indicates posterior probabilities (PPs) from the Bayesian analysis. Only branches with > 0.80 PP are shown. Branches with > 90% bootstrap support (BS) and > 0.95 PP are marked in bold. Broken lines represent branches that are collapsed in the parsimony strict consensus tree. Species vouchered from cultivated plants are marked with a star. Wild accessions from continental Africa and Madagascar are marked in colour to indicate the phytochorion of the species, and a key to the vegetation types is presented in Figure 2. The recognized clades are marked with a full line on the right-hand side of the figure and named. The Australasian, Pacific Island and Asian group is marked with a broken line.
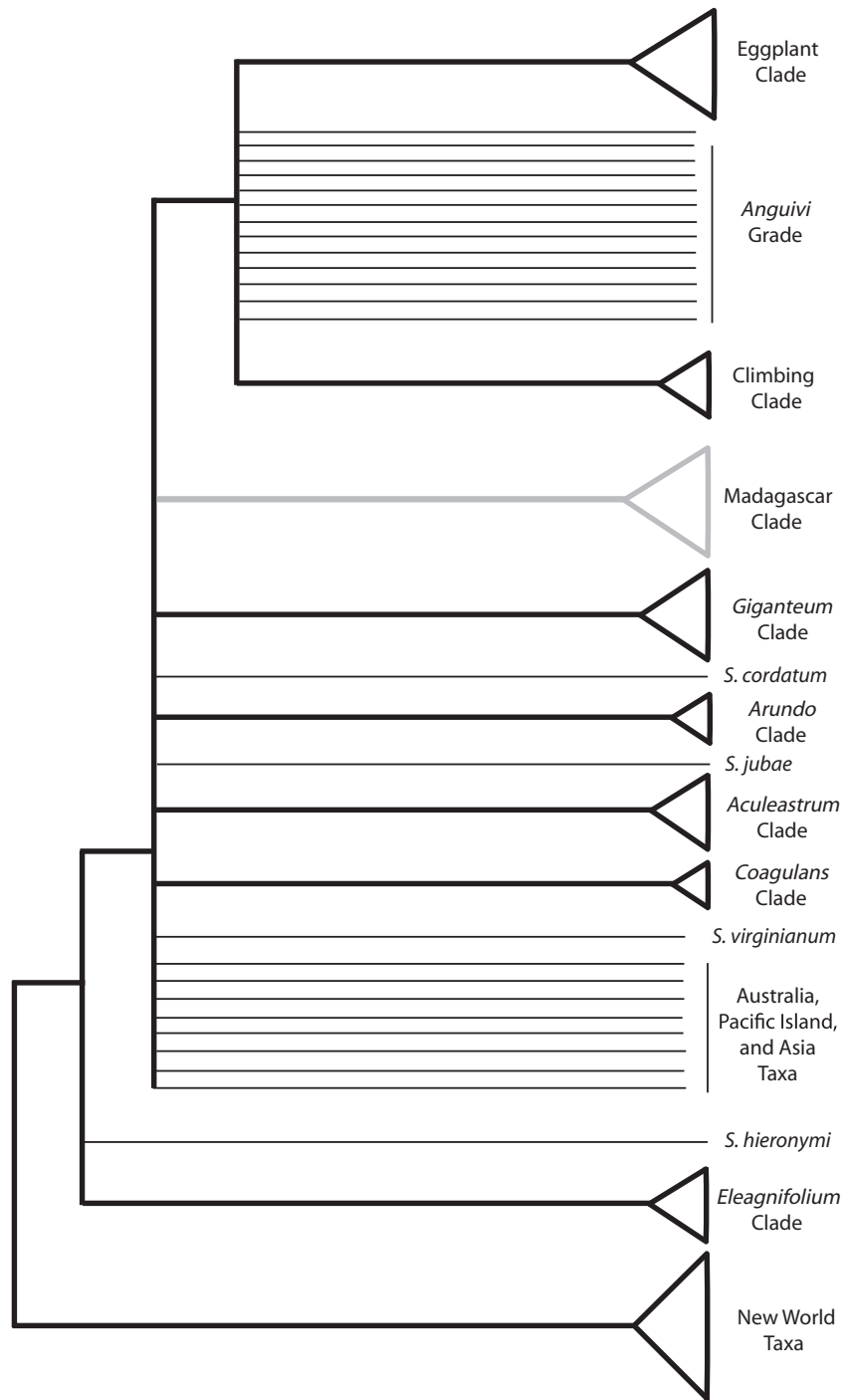
Figure 4. A simplified phylogenetic tree summarizing the clades recognized in this study. Clades are marked with triangles proportional to the number of species in each clade. All clades and branches accepted in this summary have a posterior probability (PP) of > 0.95 and bootstrap support of > 90%, except the Madagascar clade with a PP of 1.00 and bootstrap support of 73%, which is marked in grey. Accessions that do not fall within the clades are labelled individually or assigned to the *Anguivi* grade or the Australasian, Pacific Island and Asian group.

