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1Shedding new light on the origin and spread of the brinjal 2eggplant (*Solanum melongena* L.; Solanaceae) and its wild 3relatives

4

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19

20ABSTRACT

21**PREMISE OF THE STUDY:** While brinjal eggplant (*Solanum melongena* L.) is the second most
22important solanaceous vegetable crop, we lack firm knowledge of its evolutionary relationships. This
23in turn limits efficient use of crop wild relatives in eggplant improvement. Here, we examine the
24hypothesis of linear step-wise expansion of the eggplant group from Africa to Asia.

25**METHODS:** We use museum collections to generate nuclear and full-plastome data for all species of
26the eggplant clade. We combine a phylogenomic approach with distribution data to infer a
27biogeographic scenario for the clade.

28**KEY RESULTS:** The eggplant clade has Pleistocene origins in northern Africa. Dispersions to
29tropical Asia gave rise to *Solanum insanum*, the wild progenitor of the eggplant, and to Africa distinct
30lineages of widespread and southern-African species. Results suggest that spread of species to
31southern Africa is recent and was likely facilitated by large mammalian herbivores feeding on
32*Solanum* fruits (African elephant and impala).

33**CONCLUSIONS:** Rather than a linear 'Out Of Africa' sequence, our results are more consistent with
34an initial dispersion event into Asia, and subsequent wide dispersion and differentiation across Africa

35driven by large mammalian herbivores. Our evolutionary results will impact future work on eggplant
36domestication and use of wild relatives in breeding of this increasingly important solanaceous crop.

37

38**KEY WORDS** Eggplant (aubergine), crop wild relatives (CWRs), phylogenomics, chloroplast
39genome, biogeography, molecular dating, dispersion, mammalian herbivores

40INTRODUCTION

41 Crop wild relatives (CWRs) are likely to play a significant role in securing 21st century food
42 security (Dempewolf et al., 2014), due to their potential for use in breeding to withstand adverse
43 impacts of climate change, increasing scarcity of nutrients, water and other inputs, and new pests and
44 diseases (Hopkins and Maxted, 2010). Understanding the phylogenetic relationships, geographic
45 origins and spread of CWRs is critical for improving their use in future plant breeding in the face of
46 environmental and climate change.

47 The brinjal eggplant, *Solanum melongena* L. (also known as the aubergine; Solanaceae) is the
48 second most important economically important solanaceous vegetable crop after tomato (FAO,
49 2017). The brinjal eggplant has a long history of cultivation (see Daunay and Janick, 2007; Wang et
50 al., 2008), and is thought to have been domesticated in Asia several times (Daunay and Hazra, 2012;
51 Meyer et al., 2012). Increasing genetic diversity in the cultivated crop is a major target in brinjal
52 eggplant breeding (Muñoz-Falcón et al., 2009). Improvements in yield, fruit and postharvest quality
53 (Vilanova et al., 2010), resistance to plant pathogens (Pautasso et al., 2012; Bebbler et al., 2014), and
54 introduction of abiotic stress traits such as tolerance to increased drought, temperatures, and extreme
55 precipitation are all important, especially in the face of climate change model predictions of higher
56 temperatures and extreme weather patterns worldwide (Cattivelli et al., 2008). Crop wild relatives are
57 an increasingly important source for traits and genes for brinjal eggplant improvement (Daunay et al.,
58 1991; Muñoz-Falcón et al., 2009; Hurtado et al., 2012; Kaushik et al., 2016), and knowledge about
59 their distribution, traits and threat status has been the focus of recent studies (Syfert et al., 2016;
60 Kinsell et al., unpublished).

61 *Solanum* L., with c. 1,400 species, is one of the largest genera of flowering plants (Frodin,
62 2004) and has been the subject of much recent taxonomic and phylogenetic work (e.g., see references
63 in Särkinen et al., 2013; Vorontsova and Knapp, 2016). The species-level taxonomy of *S. melongena*
64 and its wild relatives has long been recognised as complex (Lester and Hasan, 1991; Daunay and
65 Hazra, 2012), but recent revision and clarification of taxonomic limits in the group (Knapp et al.,
66 2013; Vorontsova and Knapp, 2016) has provided a set of species identities for use in further analyses.
67 Previous analyses recognised only two species in the Eggplant clade (e.g., Lester and Hasan, 1991;
68 Weese and Bohs, 2010), but further work with African solanums suggested the clade comprised ten
69 species characterized in part by their andromonoecious breeding system (see Table 1 in Knapp et al.,
70 2013). Even though the number of taxa recognised increased, several extremely widespread species
71 (e.g., *S. campylacanthum* A.Rich. across eastern Africa) include much geographical variation,
72 suggesting a role for ecological structuring in these taxa (Ranil et al., 2016; Vorontsova and Knapp,
73 2016).

74 *Solanum melongena* and its wild relatives are members of the largest clade of the genus, the

75Leptostemonum Clade (the ‘spiny’ solanums; Bohs, 2005; Weese and Bohs, 2010; Särkinen et al.,
762013), and within that, a monophyletic group comprising almost all Old World spiny solanums (Stern
77et al., 2011; Vorontsova et al., 2013; Aubriot et al., 2016). The Eggplant clade has been recognised as
78monophyletic in previous analyses (e.g., Stern et al., 2011; Weese and Bohs, 2010), but sampling of
79Old World taxa was limited. Using the same set of genebank accessions Weese and Bohs (2010) tested
80Lester’s (Lester and Hasan, 1991) evolutionary scenario of brinjal eggplant evolution, but showed that
81the weedy species *S. linnaeanum* Hepper & P.M.-L.Jaeger also belonged to the group. Their analysis
82(Weese and Bohs, 2010) supported the scenario of an African origin for the group with step-wise
83expansion to tropical Asia and migration back to the Middle East as feral forms. Vorontsova et al.
84(2013) expanded the dataset by including many African taxa and still recovered a monophyletic
85Eggplant clade, but with little internal resolution. Their results placed the narrow Kenyan endemic *S.*
86*agnewiorum* Voronts. within the monophyletic Eggplant clade, a surprising result given its small fruit
87and hermaphroditic flowers. Inclusion of more species from Africa and southeast Asia (Aubriot et al.,
882016) revealed that two additional African species with hermaphroditic flowers were members of the
89monophyletic group (*S. lanzae* J.-P.Lebrun & Stork and *S. usambarensis* Bitter & Dammer). These
90studies used both plastid and nuclear molecular markers, and although the circumscription of the
91Eggplant clade improved, resolution within it was still poor. Although the brinjal eggplant and its wild
92relatives have clear morphological, molecular and eco-geographical differences (see Meyer et al.,
932012; Knapp et al., 2013; Ranil et al., 2016), they have been difficult to resolve using traditional
94molecular markers (Vorontsova et al., 2013; Aubriot et al., 2016).

95 High-throughput sequencing and DNA library preparation improvements have made obtaining
96whole plastid genomes from total DNA extraction affordable for many non-model organisms driving a
97rapid increase in the number of genomes in public sequence repositories (see Tonti-Filippini et al.,
982017). It has been suggested that complete plastid genomes can be used as ‘superbarcodes’ thus
99providing an abundance of characters to increase resolution in poorly resolved phylogenies (Williams
100et al., 2016).

101 Here we use sequences of whole chloroplast genomes to improve circumscription of and
102resolution in the Eggplant clade, and to test hypotheses concerning the origin of the close relatives of
103the cultivated eggplant, *Solanum melongena*. To account for morphological and geographical
104variability of the species, we designed a two-fold approach. First, we used Sanger data to test species
105circumscriptions for four widespread species of the Eggplant clade; we investigated two nuclear loci,
106ITS and the *waxy* (GBSSI) gene, and one plastid intergenic spacer, *ndhF-rpL32*, to check for
107topological incongruences. Second, based on this first analysis, we generated a plastome phylogeny of
108the Eggplant clade that we used to re-assess Lester and Hasan’s (1991) hypothesis of linear step-wise
109migration from Africa to Asia and use ancestral areas reconstruction to investigate biogeography and

110 dispersion of the Eggplant clade as currently circumscribed. We relate dispersion and spread in
111 widespread eastern African species to large mammalian herbivores that feed on *Solanum* fruits
112 (Pringle et al., 2014; Kartzinel et al., 2015). Our results have implications for future research on wild
113 sources of genetic variability for eggplant improvement, particularly in the context of global climate
114 change and efforts to develop the genetic basis for sustainable pest control.

