Morphological trait evolution in *Solanum* (Solanaceae): Evolutionary lability of key taxonomic characters

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DOI https://doi.org/10.1002/tax.12990

**Abstract** *Solanum* is one of the world’s largest and economically most important plant genera, including 1245 currently accepted species and several major and minor crops (e.g., tomato, potato, brinjal eggplant, scarlet eggplant, Gboma eggplant, lulo, and pepino). Here we provide an overview of the evolution of 25 key morphological traits for the major and minor clades of this giant genus based on stochastic mapping using a well-sampled recently published phylogeny of *Solanum*. The most evolutionarily labile traits (showing >100 transitions across the genus) relate to plant structure (growth form and sympodial unit structure), herbivore defence (glandular trichomes), pollination (corolla shape and colour), and dispersal (fruit colour). Ten further traits show evolutionary lability with >100 transitions across the genus (e.g., specialised underground organs, trichome structure, leaf type, inflorescence position and branching, stamen heteromorphism). Our results reveal a number of highly convergent traits in *Solanum*, including tubers, rhizomes, simple leaves, yellow corollas, heteromorphic anthers, dioecy, and dry fruits, and some unexpected pathways of trait evolution that could be explored in future studies. We show that informally named clades of *Solanum* can be morphologically defined by trait combinations providing a tool for identification and enabling predictive phylogenetic placement of unsampled species.

**Keywords** ancestral trait reconstruction; morphology; phenotypic character evolution; *Solanum*; stochastic mapping; systematics

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

## INTRODUCTION

*Solanum* L. is one of the world’s largest and economically most important plant genera with 1245 currently accepted species (http://solanaceaesource.org/). Twenty-four of these are major crops (Knapp & al., 2004), including the potato (*S. tuberosum* L.), tomato (*S. lycopersicum* L.), and brinjal eggplant (*S. melongena* L.), as well as some lesser-known cultivated species, such as pepino (*S. muricatum* Aiton), lulo/naranjilla (*S. quitoense* Lam. and relatives), tree tomato or tamarillo (*S. betaceum* Cav.), cocona (*S. sessiliflorum* Dunal), scarlet eggplant (*S. aethiopicum* L.), Gboma eggplant (*S. macrocarpon* L.), and bush tomato (*S. centrale* J.M.Black).
Agriculture has benefited from the morphological diversity found in *Solanum* through exploitation of variation in traits such as underground storage organs and fruit morphology. Breeding programmes have also used the wide range of diversity present in gene pools of the various crops and crop wild relatives (CWRs), to enhance quality and yield (e.g., Gur & Zamir, 2004; Semel & al., 2006; Lippman & Zamir, 2007), abiotic stress tolerance, and disease resistance in cultivated potato, tomato, and eggplant (e.g., Prohens & al., 2013, 2017; Dempewolf & al., 2017; Villanueva & al., 2021). One of the best examples of the use of wild diversity in crop breeding is the single cross between the cultivated tomato and *S. habrochaites* S.Knapp & D.M.Spooner, a green-fruited wild tomato relative from the northern Andes, which increased fruit soluble solid content in tomato by 22% and brought significant profit for industry (Tanksley & al., 1996; Tanksley & McCouch, 1997; Bernacchi & al., 1998).

*Solanum* has served as a model system for research into the genetic basis of several important morphological traits. Examples include quantitative trait locus (QTL) mapping studies of major crop species, which have helped to explore morphological traits relevant to plant breeding (e.g., D’Hoop & al., 2008, 2014), as well as evolutionary developmental studies involving traits such as genetic control of fleshy fruits (Pabón-Mora & Litt, 2011; Tomato Genome Consortium, 2012), anther cone cohesion (Glover & al., 2004), leaf shape and lobing (e.g., Geeta & al., 2012; Chitwood & al., 2013; Wu & al., 2018a; Nakayama & al., 2021), breeding systems (self-incompatibility and clonality; Vallejo-Marín & O’Brien, 2007), as well as traits related to chemical defences and animal-plant interactions (e.g., Tingeys & Gibson, 1978; Tingeys & Laubengayer, 1981; Avé & Tingeys, 1986; D’Hoop & al., 2008), and pathogen resistance (e.g., Gebhardt & Valkonen, 2001; Jupe & al., 2012; Thaler & al., 2012).

Despite agricultural interest and ongoing research, much of the morphological diversity in *Solanum* (Fig. 1) remains underutilized and unexplored. Species of *Solanum* are highly variable in both vegetative and reproductive morphology, for example in growth form that ranges from ephemerals in the world’s driest deserts to tiny annual herbs growing at 4000 m elevation to large trees and herbaceous climbers from pre-montane and lowland rainforests (Fig. 1A–F). New and unexpected morphological diversity continues to be discovered as baseline taxonomic work advances in *Solanum*, with some recent discoveries including a species with heart-shaped anthers (*S. anomalostemon* S.Knapp & M.Nee; Knapp & Nee, 2009), tuber-bearing shrubs (Asterophorum clade; Gouvêa & Stehmann, 2019), species with leaky dioezy and fluid sex expression (Martine & al., 2009; McDonnell & al., 2019) and another with resin-glands (Silva Sampaio & al., 2021).

*Solanum* has traditionally been characterised by its relatively uniform floral morphology with sympetalous, five-parted flowers with a central anther cone of poricidal dehiscent anthers (Fig. 1M–RT, X). Prior to molecular phylogenetic studies, the genus was divided into sections based on morphological characters (Dunal, 1852; D’Arcy, 1972; Hunziker, 2001); most of these divisions have subsequently been shown to be para- or polyphyletic (Olmstead & Palmer, 1997; Bohs, 2005; Weese & Bohs, 2007). These traditional formal infrageneric systems have since been replaced by a system of informally named clades that reflect polyphyletic groups (Fig. 2) (Bohs, 2005; followed by subsequent studies, e.g., Stern & al., 2011; Särkkinen & al., 2013; Tepe & al., 2016; Gagnon & al., 2022). Morphological characterisation of some of these clades has been difficult, however, and the robustness of proposed morphological synapomorphies has not been tested. The use of DNA sequence data has also changed the circumscription of *Solanum* by showing that taxa with stamen heteromorphy and/or another modifications previously segregated for these characters are nested within the genus (e.g., *Cyphomandra* Mart. ex Sendtn., *Lycopersicon* Mill., *Normania* Lowe; Spooner & al., 1993; Bohs & Olmstead, 1997, 2001; Olmstead & Palmer, 1997; Tepe & al., 2016). These changes have had a minimal effect on the size of *Solanum* but have expanded the morphological diversity included within the genus, especially in relation to androecium characteristics.

The current clade-based informal infrageneric system divides *Solanum* into 49 lineages (called here minor clades), which are grouped into 12 larger clades (called here major clades) and further into three main groups (Figs. 2, 3) (Bohs, 2005; Gagnon & al., 2022): (1) the small Thelophodium clade consisting of three species sister to the rest of *Solanum*; (2) Grade I, previously referred to as Clade I (Särkkinen & al., 2013) with ca. 339 non-spiny (non-prickly) species including the cultivated tomato, potato and pepino; and (3) Clade II, the largest monophyletic lineage in the genus that includes 73% of *Solanum* (903 currently accepted species) including the tree tomatoes and all cultivated eggplants and their relatives. Within Grade I are 4 major and 16 minor clades (Fig. 2A,B); major clades are VANAns (Valdiviense, Archae-solanum, Normania, and African non-spiny), DulMo (Dulcamaroid and Morelloid), Regmanda, and the Potato clade, which includes several economically important minor clades (e.g., Tomato, Petota, Euberosum, Basarthurm; Gagnon & al., 2022). Clade II contains seven major clades, the largest of which is the Leptostemonum clade with ca. 580 species, and 32 minor clades (Fig. 2C–E) including the Eastern Hemisphere Spiny clade (hereafter EHS, previously known as the Old World clade; Gagnon & al., 2022).