Madagascar have poor support in the overall analysis, some significant patterns have emerged. Our results show that the traditional sections *Oliganthes* and *Melongena* are polyphyletic and the distinction between them is artificial (see below). Some of the well-supported clades identified here (e.g. the eggplant clade) have been recognized previously (Weese & Bohs, 2007). Others, such as the climbing clade, are new.

Morphological synapomorphies for clades defined using molecular data in *Solanum* are sometimes elusive (Bohs, 2005) and combinations of characters tend to be more useful. The *Coagulans* and *Aculeastrum* clades do not share any obvious morphological synapomorphies, although both occur in East and North-East Africa. *Solanum coagulans* and *S. melastomoides* of the *Coagulans* clade share heterandry (unequal stamen length characterized by one filament being longer than the other four) and black seeds. Heterandry in the form of differential stamen size also occurs in the *Giganteum* clade (see below for a discussion of all instances of heterandry). The members of the *Aculeastrum* clade have often been combined into a single broadly defined species, *S. aculeastrum* Dunal, but are distinct (Vorontsova *et al.*, 2010). They share a tall shrub-like habit and all inhabit montane forests; species in the group range from hermaphroditic (*S. thomsonii* C.H.Wright) to strongly andromonoecious (*S. aculeastrum*).

The members of the *Arundo* clade are all species of arid East African savannahs and have been recognized previously as section *Ischyracanthum*, defined by a thick pericarp, curved stem prickles and straight leaf prickles. *Solanum jubae* Bitter is from similar habitats, but lacks prickles and has smaller fruits with a thinner pericarp, and is morphologically different from the other two taxa in the clade; it has been thought to be closely related to *S. somalense* Franch. (here part of the *Giganteum* clade) and *S. pampaninii* Chiov. (not included in this analysis).

The *Giganteum* clade is strongly supported as including both *S. giganteum*, with its traditionally recognized relatives (*S. schimperianum* Hochst. ex A.Rich, *S. tettense* Klotzsch, *S. goetzei* Dammer, *S. schumannianum* Dammer and *S. schleibenii* Werderm.), and the members of Bitter's section *Anisantherum* (*S. somalense* and *S. pubescens* Willd.). *Solanum giganteum* and relatives have complex, many-branched inflorescences of small flowers and small red berries, whereas *S. somalense* and *S. pubescens* have larger heterandrous flowers with one stamen conspicuously longer than the rest. The species are all erect shrubs to small trees and share multangulate trichomes with more than eight lateral rays. *Solanum giganteum* is a widespread pioneer and occurs in montane forests from tropical Africa to India. Other species previously thought to be related to the Indian *S. pubescens*, such as *S. wightii* Nees (a narrow endemic of the Nilghiri Hills in India), have not been analysed, but may also be part of this clade. *Solanum anomalum* Thonn. is the only species of *Solanum* known to be endemic to West African wet coastal forest and is sister to the rest of the *Giganteum* clade.