115

116 MATERIALS AND METHODS

117 **Taxon sampling**—*Sampling for preliminary Sanger analysis*—For Sanger analysis, we
118 sampled across the distribution range of four widespread species (*S. campylacanthum*, *S. cerasiferum*
119 Dunal, *S. incanum* L. and *S. insanum* L.) in order to test species monophyly and reveal any geographic
120 patterns. For the widespread and weedy eastern African species *S. campylacanthum*, we sampled three
121 specimens from the northernmost part of its distribution area (Ethiopia), one from Tanzania and two
122 from the southernmost part (Namibia and South-Africa). Both *S. cerasiferum* and *S. incanum* are
123 distributed across northern sub-Saharan Africa, with *S. incanum* also extending into regions of Middle
124 East and central Asia as far as Pakistan (Vorontsova and Knapp, 2016). For *S. cerasiferum* we used
125 specimens from Ethiopia and the Central African Republic, and for *S. incanum* one specimen from the
126 westernmost part of the distribution range (Burkina Faso), two from the centre (Kenya and Oman), as
127 well as one from the easternmost part (Pakistan). *Solanum insanum*, the wild progenitor of the
128 cultivated eggplant (Meyer et al., 2012; Ranil et al., 2016), is distributed across tropical Asia, but also
129 occurs in Madagascar; it does not occur in Africa with no populations in East Asia and Africa (Ranil et
130 al., 2016); we sampled two specimens from tropical Asia (China and India) and one individual from
131 Madagascar. Our sampling is not designed to explore the structure of relationships between the
132 populations of *S. insanum* and *S. melongena*; this will require population level sampling across the
133 range of both taxa (e.g., Meyer et al., 2012; W. Jinxiu, pers. comm.).

134 To place our study within the wider framework of Old World spiny solanums, we also
135 sampled closely related species (sensu Vorontsova et al., 2013, Aubriot et al., 2016). A clade of four
136 tropical Asian species (“*Solanum violaceum* and relatives” sensu Aubriot et al., 2016), as well as three
137 African species (*S. nigriviolaecum* Bitter, *S. polhillii* Voronts. and *S. supinum* Dunal) were found to be
138 closely related to the Eggplant clade (Vorontsova et al., 2013; Aubriot et al., 2016); therefore we
139 included in our sampling one accession of *S. violaceum* Ortega and one accession for each of these
140 three African species. Two informal groupings of a large number of African and Asian species, the
141 ‘Anguivi grade’ and the ‘Climbing clade’ (Vorontsova et al., 2013; Aubriot et al., 2016) were also
142 sampled in order to better test the circumscription of the Eggplant clade. We selected six species of the
143 ‘Anguivi grade’, including the two cultivated African solanums, the Gboma eggplant (*S. macrocarpon*
144 L.) and the Scarlet eggplant (*S. aethiopicum* L.), as well as their wild progenitors (*S. dasyphyllum*

145 Schumach. & Thonn. and *S. anguivi* Lam. respectively). Most species of the ‘Anguivi grade’ have
146 geographic distributions centred in continental eastern Africa, but several species occupy disjunct
147 regions such as the Seychelles and India (see Vorontsova et al., 2013; Vorontsova and Knapp, 2016;
148 Aubriot et al., 2016 for details on geographic distributions). To identify potential long-distance
149 dispersal events, we sampled one species with a tropical Asian distribution (*S. trilobatum* L.) and
150 another that occurs within the Middle Eastern region (*S. glabratum* Dunal). We used an eastern
151 African scandent shrub from the ‘Climbing clade’, *S. richardii* Dunal, to root all the trees. Sampling
152 for this analysis includes 36 accessions (24 species), accounting for all 13 species of the Eggplant
153 clade and for 11 additional spiny solanum species from Africa and Asia.

154

155 **Sampling for whole chloroplast genomes analysis**—After using Sanger sequencing for initial
156 assessment of species delimitation in widespread species we generated full plastome data for all
157 species of the Eggplant clade, with the exception of the cultivated brinjal eggplant for which we had
158 two sets of Illumina reads at our disposal. If a species was not shown to be monophyletic based on
159 preliminary Sanger analyses, one accession per lineage was included. All outgroup species used in the
160 preliminary analysis were included in the full-plastome analysis, with the exception of *S.*
161 *nigriviolaceum* for which we had insufficient DNA extract available.

162

163 **DNA extraction, amplification, sequencing and data assembly**—Silica gel dried or herbarium
164 material was ground using a Mixer Mill MM 300 with glass beads (Qiagen Inc., Valencia, CA, USA)
165 and with molecular grade sand. Total genomic DNA was extracted using the same two-step protocol
166 than the one described by Aubriot et al. (2016). We have also extracted chloroplast DNA from fresh
167 leaves of *Solanum melongena* ‘Black Beauty’ following Shi et al. (2012).

168 Amplified DNA regions used in the preliminary Sanger analysis were selected based on
169 previous broad-scope studies on *Solanum* phylogenetics (Särkinen et al., 2013; Aubriot et al., 2016).
170 These latter have shown that the plastid intergenic spacer *ndhF-rpL32*, the internal transcribed spacer
171 (ITS) and the granule-bound starch synthase I (GBSSI) or *waxy* gene are particularly fitted for
172 resolving phylogenetic relationships as the species level. Considering the abundant literature on DNA
173 barcoding of landplants and on phylogenetics of *Solanum*, the use of these three rapidly evolving and
174 *a priori* unlinked DNA regions should be reliable for testing current species boundaries. We
175 downloaded 62 sequences from GenBank, and generated 61 for this study (see [Appendix](#)). For each
176 additional accession, the three DNA regions were amplified and sequenced following the same
177 procedures and techniques than those described in Aubriot et al. (2016). Sanger reads were assembled
178 and edited in Geneious v.7.1.9 (Biomatters Ltd., Auckland, New Zealand). All sequences were
179 automatically aligned with MAFFT v.7.305 (Katoh and Standley, 2013), using the L-INS-i algorithm.

180 Newly generated sequences are deposited in GenBank and listed in the **Appendix**.

181 Starting quantities of total genomic DNA for the 25 samples used in the phylogenomic study
182 were determined by measurement with a Qubit 2.0 Fluorometer (Life Technologies Corp., Carlsbad,
183 CA). DNAs were diluted to approximately 3.8 ng/μl and libraries were prepared using the TruSeq
184 Nano DNA Library Prep Kit (Illumina, San Diego, CA, USA) following manufacturer instructions.
185 Sequencing was performed at the Natural History Museum (London) sequencing facility using the
186 Illumina MiSeq platform (2 × 250 bp) and loading concentration of 6 pM. Illumina adapters were
187 removed, and all reads were quality-trimmed and quality-filtered using Trimmomatic 0.35 (Bolger et
188 al., 2014) with default settings.

189

190 **Plastome assembly, annotation and alignment**—All paired reads were *de-novo* assembled
191 with IDBA-UD 1.1.1 (Peng et al., 2012), using maximum k-value = 250 bp and minimum k-value =
192 250 bp. Resulting contigs were uploaded into Geneious v.7.1.9 (Kearse et al., 2012) where they were
193 quality-checked and length-filtered. Segments of the *de novo* plastomes were then circularized by
194 matching end points. A high coverage plastid genome (800×) was also assembled *de novo* for
195 *Solanum melongena* ‘Black Beauty’ from the collected reads using the built-in Geneious assembler
196 platform with zero mismatches and gaps allowed among the reads. A similar procedure was conducted
197 using Velvet v1.2.10 (Zerbino and Birney, 2008) with k-mer length 37, minimum contig length 74 and
198 default settings by applying 800× upper coverage limit. The results of the two *de novo* methods were
199 compared and inspected. Sanger-based gap closure and IR junction verification was carried out
200 following Moore et al. (2007).