What remains to be systematically evaluated in *Solanum* is how morphological traits vary across these clades, and how evolutionarily labile or conserved these traits are across the phylogeny. Such a study has the potential of highlighting homoplasies (independent evolution of similar-looking morphological traits) and provides the backbone for evolutionary developmental studies. Growth form is one trait that varies widely across the genus and whose variation is linked to the sympodial growth system in *Solanum*, where axillary buds continue shoot development after each inflorescence (Danert, 1958, 1970), often giving the stems a zig-zag
Fig. 1. Morphological diversity across Solanum. A. Annual herb (Morelloid clade, S. weddellii Phil.); B. Herbaceous vine (Herpystichum clade, S. brevisulphatum Dunal); C. Woody vine (Tomato clade, S. jaglandifolium Dunal); D. Single-stemmed shrub (Pteroeide clade, S. mite Ruiz & Pav.); E. Shrub (Torva clade, S. glutinosum Dunal); F. Tree (Crinitum clade, S. sycophanta Dunal); G. Simple glandular trichomes (Tomato clade, S. habrochaetes S.Knapp & D.M.Spooner); H. Stellate glandular trichomes (Torva clade, S. asperolanatum Ruiz & Pav.); I. Mix of simple glandular (short) and eglandular (long) trichomes (Tomato clade, S. arcuam Peralta); J. Stellate glandular trichomes (Erythrorhtrichum clade, S. acicularis Sw.); K. Needle-like prickles on calyx (EHS clade, S. betaceum Schumach. & Thorn.); L. Broad-based prickles on trunk (Crinitum clade, S. kioniotrichum Dunal); M. Campanulate pale lilac corollas (Morelloid clade, S. limacanum Hepper & P.-M.L.Jaeger); N. Rotate purple corollas with abundant interpetalar tissue (Herpystichum clade, S. trifolium Dunal); O. Deeply stellate yellow-green corollas lacking interpetalar tissue (Pteroidea clade, S. anceps Ruiz & Pav.); P. Campanulate pale lilac corollas (Morelloid clade, S. fiebrigii Bitter); Q. Urceolate white-purple corollas (Pachyphylla clade, S. diversifolium Dunal); R. Bilaterally symmetric corollas with heteromorphic anthers (Normania clade, S. corneliomulleri J.F.Machr.); S. Bilaterally symmetric corollas with heteromorphic anthers (Androceras clade, S. grayi Rose var. grandiflorum Whalen); T. Apical and basal anther modifications (i.e., horn-like projections; tomato clade, S. trisectum Dunal); U. Homomorphic stamens, most common state in Solanum (Anarrhichomenum clade, S. appendiculatum Dunal); V. Broadly stellate purple corollas (EHS clade, S. amotapense Svenson); W. Broadly stellate purple corollas (EHS clade, S. betaceum Schumach. & Thorn.); X. Globose fleshy berries with colour variation through maturation from yellow (unripe) to red (fully mature; Cyphonandropsis clade, S. amatapense Svenson); Y. Bilaterally symmetric corollas with heteromorphic anthers (Androceras clade, S. appendiculatum Dunal); Z. Globose fleshy berries (Thelopodium clade, S. thelopodium Sendtn.).
Fig. 2. Phylogeny of *Solanum* highlighting the informally named infrageneric clades based on Bayesian analysis of 742 *Solanum* species (60% of total known diversity) with two nuclear and seven plastid regions by Gagnon & al. (2022). Infrageneric clades are colour-coded and numbered reflecting the currently recognised major and minor clades of *Solanum* (Table 1): bright red shades highlight minor clades within VANAnS clade, dark reds DulMo, blues Potato clade, purples Brevantherum, orange shades Geminata, yellows Cyphomandra, purple Wendlandii-Allophyllum, pink Nemorense, and green shades indicate minor clades within the large Leptostemonum clade. Nodes without circles have maximum branch support (1.0 posterior probability), nodes with black circles strong support (≥0.95), and nodes with white circles moderate to weak support (0.75–0.94). Dashed lines indicate nodes with nuclear-plastome discordance highlighted in Gagnon & al. (2022) collapsed in our analyses. A, Minor clades 1–7 (Thelopodium, Valdiviense, ANS [African Non-Spiny], Normania, Archaeosolanum, Dulcamaroid, Morelloid); B, Minor clades 8–17 (Regmanda, Pteroidea, Herpystichum, *S. oxycoecoides*, Anarrichomenum, Articulatum, Basarthrum, Etuberosum, Tomato, Petota); C, Minor clades 18–27 (*S. anomalostemon*, Trachytrichium, Gonatotrichum, Inornatum, Brevantherum, Reductum, Geminata, *S. graveolens*, Cyphomandropsis, Pachyphylla); D, Minor clades 28–46 (Allophyllum, Wendlandii, Nemorense, *S. polygamum*, Acanthophora, Lasiocarpa, Gardneri, Thomasiifolium, Erythrotrichum, Sisymbriifolium, Crinitum, Androceras, *S. campechiense*, Carolinense, Bahamense, Micracantha, Asterophorum, *S. multispinum*, Torva); E, Minor clades 47–49 (*S. eucanthum*, Elaeagnifolium, EHS [Eastern Hemisphere Spiny]).
appearance. Concaulescence of shoot axes results in varying numbers of leaves along each shoot, and in the apparent pairing of leaves at nodes in some species. Sympodial unit structure has been used to define some clades (e.g., Pteroidea with a single leaf in each unit, Knapp & Helgason, 1997; Geminata with paired leaves, Knapp, 2002a) and is useful when combined with branching pattern (Tovar & al., 2021). Trichome structure has traditionally been a very important taxonomic character in *Solanum*, where many clades are defined by the presence or absence of particular trichome types (e.g., stellate trichomes in Leptostemonum clade, Seithe, 1962, 1979; Roe, 1971; “bayonet” trichomes in parts of the Potato clade, Seithe & Anderson, 1982). Leaf division (i.e., degree of leaf lobing) varies from simple entire to irregularly bipinnatifid but has not been previously used for defining clades, perhaps due to variability within both species and individuals (e.g., *S. dulcamara* L.; Knapp, 2013). Other vegetative traits previously used in *Solanum* taxonomy include presence of specialised underground organs (e.g., such as tubers and rhizomes; Spooner & al., 2004, 2016, 2019; Bennett, 2008; Tepe & al., 2016; Knapp & al., 2017), prickles (Seithe, 1962, 1979), and pseudostipules (Roe, 1972; Tepe & al., 2016).

Sexual system (sensu Cardoso & al., 2018) has been used in *Solanum* taxonomy (Symon, 1970, 1979b; Levine & Anderson, 1986; Whalen & Costich, 1986; Anderson & Symon, 1989; Knapp & al., 1998; Dupont & Olesen, 2006; Anderson & al., 2015; Ndem-Galbert & al., 2021), and varies from cosexual (i.e., hermaphroditic) to various degrees of andromonoecy and dioecy. Inflorescence position, determined

Fig. 2. Continued.
by variation in fusion of inflorescence and sympodial stem axes in *Solanum* (Danert, 1958), has also been used to define some clades (Knapp, 2002b; Bohs, 2005) and position varies from terminal, internodal, axillary, leaf-opposed or along spur-shoots. Inflorescences themselves vary from unbranched (simple) to multi-branched. Corolla symmetry appears strongly linked to stamen heteromorphism, both of which have been used in previous taxonomic studies (Bohs et al., 2007). Other reproductive characters that have been suggested as useful for *Solanum* taxonomy are presence of swollen anther connectives (D’Arcy et al., 1990; Bohs, 1994; Cocucci, 1996), anther shape (Knapp, 2001; Bohs, 2005), pedicel insertion and articulation (Knapp, 2001, 2013; Tepe et al., 2016), fruit type (Symon, 1979a, 1984; Whalen, 1984; Knapp, 2001, 2002b; Chiarini & Barbosa, 2007), and stone cells (Symon, 1994; Knapp, 2002b; Chiarini & Barbosa, 2007).
Here we examine morphological trait evolution across *Solanum* clades with the aim of: (1) providing an overview of current morphological knowledge and diversity across the genus in a phylogenetic context based on the well-sampled phylogeny of Gagnon & al. (2022); (2) identifying evolutionarily labile and conserved traits across *Solanum*; and
Fig. 2. Continued.
Fig. 3. Overview of morphological diversity across *Solanum* and the informally named infrageneric groups referred to as major and minor clades. A, Division of *Solanum* into three main lineages with a graphical summary of species diversity within these large groups; B, Species diversity across major clades of *Solanum*; C, Sampling density across the largest minor clades of *Solanum* in the current species-level molecular phylogeny (Gagnon & al., 2022) showing clades with ≥10 currently accepted species. Total number of accepted species is reported for each clade based on current taxonomy in SolanaceaeSource; D, Trait diversity across major clades of *Solanum*, showing the estimated proportion of species from each major clade that possess the traits visualised including species not yet sampled in the phylogeny. Clade colouring in B and D follows Fig. 2. EHS = Eastern Hemisphere Spiny clade (previously known as “Old World Spiny”).
Scoring was done from the taxonomic literature and descriptions included in the SolanaceaeSource database (PBI Solanum Project, 2022), and from herbarium specimens identified by Solanum experts (e.g., Symon, 1994; Knapp & Helgason, 1997; Contreras & Spooner, 1999; Bennett, 2008; Peralta & al., 2008; Tepe & Bohs, 2011; Knapp, 2013; Knapp & Vorontsova, 2016; Särkinen & al., 2018; Knapp & al., 2019) (suppl. Table S2). Terminology from descriptions was standardised based on our (sometimes incomplete) knowledge of character homology. Polymorphisms were included in all traits when multiple states were known to be present within a species.

We coded sympodial structure following Danert (1970) with numbers of leaves (1, 2, 3 or many) between each inflorescence, coupled with whether leaves are found in pairs at each node (i.e., geminate or not; Table 1). Internodal inflorescences were coded as those that arise along the stem not associated with leaves (axillary buds), while leaf-opposed inflorescences arise in conjunction with a leaf or leaf pair. Trichome structure was coded combining the developmental pathways suggested by Seithe (1962, 1979) and the structure-based terminology of Roe (1971). Simple trichomes included unbranched trichomes including 2-celled “bayonet” trichomes (Fig. 1G) (Seithe & Anderson, 1982). All branched or forked trichomes and echinodendritic trichomes (e.g., Knapp, 2002a) were scored as dendritic. Stellate trichomes included geniculate trichomes (simple trichomes clearly derived from stellate trichomes), bristles, densely compacted multi-angeluate stellate trichomes that have been referred to as echinoid, as well as lepidote scales developmentally derived from stellate trichomes (Fig. 1H,J) (Seithe, 1962, 1979; Stern & al., 2013). Presence of glandular tips on trichomes was coded separately because they are found on all trichome types independent of structure (Fig. 1I,J). The degree of leaf lobing was categorised by roughly quantifying the depth of the sinus as distance to the midrib from the leaf margin. Simple leaves included leaf blades with entire, serrate, or crenate margins. Leaf blades lobed a quarter to halfway to the midrib were coded as lobed. Compound leaves were defined as leaves with blades divided all the way to the midrib, although leaflets in most of these Solanum species are variously decurrent along the leaf midrib thus leaves are more strictly pinnatifid.

Species known to consistently have both short- and long-styled flowers on the same plant were coded as andromonoecious, and species with individuals possessing only short- or long-styled flowers were coded as dioecious; all other species were coded as coxoeval (i.e., hermaphroditic). Three states of corolla shape were recognised reflecting the amount of interpetal tissue between lobes: deeply stellate corollas without apparent interpetal tissue (i.e., deeply stellate, Fig. 1P,Q,T), and two states with increasing amount of interpetal tissue, broadly stellate (Fig. 1R) and rotate (Fig. 1S,U,W), respectively. Our coding is a measure of corolla division only and does not take into account orientation of corolla lobes because corolla lobes in Solanum often

[...]