The morphologically extremely divergent species endemic to Madagascar (D'Arcy & Rakotozafy, 1994) are all closely related, suggesting an *in situ* radiation, although this grouping has low support (see below).

One well-supported clade comprises a group of taxa designated here as the 'eggplant–*Anguivi*–climbing' clade containing two well-defined clades (eggplant and climbing clades) and a complex, poorly resolved grade of species from Africa, the Near East and Asia (the *Anguivi* grade). The climbing clade is a strongly supported group of three species that share a weak climbing habit with shoots attaching themselves to surrounding vegetation by their sharp recurved prickles, but no other apparent synapomorphies. *Solanum richardii* is strongly andromonoecious, but the other taxa have hermaphroditic flowers.

The *Anguivi* grade is a morphologically variable group. The close relationship between the Canary Island endemics *S. lidii* and *S. vespertilio* (both of which are heterandrous with one enlarged stamen; see Anderson *et al.*, 2006; Prohens *et al.*, 2007a,b) is not at all surprising, nor is the relationship between the cultivated species, *S. macrocarpon* and *S. aethiopicum*, and their wild progenitors, *S. dasyphyllum* and *S. anguivi*. Our results confirm the separation of the Asian species *S. violaceum* Ortega from the mostly African species *S. anguivi*. Both of these species were classified as *S. indicum* L. in many floras, a name that has now been rejected (Hepper, 1978; McNeill *et al.*, 2006).

The eggplant clade was defined by Weese & Bohs (2010), and all the species they included are also part of this clade here. The South African *S. umtuma* is morphologically intermediate between *S. linnaeanum* and the other members of the eggplant clade, and is analysed here for the first time. It groups with the other South African eggplant relatives *S. linnaeanum* and *S. lichtensteinii*. This suggests a South African diversification rather than the introgression proposed by Weese & Bohs (2010). Most species of the eggplant clade are andromonoecious with one or a few basal hermaphroditic flowers and the more distal staminate flowers functioning as pollen donors: domestication of the eggplant took advantage of this characteristic with humans selecting for large fruits (Wang, Gao & Knapp, 2008). *Solanum agnewiorum* is only weakly andromonoecious, and the two accessions labelled *S. 'anguivi'* may represent an undescribed small-

fruited species superficially similar to the widespread and polymorphic *S. anguivi* in the *Anguivi* grade. A lack of clear structure in the eggplant clade does not allow us to conclude whether the strength of andromonoecy has a phylogenetic component.

Andromonoecy (and dioecy) have evolved several times in *Solanum* (Anderson, 1979; Symon, 1979; Whalen & Costich, 1986; Anderson & Symon, 1989), and we see similar multiple occurrences in the African species. The presence of andromonoecy in the taxa sampled is presented in Table 1. Andromonoecious and non-andromonoecious (hermaphroditic) species are present in the eggplant clade, climbing clade, Madagascar clade and *Aculeastrum* clade. It is probable that andromonoecy is a synapomorphy of part of the eggplant clade. Experimental data suggest that the strength of andromonoecy is a single physiological variable or a linked series of traits in which fewer larger fruits are developmentally associated with larger corollas and longer anthers in the female-fertile flowers (Miller & Diggle, 2007). Larger fruit size is also broadly correlated with a difference in pericarp colour; large fruits tend to be yellow and small fruits red. Hence, the full suite of seemingly independent characters separating the traditional sections *Oliganthes* and *Melongena* could represent the direct effects of andromonoecy.