201 Sequence inconsistencies were checked by mapping each set of reads to their respective
202 plastome as described in Wysocki et al. (2015). Assembled plastomes were aligned to the completely
203 annotated bittersweet (*Solanum dulcamara* L.) plastome available on GenBank (NC035724;
204 Amiryousefi et al., unpublished). Annotations were transferred from the references to the assembled
205 plastomes using a similarity threshold of 80%, and were then checked and refined manually. All 25
206 plastomes were aligned with MAFFT v.7.305 using the FFT-NS-2 algorithm, and the alignment was
207 inspected for structural mutations. The pairwise distances between each pair of plastomes were
208 calculated and analysed using the Kimura Maximum Composite Likelihood model implemented in
209 MEGA 7.0 (Kumar et al., 2016).

210

211 **Phylogenetic analyses and dating**—Sanger and genomic alignments were subjected to both
212 maximum likelihood (ML) and Bayesian inference (BI) analyses. All analyses were run via the
213 CIPRES Science Gateway (Miller et al., 2010) using RAxML-HPC v.8.1.24 (Stamatakis, 2014) for
214 ML and MrBayes 3.2.6 (Huelsenbeck and Ronquist, 2001) for BI. In all analyses gaps were treated as

215missing data (N) and *Solanum richardii* served as the outgroup. Sanger alignments were analysed both
216separately and as combined datasets. RAxML analyses were run by using the rapid bootstrap
217algorithm with 1,000 bootstrap iterations. The GTR + G rate substitution model was applied to each
218matrix in order to fit the substitution models implemented in BI (see below); the proportion of
219invariable sites was not estimated as it is not recommended by RAxML developer (Stamatakis, 2016).
220Bootstrap replicate trees were used to draw bipartitions on the optimal ML tree; nodes with bootstrap
221support values (BS) below 50% were pruned to obtain the ML 50% majority-rule tree. For BI
222analyses, the best-fitting nucleotide substitution model inferred with MrModeltest v.2.3 (Nylander,
2232004) via estimation of the Akaike information criterion was assigned to each of DNA region. The
224regions *ndhF-rpL32* and ITS followed a GTR + I + G substitution model, whereas the GTR + I model
225better fitted for the *waxy* region. MrBayes analyses constituted of two independent parallel runs of
226four Markov chains each, run for 10 million generations and trees were sampled every 1000
227generations. Adequate mixing of Markov chains and convergence of the two runs were confirmed with
228Tracer v1.6 (Rambaut et al., 2014); after a 10% burn-in, remaining trees were used to generate a 50%
229Bayesian majority-rule consensus tree. Congruence between the topologies obtained for each of the
230three markers was visually inspected before concatenating them into a combined matrix that was
231divided into three partitions, to which the best-fitted substitution models were applied. The combined
232matrix was run under the same conditions detailed above for the single marker matrices.

233 We used the same BI and ML approaches to analyse the phylogenomic dataset. The plastome
234matrix was analysed with MrModeltest, and the GTR + I + G nucleotide substitution model was
235selected as best-fitting the data. For same reasons than stated above, this model was implemented in
236MrBayes whereas the GTR + G rate substitution model was preferred for RAxML analyses. All
237conditions of MrBayes and RAxML runs were identical to those implemented for analyses of Sanger
238alignments.

239 Relative divergence times, together with the topology were estimated using BEAST v.1.8.4
240(Drummond et al., 2012), with a GTR + I + G rate substitution model applied to the plastome matrix.
241A Yule speciation tree prior and a relaxed uncorrelated clock-model that allows rates to vary
242independently along branches (Drummond et al., 2006) were used with all other parameters set to
243default. We used two temporal constraints to calibrate the BEAST analyses: (1) age of the Eggplant
244clade (mean = 1.54 Myr; standard deviation = 0.5), (2) age of the root (mean = 3.38 Myr; standard
245deviation = 0.5). These were derived from the Solanaceae-wide phylogeny of Särkinen et al. (2013),
246with uncertainty regarding these dates incorporated by assigning normal prior distributions to the two
247calibration points (Couvreur et al., 2008; Evans et al., 2014). Four independent BEAST analyses were
248run, each 100 million generations, sampling every 10,000 generations. Convergence of all parameters
249was assessed using Tracer 1.5 (Rambaut et al., 2014), the first 10% of each of the four Markov chains

250 was removed as burn-in, and chains were combined with LogCombiner 1.7.2. (Drummond et al.,
251 2012) to calculate the maximum clade credibility tree.

252

253 **Biogeographic inference and dispersion analysis**—Species distributions were determined from
254 collection data stored in Solanaceae Source Database (2017, <http://www.solanaceaesource.org/>);
255 cultivated species (*Solanum melongena*, *S. aethiopicum*, *S. macrocarpon*) were excluded from the
256 biogeographic analysis. Because several species are widespread, with distribution areas that
257 encompass all eastern Africa (*S. campylacanthum*) or that extend from western Africa to Pakistan (*S.*
258 *incanum*), circumscription of biogeographic areas that are meaningful in terms of patterns of species
259 distribution and that are coherent climatically and biogeographically speaking is challenging. We
260 defined seven biogeographic areas based on climatic and biogeographic evidence (see below): (A)
261 Tropical Asian region; (B) Somalian and Middle East region; (C) Sudanian region; (D) Congolian
262 region; (E) Zambesian region; (F) Southern African region; (G) Malagasy region (see Fig. 1A). Four
263 of these (C, D, E and F) directly correspond to those of Linder et al. (2012). Linder's regions are
264 statistically defined using patterns from groups of vascular plants and vertebrates, and were shown to
265 be robust between groups. This biogeographic framework is well suited for these solanums with 10 of
266 23 taxa included in our analysis restricted to one region, and several clades that are characteristic of a
267 set of connected biogeographic regions (Southern African clade; Fig. 1B).

268 Boundaries of the biogeographic regions used in this study are subject to some uncertainty due
269 to contrasting climatic patterns (e.g. the wet aseasonal Congolian region vs the drier and more
270 seasonal Sudanian region). Areas around the Tanzania/Kenya border in east Africa correspond to a
271 zone of high mountainous complexity (i.e. Albertine Rift and Kilimanjaro Massif), and have been
272 previously assigned to either the Somalian or the Zambesian regions, depending on the data types used
273 (White, 1983, 1993; Linder et al., 2012). This region has also been identified as a centre of diversity
274 for African spiny solanums (Syfert et al., 2016; Vorontsova and Knapp, 2016). In addition, two of our
275 sampled species, *S. polhillii* and *S. usambarense*, are restricted to this transitional region (Vorontsova
276 and Knapp, 2016) and assigning species to particular biogeographic region was challenging; therefore
277 we accounted for this complexity by assigning these two species to both the Somalian and the
278 Zambesian regions.

279 Handling of the Middle East area presents another challenge as this region does not account
280 for any endemic species of spiny solanums in our sampling (Aubriot et al., 2016). Only *S. glabratum*
281 and *S. incanum* are present in the Middle East, both have distribution ranges centred on northeastern
282 Africa (i.e., Sudanian region). The Red Sea is not a strong dispersal barrier, being only about 25 km
283 wide at its southernmost and narrowest (natural) point, and we combined the Middle East with the
284 Sudanian region, hence delimiting our region B. Similarly, it is difficult to draw the eastern boundary

285 of region B as the Middle East acts as a biogeographic crossroads between Asia and Africa, its biota
286 being of composite origin (Buerki et al., 2012). Among all spiny solanums native of the Middle East
287 region, two are distributed from eastern tropical India to the Arabian Peninsula (*S. pubescens* Willd.,
288 *S. virginianum* L.) while others are not present in tropical regions as their distributions are restricted to
289 dry regions between northeastern Africa and northwestern India (*S. cordatum* Forssk., *S. forskalii*
290 Dunal, *S. glabratum*, *S. incanum*, *S. platananthum* Dunal). Given such distribution patterns, we used
291 the Thar Desert of India as the eastern boundary of zone B (Sudanian region and Middle East). This
292 delimitation also corresponds to the western limit of the Asian monsoon climatic regime, acting as a
293 proxy of the limit between the tropical areas of region A (Tropical Asia) and the mostly dry areas of
294 region B (Holt et al., 2013).