MATERIALS AND METHODS

Supermatrix topology. — The phylogenetic framework is based on the combined supermatrix assembled by Gagnon & al. (2022) that includes 742 species of Solanum (60% of the 1245 currently accepted species; suppl. Table S1) and covers all minor clades with 36%–100% species sampling in each (Fig. 3A–C, suppl. Table S2) (Gagnon & al., 2022). All outgroup sequences of Jaltomata Schltdl. were excluded because coding all morphological diversity present in the sister genus was beyond the scope of this study. Instead, we incorporated the uncertainty of the root state in our ancestral state reconstruction methods (see below). Nodes corresponding to areas of high nuclear-plastome discordance along the backbone of Grade I and Clade II in phylogenomic analyses (Gagnon & al., 2022) were collapsed using the TreeTools package v.1.9.2 (Smith, 2019) to account for phylogenetic uncertainty and topological conflict. The ultrametric Bayesian topology from Gagnon & al. (2022) was used as input for all analyses. We chose to use a chronogram that assumes no correlation between morphological and molecular change.

Morphological traits. — A total of 25 morphological traits was evaluated, including 8 vegetative traits, 2 inflorescence traits, sexual system (sensu Cardoso & al., 2018), 7 floral traits, and 7 fruit-related traits (Table 1; suppl. Table S3). We selected the traits for scoring because they have previously been used in Solanum taxonomy and are of potential interest to the wider research community and in future crop breeding programmes. All species present in the phylogeny (after excluding 17 unpublished species for which full morphological descriptions are not yet available) resulted in 725 coded Solanum species (58% of all species; suppl. Table S3).
Table 1. Results of the ancestral trait reconstruction analyses (stochastic mapping) of 25 morphological traits across *Solanum*.

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<th>Trait States</th>
<th>Best model based on AIC</th>
<th>Observed mean number of transitions (95% HPD)</th>
<th>Results</th>
<th>Main references used for scoring states (see full list in suppl. Table S2)</th>
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</thead>
<tbody>
<tr>
<td>1. Growth form</td>
<td>Herb, shrub, single-stemmed shrub, tree, herbaceous vine, woody vine, epiphyte</td>
<td>ARD 110 (65–166)</td>
<td>Highly evolutionarily labile with &gt;100 transitions</td>
<td>Spooner &amp; al., 2004, 2016, 2019; Bennett, 2008; Knapp &amp; al., 2017</td>
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<tr>
<td>2. Specialised underground organs</td>
<td>Absent, rhizomes, underground storage organs</td>
<td>ARD 64 (51–78)</td>
<td>Evolutionarily labile with 50–100 transitions</td>
<td>Seithe, 1962, 1979; Clark &amp; al., 2015</td>
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<tr>
<td>5. Glandular trichome type</td>
<td>Absent, simple glandular, stellate glandular</td>
<td>ARD 210 (158–265)</td>
<td>Highly evolutionarily labile with &gt;100 transitions</td>
<td>Peralta &amp; al., 2008; Kang &amp; al., 2014; Watts &amp; Kariyat, 2022</td>
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<tr>
<td>6. Pseudostipules</td>
<td>Absent, present (single), present (pair)</td>
<td>SYM 9 (7–11)</td>
<td>Highly conserved with &lt;10 transitions</td>
<td>Spooner &amp; al., 2004, 2016, 2019; Peralta &amp; al., 2014</td>
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<tr>
<td>7. Sympodial unit structure</td>
<td>Plurifoliate, trifoliate, dilolate non-geminate, dilolate geminate, unifoliate</td>
<td>ARD 215 (151–277)</td>
<td>Highly evolutionarily labile with &gt;100 transitions</td>
<td>Danert, 1958; Child, 1979</td>
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<tr>
<td>8. Leaf division (i.e., type)</td>
<td>Simple, lobed, compound</td>
<td>ARD 73 (63–84)</td>
<td>Evolutionarily labile with 50–100 transitions</td>
<td>Geeta &amp; al., 2012</td>
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<td>10. Inflorescence branching</td>
<td>Unbranched, forked, multi-branched</td>
<td>ARD 90 (61–116)</td>
<td>Evolutionarily labile with 50–100 transitions</td>
<td>Lippman &amp; al., 2008</td>
</tr>
<tr>
<td>12. Corolla shape</td>
<td>Deeply stellate, broadly stellate, rotate</td>
<td>SYM 271 (214–334)</td>
<td>Highly evolutionarily labile with &gt;100 transitions</td>
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<tr>
<td>14. Corolla colour</td>
<td>White, green, purple, yellow</td>
<td>ARD 180 (120–234)</td>
<td>Highly evolutionarily labile with &gt;100 transitions</td>
<td>Passarelli &amp; Bruzzone, 2004</td>
</tr>
<tr>
<td>15. Stamen heteromorphism</td>
<td>Absent, anther, filament</td>
<td>ARD 51 (24–71)</td>
<td>Evolutionarily labile with 50–100 transitions</td>
<td>Bohs &amp; al., 2007</td>
</tr>
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</table>
change orientation through anthesis. For example, the urceolate corollas of *S. diversifolium* Dunal were coded as deeply stellate based on lobe length relative to the tube (Fig. 1V). Corolla colour was coded as four states: white, green, purple (including blues and pinks), and yellow (including pale, dull and bright yellows). The colour of the central “eye” of the corolla was not included in the coding, and corollas described with multiple colours in species descriptions (e.g., yellow-green) were coded as multistate (yellow + green). For anther modifications, when present, we recognised four states, homology of these states remains to be tested: long basal anther projections (called horns), short basal anther extensions (called sacks), long, fused (i.e., connivent) apical appendages, and short, loose (i.e., not connivent) apical anther beaks.

Fruit type was coded as either fleshy (containing fleshy mesocarp when fully ripe, including juicy, spongy, or woody indehiscent berries as well as the explosively dehiscent berries of the Gonatotrichum clade) or dry (including all dehiscent berries that lack fleshy mesocarp when fully ripe). Fruiting pedicel articulation was coded as five states based on distance from the inflorescence rachis. Fruiting calyx modifications were coded as four states: inflated (papery, lantern- or balloon-like enlarged calyces loosely covering at least >50% of the fruits), appressed (enlarged calyces tightly surrounding at least 50% of the fruits), swollen (thickened calyx tube and/or lobes often with a doughnut shaped ring of swelling; Fig. 1Z), or absent. Mature fruit colour was coded based on the external colour (i.e., not accounting for flesh colour) with six states following corolla colour with the addition of orange and red (Fig. 1Y–AD). Species with striped or multi-coloured mature berries, as well as those that change colour more than once (e.g., immature fruits green, intermediate mature fruits AD–Y).

<table>
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<tbody>
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<td>17. Anther modifications</td>
<td>Absent, appendage, horn, beak, sack</td>
<td>ER</td>
<td>7 (5–9)</td>
<td>Highly conserved with &lt;10 transitions</td>
<td>Francisco-Ortega &amp; al., 1993; Peralta &amp; al., 2008; Knapp &amp; Nee, 2009; Barboza, 2013</td>
</tr>
<tr>
<td>19. Pedicel insertion</td>
<td>Flat, cup-shaped</td>
<td>ER</td>
<td>2 (2–2)</td>
<td>Highly conserved with &lt;10 transitions</td>
<td></td>
</tr>
<tr>
<td>20. Pedicel articulation</td>
<td>Basal, near-basal, basal 1/4–1/2, distal 1/2, absent</td>
<td>ER</td>
<td>10 (8–12)</td>
<td>Conserved with 10–49 transitions</td>
<td></td>
</tr>
<tr>
<td>21. Fruit type</td>
<td>Fleshy, dry</td>
<td>ER</td>
<td>14 (13–15)</td>
<td>Conserved with 10–49 transitions</td>
<td></td>
</tr>
<tr>
<td>22. Fruit colour</td>
<td>Green, white, purple, yellow, orange, red</td>
<td>ARD</td>
<td>286 (166–298)</td>
<td>Highly evolutionarily labile with &gt;100 transitions</td>
<td>Peralta &amp; al., 2008; Dhar &amp; al., 2015</td>
</tr>
<tr>
<td>23. Fruit trichomes</td>
<td>Absent, present</td>
<td>ARD</td>
<td>68 (45–88)</td>
<td>Evolutionarily labile with 50–100 transitions</td>
<td></td>
</tr>
<tr>
<td>24. Fruiting calyx</td>
<td>Absent, appressed, inflated, swollen</td>
<td>ARD</td>
<td>62 (53–73)</td>
<td>Evolutionarily labile with 50–100 transitions</td>
<td></td>
</tr>
</tbody>
</table>

Mean number of changes modelled across 200 simulations is given based on the best model of the three models tested identified using the Akaike information criterion (AIC): Equal Rates (ER), Symmetric (SYM), and All Rates Different (ARD). Traits were categorised as evolutionarily highly labile (>100 transitions; dark grey), labile (50–100 transition; light grey), conserved (10–49 transitions), or highly conserved (<10 transitions). The 95% highest probability density (HPD) of the mean number of transitions is shown for each trait. Details of the estimated transition rates of the underlying Markov models of each trait can be found in suppl. Table S4. Some rates of rare terminal states were found to be highly elevated and are likely to be state reconstruction artefacts, the interpretation of the evolutionary rate results of these rare terminal states should be done with caution.
yellow, and mature fruits red) were scored as polymorphic. Presence of stone cells in fruits was coded from taxonomic monographs, field observations, or herbarium specimens, as they can be easily seen (and felt) in both fresh and dried specimens if they are present.