The vegetation of Africa has been subdivided into a set of vegetation types based on the coincident distribution patterns of vascular plants (called phytochoria by White, 1983, 1993; Linder *et al*., 2005). There is a high level of correlation between vegetation types and distributions of spiny *Solanum* spp., with 61 of the 73 native species restricted to one vegetation type or one vegetation type and an adjacent 'transition zone' (Jaeger & Hepper, 1986; M. S. Vorontsova & S. Knapp, in press). Vegetation types in which the African and Malagasy species sampled occur are marked in colour in Figures 2 and 3. The clades recognized here are largely confined to a single vegetation type, with only the eggplant and *Giganteum* clades including accessions from outside Africa. Four of the seven clades (eggplant clade, climbing clade, Madagascar clade and *Giganteum* clade) include species from two or more vegetation types. This suggests diversification in Africa, with frequent dispersal or vicariance between vegetation types, similar to the repeated events of dispersal and vicariance between xeric environments in South, East and parts of West Africa identified by Davis *et al*. (2002) and Sanmartín *et al*. (2010), although this pattern could also be explained by differential extinction. All the species endemic to Madagascar are part of the rather weakly supported Madagascar clade; this is in contrast with the suggestion by D'Arcy (1992) that, based on morphology, these species are closely related to New

World and Australasian species. The distinct identity of the Madagascar clade, and its lack of a clear relationship to African groups, is similar to the numerous angiosperm, invertebrate and vertebrate groups thought to have diversified in Madagascar following a dispersal event from Asia or other areas outside mainland Africa (Schatz, 1996; Plunkett, Lowry & Burke, 2001; Masters, de Wit & Asher, 2006; Yoder & Nowak, 2006; Buerki *et al*., 2013). Better sampling of Asian *Solanum* should help in the assessment of this pattern.

CONCLUSIONS

This study merely 'scratches the surface' of the unexpectedly complex evolutionary history of African spiny solanums. These results highlight the need for more extensive taxon sampling at both species and geographical distribution levels. There should be broader sampling and sequencing of additional DNA regions, particularly those from India, China and South-East Asia, where it is critical that morphological analysis of these poorly known species also be conducted. Our results suggest that the African and Malagasy clades have evolved mostly in single vegetation types, although there appears to be considerable interchange between vegetation types in some groups. Relationships between African and Asian spiny solanums are complex, and simple conclusions drawn from only a few species are likely to be premature. These relationships will be of interest not only to botanists, but also to those involved in aubergine breeding, as many wild species are crossable to the cultivated aubergine through embryo capture (Daunay & Hazra, 2012) and have broad spectra of disease and pest resistance. This study provides the framework in which this future exploration can begin.

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APPENDIX

Voucher details, species and author, source of seed or geographical region, collector and collection number (herbarium), and GenBank accession numbers for: ITS/*waxy*/*trnT-F*. BIRM samples have the seed accession number of the Solanaceae collection at the University of Birmingham, UK; Nijmegen (NIJ) accession numbers refer to the Solanaceae collection at Radboud University, Nijmegen, the Netherlands.

S. acerifolium Dunal, Costa Rica, *Bohs 2714* (UT), AY561261/AY562949/AY266249.   **S. aculeastrum Dunal**, Kenya, *Vorontsova et al. 19* (BM), HQ721833/ HQ721959/HQ721896.   **S. aculeastrum Dunal**, Uganda, NIJ 924750119, *Bohs 3251* (UT), AY996481/ AY996376/DQ812102. *S. aethiopicum* L., China, *Knapp 10121* (BM), HQ721834/HQ721960/HQ721897.