295 The history of Madagascar and of its neighbouring archipelagos (Mascarenes, Granitic
296 Seychelles and Comoros) is characterized by complex geological and climatic events that
297 accompanied their isolation from Africa and the Indian subcontinent. The Malagasy endemic flora has
298 a composite origin, with elements from Africa, the Indian subcontinent and South-East Asia (Buerki et
299 al., 2013). The spiny solanums endemic to Madagascar (not sampled here) are not closely related to
300 the Eggplant clade and form a monophyletic clade whose phylogenetic placement is still unresolved
301 (Vorontsova et al., 2013; Aubriot et al., 2016) within the larger Old World lineage of spiny solanums.
302 We sampled four species that are native to Madagascar and the Mascarenes; two are present in Africa
303 and in Madagascar (*S. anguivi* and *S. richardii*), while the two others have a distribution range centred
304 on tropical Asia, with *S. insanum* (the wild progenitor of the eggplant) present in Madagascar (Knapp
305 et al., 2013; Aubriot et al., 2016; Ranil et al., 2016) and *S. violaceum* recorded from Mauritius
306 (Vorontsova and Knapp, 2016). Hence, we treated Madagascar and the neighbouring archipelagos as a
307 distinct biogeographic area; the Malagasy region (region G).

308 The dispersal-extinction-cladogenesis (DEC) likelihood model implemented in Lagrange v.
309 20130526 (Ree and Smith, 2008) was used to investigate the biogeographic history of the Eggplant
310 clade. The analysis was performed on the BEAST maximum clade credibility tree using the following
311 set of parameters: (1) species ranges were coded using presence in the seven biogeographic regions;
312 (2) maximum range size at nodes was constrained to 3; (3) areas not formed of adjacent regions were
313 excluded from the analysis (adjacency matrix); (4) the dispersal constraints matrix was used to set the
314 dispersal rates between the seven biogeographic regions with a value of 1 for adjacent regions (e.g., E
315 and F), 0.5 between sea-separated regions (e.g., G) and 0.01 for nonadjacent regions (e.g., A and F).
316 Ancestral area reconstruction for each node was plotted on the BEAST maximum clade credibility tree
317 using pie charts (see Buerki et al., 2011 for details on the R script).

318 To assess the potential influence of fruit-eating migratory mammals in the dispersion of the
319 African widespread Eggplant clade species (*Solanum campylacanthum*, *S. cerasiferum* and *S.*

320*incanum*), a distribution map of these species together with two of their known large-mammalian seed
321dispersers (African elephant, *Loxodonta africana* (Blumenbach) and impala, *Aepyceros melampus*
322(Lichtenstein); see Pringle et al., 2014; Kartzinel et al., 2015) was reconstructed using the R
323packages *maps* and *dismo*. Shapefiles of the current distributions of the African elephant and impala
324were downloaded from the IUCN Red List of Threatened Species website (IUCN SSC Antelope
325Specialist Group, 2016; Blanc, 2008). Using georeferenced herbarium specimens, we gathered data on
3261,150 populations of *S. campylacanthum*, *S. cerasiferum* and *S. incanum*. A Venn diagram showing
327the overlap between the distributions of the widespread Eggplant clade species and the African
328elephant and impala was inferred using the R package *VennDiagram*.

329

330RESULTS

331 **Sanger reconstructions and species delimitation**—Visual comparison of 50% majority-rule
332trees obtained from single marker matrices with BI and ML showed no strongly supported topological
333conflict (BS > 75% and PP > 0.9) (only the BI consensus trees shown; see [Appendix S1a,b,c in the](#)
334[Supplemental Data with the online version of this article](#)). Topologies are overall all poorly resolved
335with the exception of few strongly supported nodes; they only differed in the degree of resolution,
336with the ITS consensus trees exhibiting higher proportions of supported nodes than those inferred from
337*waxy* and *ndhF-rpL32*.

338 The combined Sanger dataset yielded a total of 3,121 base pairs (bp) of which 256 bp were
339variable. There were no supported conflicts between the BI and ML 50% majority-rule trees, with the
340BI tree showing a much greater resolution than the ML one, albeit often with poorly supported nodes.
341The combined topology ([Appendix S1d](#)) shows that the Eggplant clade as previously defined (Voront-
342sova et al., 2013; Aubriot et al., 2016) is monophyletic (PP = 0.99) and it includes the Cape Verde en-
343demic *Solanum rigidum* Lam. Within the Eggplant clade, two of the widespread species are resolved
344as monophyletic (*S. campylacanthum*, *S. cerasiferum*) and one as paraphyletic (*S. incanum*). The three
345accessions of *S. incanum* from the eastern part of the species distribution range (Kenya, Oman and
346Pakistan) form a strongly supported lineage (BS = 99%; PP = 1) that excludes the accession from
347Burkina Faso; the latter is sister to the clade formed by the eggplant (*S. melongena*) and its wild pro-
348genitor (*S. insanum*). *Solanum melongena* is part of a polytomy that includes all three accessions of *S.*
349*insanum*; this confirms previous phylogenetic results (Vorontsova et al., 2013; Aubriot et al., 2016).
350Affinities of the species of the Eggplant clade remain largely unresolved using these markers, with the
351exception of a group of species from southern Africa (*S. aureitomentosum* Bitter, *S. lichtensteinii*
352Willd., *S. linnaeanum*, *S. umtuma* Voronts. & S.Knapp) forming a strongly supported group (BS =
35390%; PP = 1) that had been recognised in previous analyses (Vorontsova et al., 2013; Aubriot et al.,
3542016).

355

356 **Plastome phylogenomic analyses**—Plastome lengths ranged from 155,017 to 155,820 bp,
357 with a mean coverage between 10.2× and 254.8×; see [Table 1](#) and [Appendix S2](#) for details on the
358 plastomes. The plastome alignment was 159,227 bp in length, of which 3,890 bp were variable. There
359 were no supported conflicts between the BI topologies obtained with BEAST and MrBayes, and the
360 RAxML 50% majority-rule tree (see [Appendix S3](#)). Phylogenetic trees are all fully resolved with the
361 exception of a polytomy in the MrBayes and RAxML 50% majority-rule trees. For the MrBayes topo-
362 logy all other nodes have $PP \geq 0.99$ ([Appendix S3b](#)). For the BEAST and RAxML trees, 13 out of 15
363 nodes within the Eggplant clade are strongly supported (*i.e.*, $BS \geq 87\%$ and $PP \geq 0.97$; Fig. 1B and
364 [Appendix S3a,c](#)). Plastome trees confirm results from the Sanger analyses, but provide much better
365 resolution of relationships in the clade (Fig. 1B). The Eggplant clade (*sensu* Vorontsova et al., 2013;
366 Aubriot et al., 2016) is recovered as monophyletic; it is sister ($BS = 82\%$; $PP = 0.94$) to a lineage
367 formed by two African (*Solanum polhillii* and *S. supinum*) and one tropical Asian species (*S. trilob-*
368 *atum*), partly confirming previous phylogenetic results (Vorontsova et al., 2013; but see Aubriot et al.,
369 2016 for an alternative position of *S. trilobatum*). The first-branching lineage, here called ‘Kilimanjaro
370 clade’ (Fig. 1B), groups three species from the eastern African region (*S. agnewiorum*, *S. lanzae*, *S.*
371 *usambarense*). Affinities within this clade are still unresolved; in the BEAST analysis *S. agnewiorum*
372 branches first but this result is not supported ($PP = 0.41$). The next branching lineage is formed by the
373 eggplant and its wild progenitor, *S. insanum*, the two accessions of the cultivated eggplant being
374 grouped together (Fig. 1B). This lineage is sister to a monophyletic group that includes all remaining
375 species of the Eggplant clade and is composed of two sister clades: (1) the Southern African clade
376 (Fig. 1B) with four species from southern Africa (*S. aureitomentosum* Bitter, *S. lichtensteinii*, *S. lin-*
377 *naeanum* and *S. umtuma*), and (2) the Widespread clade (Fig. 1B) that includes three species with
378 large distribution ranges (*S. campylacanthum*, *S. cerasiferum* and *S. incanum*) and the Cape Verde is-
379 lands endemic *S. rigidum*. Within the Southern African clade, *S. aureitomentosum* branches first, fol-
380 lowed by *S. linnaeanum* that is sister to a moderately supported grouping formed by *S. lichtensteinii*
381 and *S. umtuma* ($BS = 83\%$; $PP = 1$). *Solanum campylacanthum* is the earliest diverging species of the
382 Widespread clade; it is sister to a lineage in which *S. cerasiferum* branches first, followed by one of
383 the two accession of *S. incanum* (from Kenya) that is in turn sister to a grouping formed by the Cape
384 Verdean *S. rigidum* and the second accession of *S. incanum* (from Burkina Faso).