**Trait evolution.** — Stochastic character mapping (SIMMAP; Huelsenbeck & al., 2003; Bollback, 2006) was performed using the phytools v.0.6-99 package (Revell, 2012) in R (R Core Team, 2021). All traits were treated as unordered and equally weighted. Polymorphic cladates were coded with equal probability of all states found to be present. Three different transition rate models were used: (1) Equal Rates (ER), i.e., a single rate for all possible transitions between states; (2) Symmetrical Rates (SYM); and (3) All Rates Different (ARD). For binary characters, only ER and ARD were run. The best-fitting model was identified using the Akaike information criterion (AIC; Akaike, 1974) and most common, with one origin of epiphytism from herbaceous ancestors (Fig. 4A). Changes in sympodial unit structure are frequent, relating to changes in growth form by enabling the modification of growth unit size, with dolfolate geminate structure being modelled as ancestral in Solanum (Fig. 4B). Plurifoliate sympodial units dominate in Grade I and dolfolate (geminate and non-geminate) units are more frequent in Clade II (Fig. 4B). Presence of glandular trichomes is highly labile across Solanum, with multiple independent origins and losses of both simple and stellate glandular trichomes (Table 1; suppl. Table S4; Fig. 4C). Corolla shape shows a mean of 271 transitions across Solanum with changes driven by the amount of interpetal tissue present (Fig. 4D). Colour in both corollas and fruits shows high evolutionary lability, with the most colours convergent in both corollas and fruits (Fig. 4E,F). Purple corollas are modelled to be ancestral in most clades in Grade I, while in Clade II white corollas are modelled as ancestral (Fig. 4E). Losses and gains of purple pigments are the most common, while transitions to yellow are less common with a minimum of five independent origins in Solanum from both white and purple ancestors (Fig. 4E; suppl. Table S4). Fruit colour shows 286 mean transitions across Solanum with frequent shifts from yellow to green, yellow to red, and purple to green, and a minimum of 58 independent origins of red fruits (Fig. 4; suppl. Table S4).

Ten further traits show evolutionary lability with 50–100 transitions across the genus, including specialised underground organs, prickles, trichome structure, leaf type, inflorescence position and branching, sexual system, stamen heteromorphism, presence of trichomes on mature fruit, and fruiting calyx modifications (Table 1; Figs. 5, 6). Underground storage organs have evolved at least four times independently, while rhizomes have been gained 30 times and lost at least 27 times across Solanum (Fig. 5A; suppl. Table S4). Prickles have a single origin in Solanum, with needle-like acicular prickles modelled as ancestral (Fig. 1K) followed by several switches between needle-like and broad-based prickles (Fig. 1L), including multiple losses of prickles (Fig. 5B). Prickles are found exclusively in clades with stellate trichomes, except for the Wendlandii and Nemorensis clades that lack stellate trichomes but have prickles (Fig. 5B,C). Stellate trichomes have evolved twice in Solanum from dendritic trichomes and have been lost several times (Fig. 5C; suppl. Table S4). Most frequent shifts include changes between dendritic to simple trichomes (Fig. 5C; suppl. Table S4). Leaves in Solanum are modelled to have been compound ancestrally with frequent switches to simple and then to lobed (Fig. 5D).
Internodal, forked inflorescences are modelled as ancestral in *Solanum* with repeated shifts in both inflorescence position and branching across the phylogeny where multi-branching inflorescences have been frequently gained and lost (Fig. 6A,B). Terminal branched inflorescences are more common in Grade 1 while unbranched internodal inflorescences dominate in the large Leptostemonum clade (Fig. 6A,B). The ancestral sexual system in *Solanum* is cosexuality (i.e., hermaphroditism) with a minimum of 17 independent origins of andromonoecy and >60 reversals back to cosexuality across *Solanum* (Fig. 6C). Dioecy has evolved at least six times in *Solanum*, once from cosexual ancestors and five times from andromonoecy (Fig. 6C; suppl. Table S4). Heteromorphic anthers have evolved at least 13 times in *Solanum* and have rarely been lost (Fig. 6D). Heteromorphic filaments are modelled ancestral in *Solanum* with frequent losses and re-gains. Androecium heteromorphism is generally present in either filaments or anthers, except for the Thelopodium clade where all species have both heteromorphic filaments and anthers (Fig. 6D). Trichomes on mature fruits are modelled as ancestral in *Solanum* with frequent losses and re-gains (Fig. 6E). Appressed fruiting calyces are common in *Solanum* with 48 independent origins, most of which are found in the Leptostemonum clade (Fig. 6F; suppl. Table S4). Inflated calyces have evolved a minimum of five times (Fig. 6F; suppl. Table S4).

Five floral and fruit traits show 10–49 changes across *Solanum* indicating relatively conserved evolution, including corolla bilateral symmetry, anther shape, pedicel articulation, fruit type and presence of stone cells in fruit (Table 1; Fig. 7). Bilaterally symmetric corollas have evolved seven times independently with frequent losses (Figs. 1X, 7A; suppl. Table S4). Tapered anther shape has evolved 6 times independently from an ancestral cylindrical shape, and corollate anthers have two independent origins (Fig. 7B; suppl. Table S4). Fruiting pedicels abscise at the basal junction between pedicel and inflorescence rachis in most *Solanum* but articulation towards the distal end has evolved in the Petota-Tomato clade and has been lost twice (Fig. 7C; suppl. Table S4). Dry dehiscent berries have evolved at least 13 times in *Solanum* and have been rarely lost once gained (Fig. 7D; suppl. Table S4). Stone cells in fruits are modelled as ancestral in *Solanum* with frequent losses (Fig. 7E).

Four highly conserved traits show <10 changes across *Solanum*, including presence of pseudostipules, enlarged anther connectives, anther modifications, and pedicel insertion type (Table 1; Fig. 8). Pseudostipules have evolved multiple times but only in two clades (Fig. 8A). Enlarged anther connectives have evolved only once but have been lost frequently (Fig. 8B). Anther modifications have evolved five times independently in *Solanum*, all outside the large Leptostemonum clade (Fig. 8C; suppl. Table S4). Cup-shaped pedicel insertion has evolved twice (Fig. 8D).

**DISCUSSION**

Morphological definition of clades. — Identifying morphological traits that characterise groups has been one of the central aims of taxonomy since its origin (Humphreys & Linder, 2009). Views on the importance of vegetative versus reproductive traits in defining genera has changed over the centuries (e.g., Stevens, 1997). Linnaeus (1735, 1753) used a so-called “sexual system” based solely on numbers of male and female parts for classifying plants into smaller units. Both Linnaeus’s contemporaries (e.g., Adanson, 1764) and subsequent taxonomists attempted more “natural” classifications, based on a wider selection of characters derived from all plant parts. Pheneticists continued this tradition by advocating the use of all characters with equal weight, in contrast to cladists who focused on the use of shared derived traits in defining groups (Williams & Ebach, 2020). A focus on a few obvious (often reproductive) traits has led to the recognition of many morphologically distinct small genera (Stevens, 1997; Humphreys & Linder, 2009). Molecular phylogenetic analyses have, however, revealed many genera (or higher-rank taxa) to be para- or polyphyletic, due in large part to the convergent evolution (i.e., evolutionary lability) of many floral and fruit traits used to define these groups prior to the advent of DNA sequence data (e.g., Orejuela & al., 2017; Bogarin & al., 2019; Koenen & al., 2020; Appelhans & al., 2021).

Traits that define clades within big genera have remained elusive in part because of the logistical difficulty of studying large groups (Minelli, 2016). *Solanum* is an example of such an unwieldy group, where the efforts of a large and collaborative team of taxonomists, field botanists, and molecular systematists now enable us to provide a broad overview of morphological diversity across the genus at species-level for the first time. Our analysis is a major step forward in quantifying morphological diversity in *Solanum*, one of the largest plant genera across the tree of life (Minelli, 2016). The analyses presented here allow us to morphologically define the informally named clades of *Solanum*, as presented in Table 2. The most-conserved traits are clearly the most useful in defining clades, but even the most-labile traits prove useful in...
defining particular clades when rare states are expressed and if used in combination (e.g., axillary inflorescences in Pteroidea clade with unifoliate sympodial units, or presence of both yellow corollas and pseudostipules in Tomato clade). Such fine-tuned understanding of variation (or lack of) enables us to confidently place all currently accepted species of *Solanum* into the informal clades with only a few exceptions (suppl. Table S1). Lastly, morphological characters used in the definition of clades can be used to create powerful identification tools, and with that in mind, the underlying data has been used to construct a freely available online interactive multi-access key to the clades (Solanum Key Consortium, 2022).

**Plant structure, roots and leaves.** — Plant structure related traits have some of the highest transition rates in *Solanum* with repeated shifts between sympodial growth patterns and herbaceous and woody growth forms (Figs. 1A–F, 4A,B). All herbaceous vines and epiphytes in *Solanum* are found in Grade I except for a single truly herbaceous vine species found in the Nemorense clade (*S. hoehnei* C.V.Morton, Fig. 4A), while woody growth forms predominate in

![Diagram of plant structure, roots, and leaves](image)

*Fig. 5.* Evolution of labile morphological traits (vegetative) in *Solanum* with 50–100 transitions based on species-level analysis using stochastic character mapping. A, Specialised underground organs; B, Prickles; C, Trichome structure; D, Leaf division. Results from the best model are shown for each character (see Table 1 and suppl. Table S4 for details) based on 200 simulations. The topology used for mapping was derived from a supermatrix phylogeny with nine loci (two nuclear and seven plastid loci; Gagnon & al., 2022) with 725 species sampled and coded for each trait (58% of all species). All minor clades are labelled; tips reflect the crown nodes of each minor clade. Piecharts indicate likelihood of modelled ancestral states along the nodes, and frequency bars (tips) reflect proportion of species sampled within each clade with each state.
Clade II. Shifts between growth forms are most prevalent in Grade I where all seven states are observed (Fig. 4A). Growth pattern in Solanum is sympodial, in which stems are composed of a series of concaulescent branches, flowering marks the end of the main shoot and axillary buds (of various numbers) continue plant growth (Danert, 1958, 1970; Child, 1979). Thus, changes in the sympodial unit structure result in variation in plant structure in general as well as inflorescence position (Danert, 1958, 1970; Child, 1979). Genetic control of the number of leaves per sympodial unit is known to involve the tomato self-pruning (sp) locus; sympodial units of sp mutants are terminated early and have fewer leaves (Paran & Van der Knaap, 2007). The great lability observed here for both traits linked to plant structure suggests that growth form has played a key role in diversification in Solanum. Symподial growth structure is perhaps the closest trait in the genus to the concept of “key innovation” seen in other large plant genera, such as insular woodiness in Begonia L. (Kidner & al., 2016) or succulence and the linked evolution of CAM photosynthesis in Euphorbia L. (Horn & al., 2012, 2014; Anest & al., 2021). Growth form variation in Solanum is often underappreciated, perhaps due to the difficulty of capturing it in photos or in herbarium specimens.