S. aethiopicum **L.**, BIRM S.0344, *Olmstead S-74* (WTU), AY996482/AY996378/DQ180394. **S. agnewiorum Voronts.**, Kenya, *Vorontsova 195* (BM), HQ721835/HQ721961/HQ721898. **S. anguivi Lam.**, Uganda, *Bohs 3250* (UT), HQ721836/HQ721962/ HQ721899. **S. anguivi Lam.**, Madagascar, NIJ A44750041, *Bohs 3266* (UT), HQ721837/HQ721963/ HQ721900. **S. anguivi Lam.**, Kenya, *Vorontsova et al. 100* (BM), HQ721838/HQ721964/HQ721901. **S. anguivi Lam.**, Uganda, *Bohs 3227* (= *Knapp 9803*, BM) (UT), AY996483/AY996380/DQ812103. **S. anguivi Lam**, Africa, *Martine 572* (CONN), AY996484/AY996383/HQ721920.   **S. anomalum Thonn.**, Gabon, *Wieringa 6207* (WAG), HQ721839/ HQ721965/HQ721902. **S. arundo Mattei**, Kenya, *Vorontsova et al. 80* (BM), HQ721840/HQ721966/ HQ721903. **S. aturense Dunal**, Costa Rica, *Soto et al. 1222* (UT), GQ163574/GQ163636/GQ163488. **S. barbisetum Nees**, China, *Knapp 10127* (BM), HQ721841/HQ721967/HQ721904. **S. betaceum Cav.**, Bolivia, *Bohs 2468* (UT), AF244713/AY996387/ DQ180426. **S. bumeliifolium Dunal**, Madagascar, *Luckow 4322* (UT), GQ163638/GQ169756/GQ163490. **S. burchellii Dunal**, Namibia, *Koberg et al. 2688* (K), HQ721842/HQ721968/HQ721905.   **S. campanulatum R.Br.**, BIRM S.0387, *Olmstead S-78* (WTU), AY996488/AY996388/DQ180395.   **S. campylacanthum Hochst. ex A.Rich.**, Kenya, *Vorontsova et al. 1* (BM), HQ721844/HQ721970/HQ721907. **S. campylacanthum Hochst. ex A.Rich.**, Kenya, *Vorontsova et al. 107* (BM), HQ721845/HQ721971/HQ721908. **S. campylacanthum Hochst. ex A.Rich.**, Uganda, NIJ 924750118, *Martine 571* (SUNY-PI), AY996489/ AY996390/EU176141. **S. candidum Lindl.**, Costa Rica, *Bohs 2898* (UT), AY562953/—/AY266250; BIRM S.0975, *Olmstead S-100* (WTU), —/AF244722/—. **S. capense L.**, South Africa, NIJ 904750116, *Bohs 2905* (UT), AY996490/AY996391/DQ392958. **S. capsicoides All.**, Peru, *Bohs 2541* (UT), AY562954/ AY561265/AY266251.   **S. catombelense Peyr.**, Namibia, *Kolberg 934* (K), HQ721846/HQ721972/ HQ721909.   **S. cerasiferum Dunal**, Ethiopia, *Friis et al. 7811* (K), HQ721847/HQ721973/HQ721910. **S. chenopodinum F.Muell.**, BIRM S.0813, no voucher, AY996393/AY996492/DQ180396. **S. clarkiae Symon**, Australia, *Symon 17109* (AD), AY996495/AY996396/DQ855033.   **S. coagulans Forssk.**, Kenya, *Vorontsova et al. 81* (BM), HQ721849/ HQ721975/HQ721912. **S. coagulans Forssk.**, Ethiopia, *Thulin 10736* (UPS), HQ721850/HQ721976/ HQ721913. **S. coagulans Forssk.**, Sudan, NIJ, A34750435, *Bohs 3274* (UT), AY996398/AY996497/ DQ812105. **S. cookii Symon**, NIJ 904750182, *Bohs 2851* (UT), GQ163643/GQ163577/GQ163495. **S. cordatum Forssk.**, Ethiopia, *Thulin et al. 11244* (UPS), HQ721851/HQ721977/HQ721914.   **S. cordatum**