385

386 **Historical biogeography of the Eggplant clade and dispersion analysis**—The most likely
387 biogeographic scenario for the Eggplant clade is displayed in Figure 1b. The Eggplant clade originated
388 in area B (Somalian and Middle East region) sometimes during the early Pleistocene. The Kilimanjaro
389 clade maintained this distribution range with the exception of *Solanum usambarense*, which expanded

390its distribution range into area E (Zambesian region). There is a high level of biogeographic uncer-
391tainty on the node separating the cultivated eggplant plus its progenitor (*S. insanum*) from the rest of
392the species in the clade. This is due to a disjunct distribution between these two clades (Fig. 1B). The
393most parsimonious scenario invokes two dispersal events leading to the most common ancestor of the
394whole clade therefore achieving a widespread distribution across regions BE and A (Tropical Asian re-
395gion). The disjunct distribution of *S. insanum* in A and G (Malagasy region) most likely results from a
396long-distance dispersal event from A to G during the last million years. The majority of inferred dis-
397persal events took place between the Southern African and Widespread clades. Southward and west-
398ward dispersal from B has been active in these two clades over the last 2 Myrs, and F (Southern
399African region) was colonized during the past 1 million years. In addition to having acted as a cradle,
400area B has been a pivotal region in shaping the current distribution of the eggplant clade. The inferred
401dispersion scenarios are illustrated in Fig. 1A.

402 The distribution of *Solanum campylacanthum*, *S. cerasiferum* and *S. incanum* together with
403their large mammalian seed dispersers is displayed in Fig. 2A. The distribution of African elephants
404and impalas covers 53.7% (617 in total) of the populations of these three widespread species (Fig. 2B).
405The elephant range currently only covers 24.3% (150) of the three *Solanum* species populations, while
406the impala distribution covers 94.4% (583); most *Solanum* populations only overlap the impala range
407(467 populations) (Fig. 2B).

408

409DISCUSSION

410 While studies focusing on the morpho-ecological and genetic diversity of the eggplant and its
411wild relatives are increasing (e.g., Gramazio et al., 2016; Kaushik et al., 2016; Ranil et al., 2016;
412Syfert et al., 2016; Acquadro et al., 2017) our study is the first designed to test phylogenetic and
413biogeographic scenarios in the Eggplant clade (*sensu* Aubriot et al., 2016). Our sampling for Sanger
414and genomic studies allowed us to test recent species delimitations and build a phylogeny for the
415Eggplant clade that is well resolved internally. This study strongly supports *Solanum insanum*, the
416only wild Eggplant clade species currently distributed within the original centre of domestication of *S.*
417*melongena* (Meyer et al., 2012), as its most likely progenitor (Fig. 1A,B). The Somalian and Middle
418East region is identified as the cradle of the Eggplant clade with recent dispersions to southern/western
419Africa and tropical Asia; distribution data suggest that large savannah herbivores contributed to the
420geographical expansion of several of the species (Fig. 2A,B). The results do not, however, provide a
421definitive biogeographic scenario for the disjunct distribution between *S. insanum* + *S. melongena* and
422the rest of the species of the Eggplant clade that are all restricted to Africa and western Asia (see node
42310 in Appendix S4a).

424

425 **Phylogenetic relationships and species concepts in the eggplant clade**—Within the Eggplant
426 clade, four species concepts are particularly challenging: *Solanum campylacanthum*, *S. cerasiferum*, *S.*
427 *incanum* and *S. insanum* (the three first species belong to the Widespread clade, the last is sister to *S.*
428 *melongena*; Fig. 1B). Widespread across Africa and Asia, these species are also extremely
429 polymorphic, with morphological characters that vary within and between populations (Knapp et al.,
430 2013; Ranil et al., 2016). Olet and Bukenya-Ziraba (2001) suggested that *S. campylacanthum* (as “*S.*
431 *incanum*”) and *S. cerasiferum* belong to the same biological species; our phylogenetic results support
432 the monophyly of these taxa and confirm they represent two distinct lineages. Sanger and full-
433 plastome data unambiguously confirm *S. insanum* as the wild progenitor of the cultivated brinjal
434 eggplant. While the two eggplant accessions are sister in the plastome topology, pairwise distances
435 between the two plastomes of the eggplant and plastome of *S. insanum* are identical ($1E-4$) and *c.* 25
436 times smaller than the mean interspecific pairwise distances of the dataset ($2.8E-3$). Strong plastome
437 identity between the brinjal eggplant and its wild progenitor is not surprising as they are known to
438 interbreed relatively freely when in sympatry (e.g., Davidar et al., 2015; Mutegi et al., 2015). Our
439 results also illustrate the fact that, while the cultivated eggplant and *S. insanum* present distinctive
440 morphological features (Ranil et al., 2016), diagnostic molecular data are still lacking. *Solanum*
441 *incanum* is recovered as paraphyletic, with the sample from the westernmost part of the distribution
442 range (Burkina Faso) that does not group unambiguously with the other *S. incanum* accessions.
443 Genomic data resolve the Cape Verde endemic *S. rigidum* nested within *S. incanum*, strongly
444 supported as sister to the sample from Burkina Faso. The plastid genome of *S. rigidum* is very similar
445 to that of the two accessions of *S. incanum*; mean pairwise distance (MPD) between these three
446 plastomes is $3.5E-4$. The phylogeny does not reflect morphological characters; *S. rigidum* is
447 morphologically similar to *S. cerasiferum* and readily distinguishable from *S. incanum* by its deeply
448 lobed leaves and sparser indumentum. This result can be interpreted in two ways. *Solanum rigidum*
449 may be a recent morpho-geographical segregate of the continental *S. incanum*, both taxa having
450 conserved their ancestral chloroplast genome. Internal transcribed spacer (ITS) data (Appendix S1a)
451 resolve *S. rigidum* as sister to *S. macrocarpon* (gboma eggplant) and *S. dasyphyllum*, albeit this result
452 is poorly supported (PP = 0.82); this would suggest a hybrid origin via chloroplast capture with
453 contributions from *S. incanum* (as the maternal parent of the cross) and arguably from *S. macrocarpon*
454 or its wild progenitor, *S. dasyphyllum* (see also Knapp and Vorontsova, 2013). Chloroplast capture
455 revealed by whole plastid genome sequences has been reported in the tomato clade (*Solanum* sect.
456 *Lycopersicon*; Poczai et al., unpublished) as well as among species of *Gossypium* (Chen et al., 2017)
457 and *Gaultheria* (Zhang et al., 2017). Obtaining broader geographic sampling of Eggplant clade
458 species, particularly *S. rigidum* and accessions from western Africa, using data suited to this
459 taxonomic depth, such as nuclear SSRs or SNPs (e.g., van Loo et al., 2015; Acquadro et al., 2017)

460 may help better resolve circumscription of *S. incanum* and *S. rigidum*.