In comparison to the high evolutionary lability of aboveground growth form, the evolution of specialised underground organs is less, albeit still evolutionarily labile. Our analyses show repeated gains and losses of rhizomes and four origins of underground storage organs in Solanum; three of the transitions have resulted in stem and root tubers (Petota, Carolinense, and Asterophorum clades, the latter two members of Leptostemonum), while the fourth has given rise to a swollen caudex (S. montanum Cav., Regmandra clade; Fig. 5A). Although tubers are often associated with herbaceous species (e.g., potatoes), in the Leptostemonum clade they are found in woody shrubs (members of the Asterophorum clade; Fig. 5A). Rhizomes appear evolutionarily more labile compared to tubers, and the relationship between rhizomes and tubers bears further investigation as both are largely found in the same clades (Fig. 5A; Table 2).

**Plant defence: Glands, trichomes and prickles.** — Glandular trichomes are involved in herbivore resistance and in Solanum contain a variety of different chemical compounds (Weinhold & Baldwin, 2011; Glas & al., 2012; Fan & al., 2019). The high evolutionary lability of glandular trichomes observed in Solanum with frequent gains and losses is not surprising, considering many species show infraspecific variation in glandular pubescence between populations and individuals (e.g., S. nigrum L., S. retroflexum Dunal, S. villosum Mill.; Manoko, 2007; Särkinnen & al., 2018). Glandular trichomes are most prevalent in simple-haired clades; only seven (minor) clades have stellate glandular trichomes (Fig. 4C). Morphological variation in simple glandular trichomes has been studied extensively in the Tomato clade where seven distinct types have been identified (types I–VII; Simmons & Gurr, 2005); each type has distinct genetic control (Schlimmiller & al., 2009, 2012; Zhang & al., 2015; Chang & al., 2018; Chalvin & al., 2020) and potentially distinct function. Some of these with single-celled glandular tips contain high amounts of acyl sugars and are involved in insect resistance (types I and IV; e.g., Weinhold & Baldwin, 2011), while trichomes with multicellular glandular tips secrete terpenes with various functions (type VI; e.g., Glas & al., 2012; Fan & al., 2019).

Prickles in Solanum are epidermal in origin and are thought to be modified multicellular stellate trichomes with layers of elongate and lignified cells (Seithe, 1962, 1979; Whalen, 1984). Our results show that the single origin of prickles corresponds to the evolution of stellate trichomes in the Leptostemonum clade (Fig. 5B,C), supporting the view that prickles have originated from the stellate trichome type. The common origin of stellate trichomes and prickles can be observed in some Leptostemonum species (e.g., S. barbisetum Nees, S. myoxotrichum Baker and S. schumannianum Dammer, all within the EHS clade) where stellate trichomes on young stems develop lignified stalks and become prickle-like with an apical stellate trichome (Vorontsova & Knapp, 2016; Aubriot & Knapp, 2022). Previous studies have proposed glandular trichomes to be involved in prickle development (Pandey & al., 2018) but these hypotheses remain unsupported based on our findings and other studies (Zhang & al., 2021). Once gained, prickles have been lost several times, where many of the losses are associated with domestication (e.g., S. aethiopicum L., S. macrocarpon, S. melongena, S. quitoense, S. sessiliflorum, S. stramonifolium Jacq.; Whalen & al., 1981; Lester & Thitai, 1989). Variation in prickle type and density observed within species and individuals shows that prickle expression is highly labile; prickles and trichomes are observed to be denser/exclusive to juvenile individuals in some species (e.g., Vorontsova & Knapp, 2016), while in others prickly and non-prickly stems can occur on the same plant (e.g., S. elaegnifolium Cav.; Knapp & al., 2017). Prickles have been shown to be under simple dominant inheritance genetically (Lester & Thitai, 1989), and QTLs and candidate genes responsible for prickle formation have been identified (Portis & al., 2015; Pandey & al., 2018; Miyatake & al., 2020; Qian & al., 2021; Zhang & al., 2021).

Trichome structure, in contrast, is less labile and defines some of the major clades in Solanum (Fig. 5C) (Dunal, 1852; Seithe, 1962, 1979; Roe, 1971, 1972). Stellate trichomes have arisen twice in Clade II (Fig. 5C). Dendritic trichomes, which never occur in clades with stellate trichomes, are modelled as ancestral in Solanum and have been lost several times (Fig. 5C). Seithe (1962, 1979) observed simple trichomes on seedling leaves of species that subsequently developed dendritic or stellate trichomes, leading her to suggest that both were derived from simple trichomes. Our results, which model dendritic trichomes as ancestral, do not support this view, and suggest that stellate trichomes are derived from dendritic ones.

**Leaves.** — Compound (i.e., deeply pinnatifid) leaves are modelled as ancestral in Solanum, with frequent shifts to simple (entire) leaves (Fig. 5D). The trait model predicts, surprisingly, direct shifts from compound to simple leaves without an “intermediate” step of leaf lobing (suppl. Table S4), as can be
seen in particular clades with both simple and compound
leaved species (e.g., Herpistichum, Pteroeida, Anarrhichome-
num, Basarthurm, and Petota; Fig. 5D), but that lack species
with “intermediate” lobed leaves. In these clades, simple
leaves may represent reduced compound leaves where only a
single leaflet remains, as this can be observed in some tomato
mutants (Berger et al., 2009). Transitions to lobed leaves are
modelled to be via simple entire leaves (suppl. Table S4), and
such transitions can be observed in Clade II, where some
species show simple, lobed, and compound leaves in a single
shoot (e.g., Wendlandii and Pachyphysa clades: S. wendlandii
Hook. f. or S. pendulum Ruiz & Pav., respectively). All species
in Leptostemonum have either simple or lobed leaves (some
deeply lobed, e.g., S. sisymbriifolium Lam., coded as lobed),
and change in shape from lobed to entire has been document-
ated in the Torva clade with developmental maturity of the
shoot (Roe, 1966). Our results disagree with previous studies
on leaf division patterns across Solanum where leaves were
modelled as ancestrally simple and entire (Geeta et al.,
2012); the difference in our results is likely due to increased
species sampling and the fact that we collapsed many nodes
along the backbone of Solanum due to the high discordance
and topological uncertainty based on phylogenetic sampling
(Gagnon et al., 2022). Genetic studies show upregulation of
KNOX genes in both compound and lobed leaves in Solanum
but not in simple leaves (Hagemann & Gleissberg, 1996;
Bharathan et al., 2002; Efroni et al., 2010).

Floral traits. — Two traits linked to pollinator attraction,
corolla shape and colour (Møller, 1995; Gómez et al., 2008,
2016; Muchhala et al., 2014; Reverte et al., 2016; Moré
et al., 2020), are shown to be some of the most evolutionarily
labile traits in Solanum (Fig. 4D,E). Variation in corolla shape in
Solanum depends on the amount of interpretal tissue pre-
sent between lobes, and changes seem frequent throughout the
genus highlighting the need to explore pollinator-linked trait
variation in buzz-pollinated plant groups.

Shifts between purple and white dominate in Solanum
with >66 gains of purple corollas (Fig. 4E). Transitions to yellow
or low are rare with a minimum of five independent origins of
yellow corollas, twice from white ancestors. A similar pattern
has been found in tribe Antirrhineae (Plantaginaceae), where
transitions from purple to yellow have been found to have oc-
curred via a white state (i.e., “loss” of previous pigment; e.g.,
Ellis & Field, 2016). Three transitions in Solanum, however,
indicate direct shifts from purple to yellow and these nodes
merit further investigation. The strength and brightness of
yellow is not homogenous across Solanum, and it is possible
that this colour arises from different pathways. Genetic con-
rol of corolla colouration (e.g., Gates et al., 2018) has not
been studied in Solanum, but flavonoids (anthocyanins: pur-
ple; flavones: yellow) and carotenoids (yellow) are compo-
ents of corolla colouration in other genera of Solanaceae
(Iochroma Benth.: Berardi et al., 2016; Larter et al., 2019;
Nicotiana L.: McCarthy et al., 2017; Petunia Juss.: Berardi
et al., 2021). We did not record the presence of multiple col-
ours in some species (e.g., corollas with shiny central “eyes”
at the base of the corolla with green, yellow, purple, or black
colouration) but this merits further investigation. Studies on
Antirrhinum L. have shown that even single mutations altering
corolla colour and reflectance can affect bee behaviour (Comba
et al., 2000; Dyer et al., 2006, 2007).

Our results indicate that the general floral “bauplan” in So-
anum has changed several times independently despite the rel-
ative morphological homogeneity in Solanum flowers based on
the buzz-pollination syndrome with poricidally dehiscent an-
thers arranged in a central cone. Changes include a minimum
of 13 origins of heteromorphic anthers, 8 origins of heteromor-
phic filaments (Fig. 6D), 7 origins of bilaterally symmetric co-
rollas (Fig. 7A), and 5 independent origins of anther modifi-
cations (Fig. 8C). Bilaterally symmetric corollas have evolved
largely in clades with heteromorphic anthers (Leptostemonum; Figs. 6D, 7A; Lester et al., 1999; Knapp, 2002b, 2010; Bohs et al., 2007). The link between
corolla and stamen zygomorphy has been well-documented and
has evolved multiple times in Solanaceae (Robyns, 1931),
where heteromorphic anthers appear to be precursors to bilater-
ally symmetric corollas (Zhang et al., 2017). Genes controlling
corolla bilateral symmetry (and heteromorphic anthers) in So-
anum have not yet been identified, but the trait is likely to affect
pollination by increasing pollinator specificity and efficiency
(Jesson & Barrett, 2002, 2005; Fenster et al., 2009). Enlarged
anther connectives have evolved once in Solanum (Fig. 8B)
again affecting pollination as they are involved in the perfume
bee pollination in the Pachyphylla clade (Sazima et al., 1993;
Taken together, our results indicate continuous shifts in pollina-
tion-related floral traits in a buzz-pollinated genus.