Forssk., Ethiopia, *Thulin et al. 11193* (UPS), HQ721875/HQ722000/HQ721939. **S. croatii D'Arcy & Keating**, Madagascar, *Miller & Randrianasolo 6179* (P), HQ721852/HQ721978/HQ721915. **S. cyaneopurpureum De Wild.**, Tanzania, *Vorontsova 192* (UT), HQ721853/HQ721979/HQ721916. **S. cyaneopurpureum De Wild.**, Burundi, NIJ 874750010, *Bohs 3164* (UT), AY996503/AY996405/DQ392959. **S. dasyphyllum Thonn.**, *Cipollini 7* (UT), AY996504/AY996406/EU176139. **S. dennekense Dammer**, Kenya, *Vorontsova 204* (BM), HQ721854/HQ721980/HQ721917. **S. dennekense Dammer**, Ethiopia, *Friis et al. 8304* (K), HQ721855/HQ721981/HQ721918. **S. dimorphispinum C.T.White**, Australia, *Bohs 3582* (UT), GQ163648/GQ163581/GQ163500. **S. elaeagnifolium Cav.**, Paraguay, *Bohs 3199* (UT), AY996412/AY996508/DQ180463. **S. erythracanthum Dunal**, Madagascar, *Dorr et al. 3277* (P), HQ721856/HQ721982/HQ721919. **S. erythracanthum Dunal**, Madagascar, *Malcomber et al. 1295* (P), HQ721857/—/HQ721921. **S. furfuraceum R.Br.**, BIRM S.1442, *Olmstead S-84* (WTU), AY996512/AY996417/DQ180401. **S. giganteum Jacq.**, Kenya, *Vorontsova 161* (UT), HQ721858/HQ721983/HQ721922. **S. giganteum Jacq.**, INRA, *Daunay MM0977* (UT), GQ163658/GQ163590/GQ163511. **S. glabratum Dunal**, Yemen, NIJ 944750142, *Bohs 2906* (UT), AY996420/AY996514/DQ812106. **S. goetzei Dammer**, Tanzania, NIJ A24750103, *Bohs 3273* (UT), GQ163591/GQ163659/GQ163512. **S. gympiense Symon**, Australia, *Bohs 3539* (UT), GQ163592/GQ163660/GQ163513. **S. heinianum D'Arcy & Keating**, Madagascar, *RHS 275* (TAN), AY996421/AY996515/GQ163515. **S. hieronymi Kuntze**, Argentina, *Nee & Bohs 50761* (NY), AY996423/AY996517/GQ163517. **S. houstonii Martyn**, NIJ 904750179, *Bohs 2977* (UT), AY996474/AY996559/DQ180412. **S. humile Lam.**, NIJ 814750065, *Bohs 3468* (UT), EU176137/EU176121/EU176157. **S. humile Lam.**, INRA, *MM1226* (UT), GQ163694/GQ163620/GQ163556. **S. inaequiradians Werderm.**, Tanzania, *Vorontsova 154* (UT), HQ721859/HQ721984/HQ721923. **S. incanum L.**, Kenya, *Vorontsova 203* (BM), HQ721860/HQ721985/HQ721924. **S. incanum L.**, NIJ 874750008, *Cipollini 81* (UT), AY996428/AY996520/GQ163522. **S. incompletum Dunal**, Hawaii, no voucher, AY996429/AY996521/GQ163523. **S. insanum L.**, India, NIJ 954750125, *Bohs 3459* (UT), EU176130/EU176114/EU176149. **S. insanum L.**, Indonesia, NIJ 944750231, *Bohs 3460* (UT), EU176132/EU176116/EU176151. **S. insanum L.** NIJ 924750202, *Bohs 3461* (UT), EU176133/EU176117/EU176152. **S. insanum L.**, China, *Knapp 10113* (BM), HQ721889/HQ722013/HQ721952. **S. insanum L.**, China, *Wang 2044* (BM), HQ721890/HQ722014/HQ721953. **S. jamaicense Mill.**, BIRM S.1209, *Olmstead S-85* (WTU), AY562956/AF244724/DQ180485. **S. jubae Bitter**, Ethiopia, *Boudet 8086* (K), HQ721861/HQ721986/HQ721925. **S. lamprocarpum Bitter**, NIJ 944750153, *Bohs 3467* (UT), GQ163671/GQ163600/GQ163529. **S. lichtensteinii Willd.**, South Africa, NIJ 954750126, *Bohs 3482* (UT), EU176128/EU176112/EU176146. **S. lidii Sunding**, Canary Islands, NIJ 934750022, *Bohs 2903* (UT), AY996434/AY996524/DQ180403. **S. linnaeanum Hepper & P.-M.L. Jaeger**, France, *Bohs 3238* (UT), EU915548/EU915550/EU915549. **S. macrocarpon L.**, BIRM S.0133, *Olmstead S-88* (WTU), AF244725/AY996436/DQ180404. **S. mahoriense D'Arcy & Rakot.**, Madagascar, *Bohs 2576* (UT), AY996437/AY996526/DQ180405. **S. malindiense Voronts.**, Kenya, *Vorontsova et al. 112* (BM), HQ721862/HQ721987/HQ721926. **S. mauense Bitter**, Kenya, *Vorontsova et al. 20* (BM), HQ721863/HQ721988/HQ721927. **S. melastomoides C.H.Wright**, Somalia, *Thulin 10963* (UPS), HQ721864/HQ721989/HQ721928. **S. melastomoides C.H.Wright**, Somalia, *Thulin et al. 10582* (UPS), HQ721884/HQ722008/—. **S. melongena L.**, China, *Knapp 10124* (BM), HQ721865/HQ721990/HQ721929. **S. melongena L.**, China, *Knapp 10115* (BM), HQ721866/HQ721991/HQ721930. **S. melongena L.**, NIJ 954750114, *Olmstead S-91* (WTU), AF244726/AY562959/DQ180406. **S. melongena L.**, USA (cultivated), *Bohs 3650* (UT), EU176119/EU176135/EU176154. **S. myoxotrichum Bak.**, Madagascar, *Bohs 2981* (UT), AY996534/AY996445/DQ392960. **S. nienkui Merr. & Chun**, China, *Wang 2073* (BM), HQ721867/HQ721992/HQ721931. **S. nigriviolaceum Bitter**, Daunay 1269 INRA France, *Bohs 3242* (UT), EU427555/EU427554/EU427553. **S. nigriviolaceum Bitter**, Kenya, *Vorontsova et al. 57* (BM), HQ721868/HQ721993/HQ721932. **S. oldfieldii F.Muell.**, Australia, *Bohs 3253* (UT), GQ163685/GQ163612/GQ163545. **S. papaverifolium Symon**, Australia, *Bohs 3528* (UT), GQ163688/GQ163615/GQ163548. **S. phoxocarpum Voronts.**, Kenya, *Vorontsova et al. 29* (UT), HQ721869/HQ721994/HQ721933. **S. platacanthum Dunal**, Yemen, *Wood 1991* (K), HQ721870/HQ721995/HQ721934. **S. polhillii Voronts.**, Kenya, *Vorontsova et al. 15* (BM), HQ721871/HQ721996/HQ721935. **S. polhillii Voronts.**, Kenya, *Vorontsova et al. 88* (BM), HQ721872/HQ721997/HQ721936. **S. praetermissum Kerr ex Barnett**, China, *Wang 2035* (BM), HQ721873/HQ721998/HQ721937. **S. procumbens Poir.**, China, *Wang 2075* (BM), HQ721874/HQ721999/HQ721938. **S. pubescens Willd.**, India, *Wang 1525* (PE), HQ721876/HQ722001/HQ721940. **S. pyracanthos Lam.**, Madagascar, *Olmstead S-95* (WTU), AY996459/AY996546/DQ180408. **S. quitoense Lam.**, Costa Rica, *Bohs 2873* (UT), AY562965/—/—; Jardín