461 Our inferred plastome phylogeny provides much better resolution at the interspecific level
462 within the Eggplant clade than previous phylogenetic investigations that either lacked taxonomic
463 representativeness (Meyer et al., 2012; Acquadro et al., 2017) or phylogenetic resolution (Vorontsova
464 et al., 2013; Aubriot et al., 2016) or both (Weese and Bohs, 2010). The topology we obtained, with the
465 exception of one internal nodes (Fig. 1B), is fully resolved with strongly supported nodes. This
466 plastome phylogeny confirms several phylogenetic hypotheses while it contradicts others. Taxonomic
467 composition and phylogenetic structure of the Eggplant clade as found by Aubriot et al. (2016) is
468 confirmed but with the addition of *Solanum rigidum* and much improved resolution and support. Three
469 species that were found in polytomy at the base of the Eggplant clade (*S. agnewiorum*, *S. lanzae* and *S.*
470 *usambarensis*) here are resolved as a basal Kilimanjaro clade; the Southern African clade and
471 Widespread clade, whose compositions globally overlap clades that were previously poorly supported
472 with Sanger data (see Aubriot et al., 2016; Vorontsova et al., 2013) are here resolved with highly
473 supported nodes. Phenetic results obtained by Acquadro et al. (2017) with a data set of 12,859 nuclear
474 SNPs, but with limited taxonomic sampling (6 Eggplant clade spp.) are not fully congruent with our
475 plastome topology; comparisons are difficult due to differences in sampling and methodological
476 approaches.

477

478 ***Effect of savannahs and mammalian dispersers on biogeography of the Eggplant clade—***

479 Our biogeographic results show that the Eggplant clade originated recently, during the last c. 3 Myr, in
480 the Somalian and Middle East region (Fig. 1A,B). Spread then occurred mostly within Africa; the
481 progenitor of the eggplant, *Solanum insanum*, is the only wild species that is not present in continental
482 Africa, but that has a Malagasy-Southeast Asian distribution. Dispersion to tropical Asia that gave rise
483 to *S. insanum* is likely to have happened during the Early Pleistocene via the Middle East region; we
484 suggest dispersion to Madagascar was a later event, possibly linked to recent human migration (see
485 Crowther et al., 2016). Our results challenge Lester and Hasan's (1991) hypothesis of an eastern
486 African origin for the 'ancestors of *S. melongena*' with subsequent spread to tropical Asia via a step-
487 wise expansion through Middle East. Our biogeographic analysis instead shows that the origin of the
488 Eggplant clade lies in northeastern Africa and the Middle East, with spread both south (Widespread
489 and Southern African clades) and east (*S. insanum* + *S. melongena*). Importantly, it shows that the
490 tropical Asian lineage of *S. insanum* did not proceed from a step-wise expansion through Middle East,
491 but instead from an early dispersion from Africa, unrelated to the southwards spread of the
492 Widespread and Southern African clades. This first attempt to provide a testable biogeographic
493 framework for the Eggplant clade shows that its history consists in a wide dispersion across the
494 African continent rather than an 'Out of Africa' phenomenon. Nesting of Asian species such as *S.*

495 *insanum* in otherwise African lineages, suggesting dispersal events in African lineages are not rare in
496 Old World spiny solanums; *S. trilobatum* and *S. violaceum* also show this pattern in our plastome
497 phylogeny (see also Aubriot et al., 2016).

498 Species of the Eggplant clade have a recent biogeographic history and several species have
499 large and complex distribution ranges, which makes it difficult to untangle biotic and abiotic factors
500 that could explain evolutionary dynamics in the clade. Many spiny solanums are plants of disturbed
501 areas, and most species of the Eggplant clade are weedy and occur in nitrogen-rich habitats of arid-
502 areas or gaps in tropical forests, in a wide range of altitudes (Vorontsova and Knapp, 2016; Knapp and
503 Vorontsova, 2013). Only the three species of the basal Kilimanjaro clade are habitat-restricted; they
504 are found in higher elevation (> 1,200 m) montane woodlands (Vorontsova and Knapp, 2016). These
505 are also either hermaphroditic (*Solanum lanzae*, *S. usambarense*) or only weakly andromonoecious (*S.*
506 *agnewiorum*) with small fruits, while strong andromonecy characterizes all other species of the
507 Eggplant clade (Vorontsova and Knapp, 2016; Vorontsova et al., 2013), with larger fruits. Our data
508 suggest that the combination of breeding system and ecology (see below) in this lineage have been
509 important factors in the dramatic expansion of its distribution range over the last 2 Myrs.

510 The increased geographical spread of members of the Eggplant clade coincides with profound
511 habitat changes in Africa. Decrease in atmospheric CO₂ concentrations and aridification beginning in
512 the late Miocene led to global increase in the biomass of plants using C₄ photosynthesis. This resulted
513 in the extension of savannahs and fire-prone environments, first in northeastern Africa and then in
514 South Africa (Cerling et al., 1997; Uno et al., 2016). Recent studies on hominin environments (Cerling
515 et al., 2011; Uno et al., 2016) found that woody grassland savannahs became persistent in northeastern
516 Africa at least 6 Myr BP, with major increases in the abundance of savannah grazing mammalian s
517 over this period (Uno et al., 2011). Open grassland and wooded grassland savannahs are typical
518 habitats for members of both the South-African and Widespread clades, and large savannah
519 mammals such as African elephants and impalas have been recorded as important herbivores and
520 seed dispersers of Eggplant clade species (Pringle et al., 2014; Kartzinel et al., 2015). In Africa
521 elephants and impalas have native distributions that overlap those of members of the Eggplant clade,
522 and particularly species of the Widespread clade (see Fig. 2A,B). Although the historical range of
523 African elephants fully encompassed the current distribution of the Eggplant clade species (see Ripple
524 et al., 2015), it appears that today the impala is likely to be more important for the seed dispersal of
525 widespread species. We suggest that the extensive geographical expansion over the last 2–3 Myr and
526 the impressive ranges of some of the extant species (e.g., *Solanum campylacanthum*, *S. cerasiferum*, *S.*
527 *incanum*) is related to the dispersal of seeds by these large, migratory mammalian herbivores.
528 Contraction of ranges of these large mammalian seed dispersers could ultimately contribute to
529 isolation of populations previously more intermixed, leading to differentiation and speciation. Human

530use of these species could have also contributed to their recent wide dispersal and spread; many
531species of the clade are used medicinally and for tanning hides (Bitter, 1923; Ranil et al., 2016;
532Vorontsova and Knapp, 2016). Fragments of *Solanum* seeds have been recorded from a 780,000 yr old
533hominin site in Israel (Melamed et al., 2016), and archaeological remains may provide additional
534information about early interactions between hominins and Eggplant clade species.

535 Disentangling the relationship between complex changes in ecology and differentiation in the
536Eggplant clade, and in spiny solanums more broadly, is challenging, especially in the light of recent
537profound environmental change; new types of data will be required to understand the evolutionary
538success of this cosmopolitan and very diverse group.

539

540 ***Eggplant domestication, still a biogeographic puzzle***—Our understanding of the evolutionary
541history and biogeography of the eggplant and its wild relatives is now better understood following the
542analyses conducted here using whole plastome and nuclear sequence data. The two nuclear regions we
543analysed here do not contradict plastome data, but nuclear genomic data for all the species of the
544Eggplant clade will be necessary to assess phylogenetic discordance and detect historical gene flow.
545Combination of plastome and denser nuclear genomic data would also open the way to in-depth
546investigation of the genomic basis of environment-specific and lineage-specific adaptations in
547eggplant CWR (e.g., Pease et al., 2016). This will ultimately provide plant breeders and physiologists
548with an estimate of the potential for selection from standing variation across eggplant CWR,
549potentially revolutionizing genetic improvement of eggplants.

550 Our study also shows that even with sampling across the full diversity of the Eggplant clade
551and a robust phylogenomic framework, our understanding of the biogeographic history of the Eggplant
552clade can still be improved; in particular dispersion of *Solanum insanum* lineages to tropical Asia and
553emergence and domestication of the brinjal eggplant. Meyer et al. (2012) suggested that *S. melongena*
554was domesticated several times from *S. insanum* (as *S. incanum*); use of *S. insanum* as a medicine
555(Ranil et al., 2016) and extensive movement of peoples across southeastern Asia support this idea.
556Combining sampling for *S. insanum* through its whole geographical range with the use of recently de-
557veloped targeted high-throughput sequencing (Kadlec et al., 2017) will provide a promising approach
558for reconstructing reliable scenarios of evolution of brinjal eggplant from its wild progenitor, *S. in-*
559*sanum*.