Fruit morphology. — Solanum is well-known for vari-
ation in fruit shape, size, colour, and texture (Fig. 1Y–AD;
Knapp, 2002c), and fruit traits have been suggested to have
been important in the diversification of the EHS clade
(Echeverría-Londoño et al., 2020) likely due to their function

![Fig. 6. Evolution of labile morphological traits (reproductive) in Solanum with 50–100 transitions based on species-level analysis using stochastic character mapping. A, Inflorescence position; B, Inflorescence branching; C, Sexual system; D, Stamen heteromorphism; E, Trichomes on mature fruits; F, Fruiting calyx modifications. Results from the best model are shown for each character (see Table 1 and suppl. Table S4 for details) based on 200 simulations. The topology used for mapping was derived from a supermatrix phylogeny with nine loci (two nuclear and seven plastid loci; Gagnon et al., 2022) with 725 species sampled and coded for each trait (58% of all species). All minor clades are labelled; tips reflect the crown
nodes of each minor clade. Piecharts indicate likelihood of modelled ancestral states along the nodes, and frequency bars (tips) reflect proportion of species sampled within each clade with each state. Version of Record](https://onlinelibrary.wiley.com/doi/10.1002/tax.12990)
in dispersal adaptations and ability to colonise new areas and habitats (e.g., Cipollini & al., 2002; Martine & al., 2019). Colour is the most evolutionarily labile fruit character in Solanum. Fleshy Solanum berries are known to be dispersed by a wide variety of vertebrates, including birds, bats, and small rodents (Symon, 1979a; Cipollini & Levey, 1997a,b,c; Knapp, 2002a), and variation in fruit colour could be linked to changes in dispersal strategies. Green fruits are the most common in Solanum (275 species sampled in the phylogeny; suppl. Table S3), but the commonness of green fruits may be an artefact of late maturing fruits or fruits that are rapidly taken by dispersers in some groups and ephemerality of this stage, where fully mature fruits are rarely collected. An example are the green fruits of the Geminata and Brevantherum clades that rapidly change in colour from green to yellow, orange, red or purple when they are mature and are quickly consumed by frugivores such as bats (Knapp, 2002a; Tovar & al., 2021). Yellow (157 spp.) and red (122 spp.) are the second most common fruit colours in Solanum, followed by purple (77 spp.), orange (65 spp.) and white (29 spp.; suppl. Table S3). Flavonoids, particularly anthocyanins, are responsible for purple, blue, and red fruit colours in Solanaceae, whereas carotenoids are typically responsible for yellow, orange, and red fruits (Gonzali & Perata, 2021). Because we only scored external colour and did not code flesh colouration, future studies should expand on the distinct colour pathways potentially present in fruit flesh and peel, especially in species such as S. lycopersicum (Tomato clade; Ronen & al., 1999; Bovy & al., 2007; Gonzali & Perata, 2021), S. betaceum (Pachyphylla clade; Acosta-Quezada & al., 2015), and S. melongena (EHS clade; Jiang & al., 2016).

Presence of trichomes on mature fruits and fruiting calyx modifications (Table 1, Fig. 6E,F) are evolutionarily labile in Solanum. Our results agree with Deanna & al. (2019) showing a stepwise and directional evolution from non-accrescent to accrescent (appressed) and inflated fruiting calyces but also indicate a second path from non-accrescent directly to inflated (suppl. Table S4). Fruiting calyx modifications (Table 1; Fig. 6F) enable physical dispersal mechanisms, for example where prickly accrescent fruiting calyces around dry berries act as trample-burrs or censer fruits where seeds shake out of the open end of the accrescent calyx with plant movement (e.g., S. eucanthatum Phil., Elaeagnifolium, Androcers and EHS clades; Symon, 1979a; Martine & al., 2019).

The remaining fruit traits in Solanum are phylogenetically conserved (Figs. 7C–E, 8D; pedicel articulation, fruit type, presence of stone cells, and pedicel insertion) and are useful for defining groups (Table 2). Stone cells (i.e., sclerotic granules or brachysclereids), hard inclusions found in the fleshy portion of some Solanum berries, have evolved a minimum of four times (Fig. 7E). Stone cells are derived from sclerenchyma with massively enlarged cell walls and vary in their number, size, shape, and colour (Bitter, 1911, 1914; Symon, 1994; Knapp, 2002c; Särkinen & al., 2018; Knapp & al., 2019). Their function remains unclear, but interestingly, in the Morelloid clade, where stone cells are common, species cultivated for their berries lack them completely (e.g., S. scabrum Mill., see Särkinen & al., 2018).

There is complex variation in fruit texture, shape, and size across Solanum not captured by our analyses that likely contributes to dispersal strategies (e.g., Cipollini & al., 2002). In our study, the single category of fleshy berries included small, soft, and juicy (e.g., tomatoes), large and spongy (e.g., eggplant), large and woody (e.g., S. syphanta Dunal), and explosively dehiscent fleshy berries (e.g., all species of the Gonoctrichum clade; Knapp, 2001, 2002c; Stern & al., 2013; S. mellobarretori Agr & Stehmann in the Leptostemonum clade; Agra & Stehmann, 2016). Phenotypic variation of fruit texture, shape, and size will be challenging to quantify in all species but will be needed to enhance understanding of diversity across Solanum. Methods developed for tomatoes (e.g., Van der Knaap & al., 2014) applied across the genus may reveal new characters and character combinations for developmental study. Links between the evolution of fruit type, size, colour, and texture combined with fruiting calyx modifications warrant further exploration because they all affect fruit and seed dispersal.

**Sexual system.** — Cosexuality, with all flowers having both male and female parts (Cardoso & al., 2018), is ancestral in Solanum (Fig. 6C). Dioecy is relatively rare in Solanum, being found in 15 species sampled so far in the molecular phylogeny, but has evolved at least six times independently, directly from a cosexual (i.e., hermaphroditic) ancestor in at least one case (Anarrhichomenum clade; Fig. 6C) and from andromonoecious ancestors in others (e.g., Martine & al., 2006, 2009). Plants with dioecious or plastic sexual systems continue to be discovered in Solanum (e.g., Knapp & al., 1998; Martine & al., 2016; McDonnell & al., 2019); 22 dioecious species are currently known in Solanum (Fig. 3D). Andromonoecy as coded here is common in Solanum and is modelled as ancestral in the Leptostemonum clade and its sister lineage with multiple gains and losses (Fig. 6C). There is large variation within species coded as andromonoecious, with a continuum from weakly andromonoecious species with stamine flowers and pistillate flowers in more or less equal proportions to strongly andromonoecious species with...
a large number of staminate flowers and a single hermaphroditic flower that produces fruits (Whalen & Costich, 1986; Miller & Diggle, 2007). Future studies in large clades where andromonoecy is common but not predominant (e.g., EHS clade) will be useful in refining our knowledge of sexual system transitions in *Solanum*; both additional taxa and sequences will be needed to untangle relationships in the species-rich EHS clade where detailed relationships are not yet clear. Small clades exhibiting the entire range of sexual systems (e.g., the Australian groups under study by Martine & al., 2019) could be used to understand the role of flower morphology and pollinator dynamics in sexual system evolution in relation to ecological conditions (e.g., Quesada-Aguilar & al., 2008).

**Future research.** — Our results open several hypotheses that could be further explored in future studies. For example, our results highlight that much work remains to be done in understanding the evolutionary and developmental origin of the distinct trichome structures found across *Solanum*. There is more morphological variation in trichome structure than