Botanico de Bogotá, Colombia, *Olmstead*, no voucher, —/AY263460/—; Ecuador, *Hieser sn*, —/—/AY266243. **S. richardii Dunal**, NIJ 944750152, no voucher, AY996462/AY996549/AY996549. **S. richardii Dunal**, Tanzania, *Vorontsova 182* (UT), HQ721843/ HQ721969/HQ721906. **S. ruvu Voronts.**, Tanzania, *Mhoro* UMBCP113 (K), HQ721877/—/HQ721941. **S. sandwicense Hook. & Arn.**, Hawaii, *Bohs 2992* (UT), AY996464/AY996551/DQ180409. **S. schimperianum Hochst. ex. A. Rich.**, BIRM S.1538, *Olmstead S-97* (WTU), AY996465/AY996552/DQ180410. **S. schliebenii Werderm.**, Tanzania, *Vorontsova 155* (UT), HQ721878/HQ722002/HQ721942. **S. schumannianum Dammer**, Tanzania, *Tepe 2797* (UT), HQ721879/HQ722003/HQ721943. **S. sejunctum Brennan et al.**, Australia, *Symon 17105* (AD), AY996466/AY996553/GQ163558. **S. setaceum Dammer**, Tanzania, *Vorontsova et al. 167* (BM), HQ721880/HQ722004/HQ721944. **S. setaceum Dammer**, Kenya, *Vorontsova et al. 84* (BM), HQ721881/HQ722005/HQ721945. **S. somalense Franch.**, Kenya, *Vorontsova 207* (BM), HQ721882/ HQ722006/HQ721946. **S. somalense Franch.**, Ethiopia, *Friis et al. 10379* (K), HQ721883/HQ722007/ HQ721947. **S. umtuma Voronts. & S.Knapp**, South Africa, *Nevhutalu et al. 921* (K), HQ721848/ HQ721974/HQ721911. **S. stipitatostellatum Dammer**, Tanzania, *Vorontsova 153* (UT), HQ721885/ HQ722009/HQ721948. **S. supinum Dunal**, Botswana, NIJ 944750174, *Bohs 3469* (UT), EU176138/ EU176122/EU176158. **S. tettense Klotzsch**, Kenya,