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884**TABLE 1** Summary of GenBank accession numbers, species name, collection information and plastome composition and coverage for taxa used in the
885NextGen analyses. Herbarium codes in column 4 follow Index Herbariorum (Thiers, 2017). Abbreviation in columns 7 to 10 are as follows: herb. =
886herbarium material; sil. = silica gel-dried material; LSC = large single copy region; SSC = Small single copy region; IRs = inverted repeat regions. **[In-**
887**formation intended for the review process only: The sequences generated for the present study are in the process of being submitted to GenBank.**
888**Once the GenBank accession numbers for all these sequences have been generated, we will update the table].**

889

GenBank accessions	Name in topologies	Species name	Voucher	Collection location	Material	Total length	LSC	SSC	IRs	Mean coverage
x	Solanum aethiopicum	<i>Solanum aethiopicum</i> L.	Vorontsova et al. 156 (BM)	Tanzania, Morogoro, Tegetero	sil.	155,608	86,219	18,563	25,413	152.5
x	Solanum agnewiorum	<i>Solanum agnewiorum</i> Voronts.	Vorontsova et al. 195 (BM)	Kenya, Eastern, Nyambene	herb.	155,586	86,163	18,587	25,418	19.5
x	Solanum anguivi	<i>Solanum anguivi</i> Lam.	Vorontsova et al. 1302 (K)	Madagascar, Fianarantsoa, Itremo Massif	sil.	155,577	86,188	18,559	25,415	124.6
x	Solanum aureitomentosum	<i>Solanum aureitomentosum</i> Bitter	Chase N.C. 5271 (BM)	Zimbabwe, Southern Rhodesia, Odzi	herb.	155,303	85,950	18,497	25,428	38
x	Solanum campylacanthum	<i>Solanum campylacanthum</i> Hochst. ex A.Rich.	Vorontsova et al. 158 (BM)	Tanzania, Tanga, Mkata Kideleko	sil.	155,017	85,667	18,506	25,422	54.5
x	Solanum cerasiferum	<i>Solanum cerasiferum</i> Dunal	Fay 2715 (K)	Central African Republic, Bamingui-Bangoran, Bozobo	herb.	155,413	86,129	18,516	25,384	17.2
x	Solanum dasyphyllum	<i>Solanum dasyphyllum</i> Schumacher. & Thonn.	Vorontsova et al. 151 (BM)	Tanzania, Morogoro, Tegetero	sil.	155,716	86,314	18,536	25,433	62.8
x	Solanum glabratum	<i>Solanum glabratum</i> Dunal	Miyazaki 606I28 (A)	Saudi Arabia, Asir, Abah	herb.	155,368	86,081	18,517	25,385	20.2
x	Solanum incanum 1	<i>Solanum incanum</i> L.	Vorontsova et al. 203 (BM)	Kenya, Eastern, Laisamis	herb.	155,657	86,276	18,539	25,421	105.3
x	Solanum incanum 2	<i>Solanum incanum</i> L.	Sanou & Traore BUR48 (K)	Burkina Faso, Houet, Saguere	herb.	155,617	86,269	18,508	25,420	92.5
x	Solanum insanum	<i>Solanum insanum</i> L.	Sampath Kumar et al. 941 (MH)	India, Tamil Nadu, Thamaraikulam	sil.	155,570	86,240	18,498	25,416	254.8
x	Solanum lanzae	<i>Solanum lanzae</i> J.-P.Lebrun & Stork	Vorontsova et al. 783 (K)	Kenya, Rift Valley, Kifuko Ranch	sil.	155,269	86,253	18,198	25,409	175

x	<i>Solanum lichtensteinii</i>	<i>Solanum lichtensteinii</i> Willd.	Crawford et al. FC139 (K)	Namibia, Kunene, Outjo	herb.	155,574	86,217	18,51 5	25,421	30.3
x	<i>Solanum linnaeanum</i>	<i>Solanum linnaeanum</i> Hepper & P.-M.L. Jaeger	Jury et al. 13209 (BM)	Morocco, Rabat-Salé-Kénitra, Moulay Bousselham	herb.	155,574	86,219	18,50 9	25,423	73.5
x	<i>Solanum macrocarpon</i>	<i>Solanum macrocarpon</i> L.	Tepe et al. 2770 (BM)	Tanzania, Morogoro, Ruvu	sil.	155,820	86,398	18,55 4	25,434	55.5
x	<i>Solanum melongena</i> 1	<i>Solanum melongena</i> L.	Meeboonya et al. RM294 (BM)	Thailand, Chumphon, Pang Wan	sil.	155,583	86,250	18,50 1	25,416	44.6
x	<i>Solanum melongena</i> 2	<i>Solanum melongena</i> L.	Poczai H07653 (H)	Finland, Helsinki, Kumpula Botanical Garden	sil.	155,569	86,236	18,50 1	25,416	800
x	<i>Solanum polhillii</i>	<i>Solanum polhillii</i> Voronts.	Vorontsova et al. 15 (BM)	Kenya, Rift Valley Mt. Suswa	herb.	155,422	86,044	18,54 4	25,417	196.9
x	<i>Solanum richardii</i>	<i>Solanum richardii</i> Dunal	Vorontsova et al. 633 (K)	Madagascar, Fianarantsoa, Vangaindrano	sil.	155,187	86,113	18,24 4	25,415	118
x	<i>Solanum rigidum</i>	<i>Solanum rigidum</i> Lam.	Malato-Beliz 141 (LISC)	Cape Verde, Maio	herb.	155,594	86,244	18,51 0	25,420	10.2
x	<i>Solanum supinum</i>	<i>Solanum supinum</i> Dunal	Kabelo 170 (K)	Botswana, Ghanzi, Okwa Valley	herb.	155,769	86,362	18,54 9	25,429	111.9
x	<i>Solanum trilobatum</i>	<i>Solanum trilobatum</i> L.	Meeboonya et al. RM243 (BM)	Thailand, Samut Songkhram, Bueng Yi San	sil.	155,289	86,218	18,24 5	25,413	95.8
x	<i>Solanum umtuma</i>	<i>Solanum umtuma</i> Voronts. & S.Knapp	Nevhutalu 921 (K)	South Africa, KwaZulu-Natal, Swart Umfolozi	herb.	155,541	86,173	18,51 4	25,427	29.5
x	<i>Solanum usambarense</i>	<i>Solanum usambarense</i> Bitter & Dammer	Vorontsova et al. 166 (BM)	Tanzania, Tanga, Magamba Forest Reserve	sil.	155,411	86,028	18,55 1	25,416	42.3
x	<i>Solanum violaceum</i>	<i>Solanum violaceum</i> Ortega	Sampath Kumar et al. 945e (MH)	India, Tamil Nadu, Palar Dam	sil.	155,748	86,309	18,60 9	25,415	147.2

890APPENDIX

891Summary of species, country, voucher (collector and number), herbarium acronym (codes follow
892Thiers 2017) and GenBank accession numbers for taxa used in the preliminary Sanger study, provided
893in the following order: ITS, *waxy* and *ndhF-rpL32*. Dashed lines indicate that the region was not
894sampled for this accession. Newly generated sequences are indicated with an asterisk following the ac-
895cession number. **[Information intended for the review process only: GenBank numbers for se-**
896**quences already published are provided. The sequences generated for the present study are in the pro-**
897**cess of being submitted to GenBank and we have used our laboratory extraction ID (XA plus three di-**
898**gits) to refer to them. Once the GenBank accession numbers for all these sequences have been gener-**
899**ated, we will update the table where appropriate].**