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**Fig. 8.** Evolution of the most conserved morphological traits in *Solanum* with <10 transitions based on species-level analysis using stochastic character mapping. **A**, Pseudostipules; **B**, Enlarged anther connectives; **C**, Anther modifications; **D**, Pedicel insertion. Results from the best model are shown for each character (see Table 1 and supp. Table S4 for details) based on 200 simulations. The topology used for mapping was derived from a supermatrix phylogeny with nine loci (two nuclear and seven plastid loci; Gagnon & al., 2022) with 725 species sampled and coded for each trait (58% of all species). All minor clades are labelled; tips reflect the crown nodes of each minor clade. Piecharts indicate likelihood of modelled ancestral states along the nodes, and frequency bars (tips) reflect proportion of species sampled within each clade with each state.
<table>
<thead>
<tr>
<th>Main group</th>
<th>Description</th>
<th>Major clade</th>
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<th>Minor clade Description</th>
<th>Geography</th>
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<tbody>
<tr>
<td>Thelopodium (3)</td>
<td>Single-stemmed (unbranched) shrubs with heteromorphic anthers and filaments</td>
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<td>apically pointed onion dome shaped and pointing upwards</td>
<td>Lowland and pre-montane South America</td>
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<tr>
<td>Grade I</td>
<td>Non-prickly herbs, shrubs or herbaceous or woody vines that lack stellate trichomes; mostly plurifoliate sympodial unit structure, many compound-leaved species</td>
<td>Regmandra (12)</td>
<td>Herbs and shrubs, leaves mostly deeply lobed to compound, thick and somewhat succulent, corollas mostly rotate, stigmas expanded and clavate, stone cells present</td>
<td>Pacific coastal deserts and dry habitats (incl. lomas) of Peru and Chile</td>
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<td><strong>VANAns</strong></td>
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<td>Woody plant with cup-shaped pedicel bases (insertion), berries red at maturity</td>
<td>Chile</td>
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<td></td>
<td><strong>African non-spiny</strong></td>
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<td>Woody shrubs or vines, mostly climbing, many species with branched dendritic trichomes, plurifoliate sympodial units, terminal inflorescences, and mostly deeply stellate purple corollas</td>
<td>Africa &amp; Madagascar</td>
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<td><strong>Normania</strong></td>
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<td>Herbs and shrubs with inflated calyces, bilaterally symmetric purple corollas, heteromorphic anthers with basal modifications (horn-like projections), unbranched internodal inflorescences</td>
<td>Macaronesia, southern Spain and Mediterranean North Africa</td>
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<td><strong>Archaesolanum</strong></td>
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<td>Soft-wooded shrubs with highly variable leaves (simple to deeply lobed) with winged petioles, rotate purple corollas, loosely erect anthers on relatively long filaments, and berries with many stone cells</td>
<td>Australia and the South Pacific (New Guinea, Australia, Tasmania, New Zealand)</td>
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<td>DulMo</td>
<td>Mostly subwoody to woody (often scandent) shrubs, some climbing with twining petioles, many species with branched dendritic trichomes, pedicels with distinctive cup-shaped bases (insertions), stone cells absent</td>
<td>Dulcamaroid (43)</td>
<td>Herbs to shrubs, with internodal or leaf-opposed inflorescences, stone cells absent</td>
<td>Global</td>
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<td><strong>Morelloid</strong></td>
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<th>Minor clade</th>
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<th>Geography</th>
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<tbody>
<tr>
<td>Grade I continued</td>
<td>Potato</td>
<td>Mostly herbs, herbaceous vines, or weakly woody vines</td>
<td>Herpystichum (10)</td>
<td>Small herbs or herbaceous vines commonly rooting along nodes with simple to 3–5–foliate leaves, flower buds distinctly onion-shaped and fruits mostly flattened along base to tip axis</td>
<td>Lowland rain forest and pre-montane forests from southern Mexico to northern Peru</td>
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<td>Pteroidea (10)</td>
<td>Understory herbs, herbaceous vines with adventitious roots and unbranched shrubs with unifoliate sympodial units, simple or pinnate leaves, and axillary inflorescences with small, deeply stellate corollas, fruits often pointed and warty</td>
<td>Lowland rain forest and pre-montane forests from Mexico to tropical South America</td>
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<td>S. oxycooides (1)</td>
<td>Somewhat woody vine with simple leaves lacking pseudostipules, and small red fruits with only a few seeds</td>
<td>Peruvian Andes &gt;3000 m</td>
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<td>Articulatum (2)</td>
<td>Somewhat woody vines with paired pseudostipules, with large, often branched inflorescences and winged seeds, resembling Basarthrum clade but lacking bayonet hairs (2-celled hairs with a short apical cell)</td>
<td>Montane forests &gt;2500 m in Costa Rica, Panama, and northern Colombia</td>
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<td>Basarthrum (16)</td>
<td>Somewhat woody vines or lax shrubs, simple to pinnately compound leaves with frequent interjected leaflets, subtended by a pair of pseudostipules, all species with bayonet hairs (2-celled hairs with a shorter apical cell), with pendant fruits typically green, striped</td>
<td>Dry to moist mid-elevation habitats in Central &amp; South America</td>
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<td>Anarrhichomenum (12)</td>
<td>Somewhat woody vines readily rooting along nodes, simple or compound leaves lacking interjected leaflets, subtended by a single (not paired) pseudostipule at most nodes, fruits orange to red and seeds winged</td>
<td>Mid-elevation habitats in Central &amp; South America</td>
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<td>Etuberosum (3)</td>
<td>Rhizomatous herbs with pinnately compound leaves with frequent interjected leaflets subtended by paired pseudostipules, with many-branched terminal inflorescences, morphologically similar to Petota clade members that have tubers, pedicels articulated at or near the base (unlike Petota clade)</td>
<td>Argentina and Chile</td>
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<td>Main group</td>
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<td>Grade I continued</td>
<td>Tomato (17)</td>
<td>Herbs to woody vines with pinnate leaves with mostly serrate to serrulate margins, some with interjected leaflets, all subtended by paired pseudostipules, all species with strong vegetative odours (glandular trichomes) and yellow corollas, with most species with distinct apical anther modifications (appendages), fruiting pedicels articulating mostly in the distal part</td>
<td>Colombia, Ecuador, Peru and Chile</td>
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<td>Petota (113)</td>
<td>Tuber-bearing herbs mostly with compound leaves with interjected leaflets with entire leaflet margins, subtended by paired pseudostipules, inflorescences always branched and terminal, corollas usually rotate, fruiting pedicels articulating mostly in the distal part, berries green to purple</td>
<td>North, Central &amp; South America</td>
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<td>Clade II</td>
<td>S. anomalostemon (1)</td>
<td>Small herb with glandular trichomes, simple to 3-foliate leaves, distinct cordate shaped anthers with apical modification (beak)</td>
<td>Dry forests in southern Peru</td>
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<td>Brevantherum</td>
<td>Non-prickly, shrubs or trees (herbs) with cylindrical anthers, some with stellate hairs</td>
<td>Argentina, Brazil and Paraguay</td>
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<td>Trachytrichium (2)</td>
<td>Shrubs with simple entire leaves, simple trichomes and unbranched inflorescences with deeply stellite white corollas, heteromorphic filaments in some species, fruits dull green, many-seeded</td>
<td>Brazilian Atlantic Forest and Cerrado</td>
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<td>Inornatum (5)</td>
<td>Herbs to small shrubs with simple entire leaves, simple trichomes, and unbranched inflorescences with deeply stellite white corollas, fruits translucent or dull green to red, with few large seeds</td>
<td>Southern United States to southern South America</td>
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<td>Gonatotrichum (7)</td>
<td>Herbs to shrubs, some species with distinctive 2-celled trichomes with a long apical cell that is bent at a 90-degree angle, inflorescences unbranched with mostly rotate white corollas, strongly heteromorphic filaments in some species, fruits translucent green, explosively dehiscent and with many seeds</td>
<td>Native to Central and South America with many species now found globally</td>
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<td>Brevantherum (80)</td>
<td>Trees or shrubs, some species with distinct branching pattern where stem forks have an inflorescence or a leaf arising from it (diachasial branching) and rank fishy vegetative odour, all species with stellate trichomes (or lepidote scales), most species with highly branched inflorescences, some with upright and stout peduncle and pedicels, mostly white corollas, fruits various colours remaining green until just before maturity</td>
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<td>Main group</td>
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<td><strong>Clade II continued</strong></td>
<td></td>
<td>Geminata</td>
<td>Non-prickly shrubs or trees with simple entire leaves and sometimes a rank vegetative odour (burning smell), anthers cylindrical</td>
<td>Reductum (2)</td>
<td>Small shrubs with dendritic hairs, broadly stellate white corollas, and one species with basal anther modifications (sack)</td>
<td>Argentina</td>
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<td>Geminata (150)</td>
<td>Shrubs or trees, many with geminate (paired/twinned) leaves, inflorescences mostly leaf-opposed and with deeply stellate white flowers with relatively stout, oblong anthers, and fruits that remain green at maturity</td>
<td>Geminata (150)</td>
<td>Shrubs or trees, many with geminate (paired/twinned) leaves, inflorescences mostly leaf-opposed and with deeply stellate white flowers with relatively stout, oblong anthers, and fruits that remain green at maturity</td>
<td>Moist lowland or montane forests from Central to South America</td>
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<td>Cyphomandra</td>
<td>Non-prickly shrubs, small trees or woody vines with rank vegetative odour (burning smell), plurifoliate or trifoliate sympodial growth, tapered anthers, and with long and mostly branching inflorescences, some species with branched dendritic trichomes</td>
<td>S. graveolens (1)</td>
<td>Woody vine with pinnately compound leaves, white broadly stellate corollas, anthers with apical modification (beaks)</td>
<td>Brazilian Atlantic Forest</td>
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<td>Cyphomandropsis (11)</td>
<td>Nr</td>
<td>Shrubs or small trees with simple entire leaves, many with dendritic trichomes, mostly white corollas, some with stone cells</td>
<td>Cyphomandropsis (11)</td>
<td>Shrubs or small trees with simple entire leaves, many with dendritic trichomes, mostly white corollas, some with stone cells</td>
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<td>Pachyphylla (42)</td>
<td>Nr</td>
<td>Shrubs (often lax and spreading) or small trees with distinct branching pattern where stem forks have an inflorescence or a leaf arising from it (dichasial branching), some species with lobed or compound leaves, corollas mostly deeply stellate, anthers with enlarged connectives, some with stone cells</td>
<td>Pachyphylla (42)</td>
<td>Shrubs (often lax and spreading) or small trees with distinct branching pattern where stem forks have an inflorescence or a leaf arising from it (dichasial branching), some species with lobed or compound leaves, corollas mostly deeply stellate, anthers with enlarged connectives, some with stone cells</td>
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<td>Wendlandii-Allophyllum</td>
<td>Prickly to non-prickly shrubs, herbs and woody vines with tapered anthers</td>
<td>Allophyllum (4)</td>
<td>Shrubs or herbs lacking prickles, with distinct branching pattern where stem forks have an inflorescence or a leaf arising from it (dichasial branching), leaves with idioblasts containing crystal sand (sand-punctate), inflorescences unbranched, few-flowered and relatively short, corollas broadly stellate or rotate, white or greenish white, some species with stone cells</td>
<td>Lowland and montane moist forests of Central and South America</td>
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<td>Wendlandii (9)</td>
<td>Woody vines with mostly broad-based recurved prickles and with large and generally many-branched inflorescences, many species with lobed or compound leaves, heteromorphic filaments, or swollen calyces in fruit</td>
<td>Wendlandii (9)</td>
<td>Woody vines with mostly broad-based recurved prickles and with large and generally many-branched inflorescences, many species with lobed or compound leaves, heteromorphic filaments, or swollen calyces in fruit</td>
<td>Mexico, and Central and South America</td>
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<th>Main group</th>
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<th>Major clade</th>
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<tbody>
<tr>
<td>Clade II continued</td>
<td>Nemorense</td>
<td>Prickly vines, shrubs or herbs, andromonoecious, with tapered anthers</td>
<td>Nemorense (4)</td>
<td>Woody or herbaceous vines or herbs with mostly broad-based recurved prickles, sympodial units mostly difoliate geminate, leaves usually lobed or compound, inflorescences unbranched and leaf-opposed with flowers with deeply stellate corollas</td>
<td>South America</td>
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<td>Leptostemonum</td>
<td>Prickly shrubs, trees, woody vines or herbs with stellate trichomes, difoliate (geminate or non-geminate) sympodial units dominate, leaves simple or lobed, mostly andromonoecious, simple inflorescences dominate, anthers tapered</td>
<td>S. polygamum (1)</td>
<td>Dioecious shrub or small tree with needle-like prickles, simple entire leaves, deeply stellate 5–6-merous white corollas, cylindrical anthers, female flowers lacking developed anthers and with large, forked stigmas, and pubescent orange fruits subtended by large leafy calyx lobes</td>
<td>Caribbean</td>
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<td>Lasiocarpa (12)</td>
<td>Shrubs or small trees with needle-like prickles, with mostly repand leaves and unbranched inflorescences, mostly broadly stellate corollas and orange fruits covered in stellate usually glandular trichomes</td>
<td>Global (mostly Central America and northern and western South America, with two species in Asia and the Pacific)</td>
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<td>Acanthophora (22)</td>
<td>Shrubs and herbs with deeply stellate corollas characterised by having a mix of stellate and simple trichomes on lower leaf surfaces but only simple trichomes on stems and upper leaf surfaces</td>
<td>Disturbed and open habitats from Mexico to South America (mostly eastern Brazil); introduced and naturalized elsewhere</td>
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<td>Gardneri (10)</td>
<td>Slender-stemmed shrubs and herbs mostly with needle-like prickles, small simple (mostly unlobed) leaves, short and laterally directed inflorescences, deeply stellate corollas, and berries with somewhat accrescent calyces covering less than half of the fruit</td>
<td>Dry habitats of eastern to central Brazil, Caribbean, Mexico and Central America, and northern Peru</td>
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<td>Thomasiifolium (9)</td>
<td>Shrubs or woody vines mostly with broad-based recurved prickles, some species with glandular-stellate trichomes, stems often with short internodes and leaves grouped at the apex, inflorescences unbranched, corollas purple, some bilaterally symmetric, fruits either large and densely pubescent with large seeds, or small and glabrous with accrescent calyces that cover less than half of the fruit</td>
<td>Eastern Brazil</td>
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<td>Clade II continued</td>
<td>Leptostemonum continued</td>
<td><strong>Erythrotrichum (35)</strong></td>
<td>Shrubs, woody vines or small trees covered in broad-based recurved prickles, with stellate glandular trichomes, trichomes dense and often reddish-brown in colour, fruits covered in stellate trichomes</td>
<td>Tropical South America</td>
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<td><strong>Sisymbriifolium (2)</strong></td>
<td>Shrubs or herbs with dense needle-like prickles, leaves deeply lobed (nearly pinnate), corollas broadly stellate to nearly rotate, white, fruits red with appressed spiny calyces that spread open at full maturity</td>
<td>Dry habitats of South America</td>
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<td><strong>Crinitum (23)</strong></td>
<td>Trees, large shrubs or woody vines with scattered broad-based prickles and large flowers with bilaterally symmetric purple corollas and long, heteromorphic anthers, berries large and hardened, oxidize black when cut open, with distinctly swollen calyces</td>
<td>Mexico and South America</td>
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<td><strong>Androceras (16)</strong></td>
<td>Herbs densely covered in needle-like prickles, with bilaterally symmetric corollas with heteromorphic anthers, dry fruits surrounded by accrescent spiny calyces</td>
<td>Southern U.S.A. and Mexico</td>
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<td><strong>S. campechiense (1)</strong></td>
<td>Small shrub covered in needle-like prickles, corollas rotate, fruits with appressed calyces lacking pedicel articulation</td>
<td>Dry forests of Mexico, and Central and South America</td>
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<td><strong>Carolinense (14)</strong></td>
<td>Rhizomatous herbs and shrubs covered in needle-like prickles, some species with tubers, corollas rotate, mostly purple, fruits green to yellow mottled, some with appressed calyces</td>
<td>Open habitats of southeastern U.S.A. and Bolivia, Argentina and Paraguay</td>
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<td><strong>Bahamense (6)</strong></td>
<td>Shrubs and trees with some needle-like prickles, deeply stellate corollas, anthers with stellate trichomes on the adaxial surface, and small juicy red or black fruits on strongly recurved fruiting pedicels</td>
<td>Caribbean</td>
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<td><strong>Micracantha (14)</strong></td>
<td>Scandent shrubs and woody vines that climb using broad-based recurved prickles with unbranched inflorescences, deeply stellate (mostly white) corollas, and mostly orange or red fruits</td>
<td>Florida to Bolivia, including the Caribbean</td>
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<tr>
<td><strong>Clade II continued</strong></td>
<td></td>
<td><strong>Leptostemonum</strong></td>
<td></td>
<td><strong>Asterophorum</strong></td>
<td>(4)</td>
<td>Brazilian Atlantic Forest</td>
</tr>
<tr>
<td></td>
<td></td>
<td>continued</td>
<td></td>
<td></td>
<td>Tuber-bearing shrubs with dilolate geminate sympodial growth, with broad-based prickles, simple leaf-opposed inflorescences with broadly stellate white corollas, and fruit with appressed calyces covering at least half of the fruit</td>
<td></td>
</tr>
<tr>
<td><strong>S. multispinum</strong></td>
<td>(1)</td>
<td>Rhizomatous small shrub covered in needle-like prickles, with white broadly stellate corollas, and yellow berries with prickly accrescent calyces that cover less than half of the fruit</td>
<td>Dry habitats of Argentina, Brazil and Paraguay</td>
<td></td>
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<tr>
<td><strong>Torva</strong> (55)</td>
<td></td>
<td>Shrubs, small trees or woody vines with mostly branched (and stout) inflorescences, with some needle-like or occasionally broad-based prickles, usually broadly stellate corollas, and fruits on stout pedicels often held upright, most species with mucilaginous pulp</td>
<td>Global (mostly tropical Americas, with a few members in Asia)</td>
<td></td>
<td></td>
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<tr>
<td><strong>S. euacanthum</strong></td>
<td>(1)</td>
<td>Herb covered in needle-like prickles and stellate glandular trichomes, with broadly stellate white corollas, and dehiscent fruits lacking mesocarp and “exploding” when ripe (probably from tension in the exocarp) with appressed calyces that cover more than half of the fruit</td>
<td>Dry habitats of subtropical Argentina</td>
<td></td>
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<tr>
<td><strong>Elaeagnifolium</strong></td>
<td>(5)</td>
<td>Rhizomatous shrubs or herbs with various degrees of both broad-based recurved and needle-like prickles, weakly bilaterally symmetric purple corollas with heteromorphic anthers and dry fruits, some with lepidote scales</td>
<td>Deserts and dry habitats in North and South America</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Eastern Hemisphere Spiny</strong> (EHS, 336)</td>
<td>Morphologically diverse group of shrubs, herbs, woody vines or small trees, mostly densely prickly (broad-based recurved and/or needle-like), some rhizomatous, many with appressed calyces that cover more than half of the fruit. Most prickly Solanum species outside the Americas are members of this clade</td>
<td>Africa, Madagascar, Asia, Australia, Pacific</td>
<td></td>
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</table>
displayed by the broad categories used in our analyses, with several losses and modifications of stellate trichomes within clades. For instance, the 2-celled geniculate trichomes in the Gonatotrichum clade with a short basal and longer apical cell are thought to represent reduced stellate trichomes (Seithe, 1979; Stern & al., 2013). This is an area of great promise for future research in developmental genetics. The widespread occurrence of glandular trichomes across the clades of Solanum provides an ideal system to test homology of genetic and developmental pathways beyond the Tomato clade. How the distinct trichome structures relate to the origin of prickles should also be further explored.