Vorontsova et al. 82 (BM), HQ721886/HQ722010/ HQ721949. **S. tettense Klotzsch**, South Africa, NIJ 944750162, *Bohs 2849* (UT), AY996430/AY996522/ GQ163528. **S. thomsonii C.H.Wright**, Tanzania, *Vorontsova 175* (BM), HQ721887/HQ722011/ HQ721950. **S. thomsonii C.H.Wright**, Tanzania, *Tepe 2793* (BM), HQ721888/HQ722012/HQ721951. **S. toliaraea D'Arcy & Rakot.**, Madagascar, *Bohs 2574* (UT), AY996472/AY996557/DQ180411. **S. tomentosum L.**, South Africa, NIJ 894750127, *Bohs 3107* (UT), AY996473/AY996558/DQ392961. **S. torvum Sw.**, BIRM S.0839, *Olmstead S-101*(WTU), AY562972/AF244729/AY266246. **S. usaramense Dammer**, Tanzania, *Vorontsova 159* (UT), HQ721891/ HQ722015/HQ721954. **S. vaccinioides Schltr.**, New Caledonia*, Bohs 3608* (UT), DQ812111/GQ163629/ DQ812110. **S. vespertilio Aiton**, BIRM S.2091, *Olmstead S-103* (WTU), AY996476/AF244727/DQ180413. **S. violaceum Ortega**, BIRM S.1849, *Bohs 3277* (UT), HQ721892/HQ722016/HQ721955. **S. violaceum Ortega**, INRA, *Dauney MM1003* (UT), GQ163670/ GQ163599/GQ163527. **S. violaceum Ortega**, China, *Knapp 10110* (BM), HQ721893/HQ722017/HQ721956. **S. violaceum Ortega**, Mauritius, *Bloomfield s.n.* (BM), HQ721894/HQ722018/HQ721957. **S. violaceum Ortega**, NIJ 924750100, *Bohs 3093* (UT) AY996560/AY996478/EU176159. **S. virginianum L.**, NIJ 934750032, *Cipollini 17* (UT), AY996561/ AY996479/EU176160. **S. zanzibarense Vatke**, Tanzania, *Vorontsova 187* (UT), HQ721895/HQ722019/ HQ721958.