900

901*Solanum aethiopicum* L., Tanzania, Vorontsova et al. 156 (BM), XAS232*, –, XAS232*. *S. ae-*
902*thiopicum* L., Olmstead S-74 (WTU), –, AY996378, –. *S. agnewiorum* Voronts., Kenya, Vorontsova
903et al. 195 (BM), KU719948, KU719870, KU720049. *S. anguivi* Lam., Madagascar, Vorontsova et al.
9041302 (K), XAS218*, –, XAS218*. *S. anguivi* Lam., Bohs 3266 (UT), –, HQ721963, –. *S. aureito-*
905*mentosum* Bitter, Zimbabwe, Chase N.C. 5271 (BM), KU719949, KU719871, XAS298*. *S. campyla-*
906*canthum* Hochst. ex A.Rich., Tanzania, Vorontsova et al. 158 (BM), XAS220*, XAS220*,
907KU719997. *S. campylacanthum* Hochst. ex A.Rich., Ethiopia, Friis 8107 (K), XAS290*, XAS290*,
908XAS290*. *S. campylacanthum* Hochst. ex A.Rich., Ethiopia, Friis et al. 10427 (K), XAS313*,
909XAS313*, XAS313*. *S. campylacanthum* Hochst. ex A.Rich., Ethiopia, Friis 11156 (K), XAS314*,
910XAS314*, XAS314*. *S. campylacanthum* Hochst. ex A.Rich., South Africa, Westfall 1661 (K),
911XAS317*, XAS317*, XAS317*. *S. campylacanthum* Hochst. ex A.Rich., Namibia, Kolberg & Ku-
912birske 600 (K), XAS318*, XAS318*, XAS318*. *S. cerasiferum* Dunal, Ethiopia, Friis et al. 7733
913(K), XAS291*, XAS291*, XAS291*. *S. cerasiferum* Dunal, Ethiopia, Friis et al. 12670 (K),
914XAS315*, XAS315*, XAS315*. *S. cerasiferum* Dunal, Central African Republic, Fay 2715 (K),
915XAS322*, XAS322*, XAS322*. *S. dasyphyllum* Schumach. & Thonn., Tanzania, Vorontsova et al.
916151 (BM), XAS223*, –, KU720000. *S. dasyphyllum* Schumach. & Thonn., Cipollini 7 (UT), –,
917AY996406, –. *S. glabratum* Dunal, South Arabia, Miyazaki 606I28 (A), KU719913, KU719834,
918KU719994. *S. incanum* L., Kenya, Vorontsova et al. 203 (BM), XAS309*, XAS309*, XAS309*. *S.*
919*incanum* L., Burkina Faso, Sanou & Traore BUR48 (K), XAS325*, XAS325*, XAS325*. *S. in-*
920*canum* L., Oman, Mandaville 6523 (BM), XAS327*, XAS327*, XAS327*. *S. incanum* L., Pakistan,
921Popov 30 (BM), XAS328*, XAS328*, XAS328*. *S. insanum* L., Madagascar, Vorontsova et al. 644
922(BM), KU719914, KU719835, KU720003. *S. insanum* L., Wang 2052 (PE), KU719884, KU719813,
923KU719964. *S. insanum* L., India, Sampath Kumar et al. 941 (MH), KU719940, KU719862,
924KU720041. *S. lanzae* J.-P.Lebrun & Stork, Kenya, Vorontsova et al. 783 (BM), KU719921,

925KU719842, KU720015. *S. lichtensteinii* Willd., Namibia, Crawford et al. 139 (K), KU719947, 926KU719869, KU720048. *S. linnaeanum* Hepper & P.-M.L. Jaeger, Morocco, Jury et al. 13209 (BM), 927KU719950, KU719872, KU720050. *S. macrocarpon* L., Tanzania, Tepe et al. 2770 (BM), XAS227*, 928–, KU720004. *S. macrocarpon* L., Olmstead S-88 (WTU), –, AY996436, –, *S. melongena* L., Thail- 929and, Meeboonya et al. RM294 (BM), XAS343*, –, XAS343*. *S. melongena* L., Olmstead S-91 930(WTU), –, AY562959, –, *S. nigriviolaceum* Bitter, Kenya, Vorontsova et al. 57 (BM), HQ721868, 931HQ721993, –, *S. polhillii* Voronts., Kenya, Vorontsova et al. 15 (BM), XAS308*, XAS308*, 932XAS308*. *S. richardii* Dunal, Madagascar, Vorontsova et al. 633 (BM), KU719915, KU719836, 933KU720006. *S. rigidum* Lam., Cape Verde, Malato-Beliz 141 (LISC), XAS337*, –, XAS337*. *S. su-* 934*pinum* Dunal, Botswana, Kabelo 170 (K), XAS335*, XAS335*, XAS335*. *S. trilobatum* L., Thail- 935and, Meeboonya et al. RM243 (BM), XAS130*, XAS130*, XAS130*. *S. umtuma* Voronts. & 936S.Knapp, South Africa, Nevhutalu 921 (K), XAS334*, XAS334*, XAS334*. *S. usambarensis* Bitter & 937Dammer, Tanzania, Vorontsova et al. 166 (BM), KU719923, KU719844, KU720023. *S. violaceum* 938Ortega, India, Sampath Kumar et al. 945e (MH), KU719941, KU719863, KU720042.

939

940FIGURE LEGENDS

941**FIGURE 1** Phylogeny and biogeography of the Eggplant clade based on whole chloroplast genome 942sequences. **(A)** Map showing the seven biogeographic areas used to infer the biogeographic history of 943the Eggplant clade. Dotted lines indicate instances of complex biome transitions. Arrows illustrate the 944dispersion events inferred from the biogeographic analysis. **(B)** Full-plastome dated phylogeny of the 945Eggplant Clade (consensus of 4 BEAST analyses; 159,227 bp matrix). All nodes have PP \geq 0.97 and 946BS \geq 87% except for the nodes designated with *. Green bars correspond to 95% HDP intervals for 947the dates of the nodes (Myr). Geographical distribution for each terminal is indicated using the biogeo- 948graphic regions subdivision. The most probable ancestral area is figured at each node of the Eggplant 949clade; high level of biogeographic uncertainty is indicated with dotted lines. Pie-charts with relative 950probabilities of ancestral states at each node are provided in [Appendix S4a,b](#). Hypothesised dispersion 951(D) and extinction (E) events are figured above the branches of the tree. Within the Eggplant clade, 952clades are given provisional names based on their distributions. Names of cultivated species are in 953bold. Pictures from top to bottom and left to right are fruits of the cultivated eggplant (*Solanum mel-* 954*ongena*), *S. incanum*, *S. linnaeanum*, *S. insanum* (eggplant wild relative) and *S. agnewiorum*. Photo- 955graph credits: (*S. melongena*, *S. insanum*) X. Aubriot; (*S. incanum*, *S. agnewiorum*) M.S. Vorontsova; 956(*S. linnaeanum*) S. Knapp.

957

958**FIGURE 2** Overlap between the distribution of the widespread Eggplant clade species in Africa and 959two of their recorded seed dispersers, the African elephant and impala **(A)** Distribution of species of

960 *Solanum* belonging to the Widespread clade (with the exclusion of the Cape Verdean *S. rigidum*; see
961 Fig. 1B for more details on this clade). The current distributions of the African elephant and impala
962 are also displayed on this map. **(B)** Venn diagram displaying the overlap of distributions between pop-
963 ulations of *S. campylacanthum* + *S. cerasiferum* + *S. incanum* and the African elephant and impala.
964 Overall, the two animals cover 53.7% of the distribution of the three *Solanum* species.

965

966 SUPPLEMENTAL DATA LEGENDS

967 **APPENDIX S1** 50% majority-rule trees from the separate and combined Bayesian analyses of the
968 ITS, *waxy* and *ndhF-rpL32* datasets.

969 **APPENDIX S2** Chloroplast genome maps of the 25 accessions sequenced; a description of the
970 general plastid structure is also supplied.

971 **APPENDIX S3** 50% majority-rule trees from the RAxML, MrBayes and BEAST analyses of the full-
972 plastome dataset.

973 **APPENDIX S4** Biogeographical scenarios for the Eggplant clade inferred by Lagrange plotted onto
974 the BEAST maximum clade credibility tree; probabilities of splits for each node are also provided.