Our results on evolutionary trends in leaf division highlight that further exploration of genes linked to leaf shape patterning across Solanum would be interesting, where lineages with considerable polymorphism within individual plants (e.g., Dulcamaroidis) should be included following approaches in Brassicaceae (Vlad & al., 2014; Streubel & al., 2018; Nikolov & al., 2019). Perhaps most intriguingly, our results indicate continuous shifts in pollination-related floral traits (e.g., corolla shape and colour) in this buzz-pollinated genus, and the drivers of this variation should be explored further in species-level studies in Solanum in relation to diversification. Such studies should aim to quantify corolla shape to include corolla lobe orientation to enable more detailed studies of trait evolution at species level.

Our overview provides a framework for studying morphological evolution in Solanum and for designing future experiments. Data from molecular genetics will enable detailed understanding of pathways involved in evolution of each trait (Smith & al., 2020) and is still largely lacking for most traits. We emphasise, however, that many of the broad categories used in our study are oversimplifications of the continuous variation observed in Solanum, and confirmation of character homology will be needed in many places. This will include observations of developmental sequences from species across the clades in genus-wide investigations of the genetic/metabolic pathways of several key traits (e.g., leaf division, corolla and stamen bilateral symmetry, corolla colour, sexual systems). Studying morphological diversity in such a large and morphologically variable group as Solanum is challenging, and we hope that our overview provides a guide for next steps and a way to further target species for future study. Our results are limited by species sampling and resolution of our phylogeny: the number and position of the trait shifts will likely increase as sampling and resolution of the underlying phylogeny increases. Increased sampling is especially needed especially in the most diverse clades of Solanum (e.g., Brevantherum, Dulcamaroid, Geminata, Torva, and EHS clades) both in terms of species and genes to further refine and better understand phylogeny and evolution of this globally important genus.

**CONCLUSION**

Our analyses provide a systematic review and synthesis of morphological diversity in the large and economically important genus Solanum at clade level using the most up-to-date and well-sampled phylogeny, thus expanding on previous works both in terms of taxa and traits (see Knapp & al., 1998; Knapp, 2001, 2002c; Bohs & al., 2007). Traits related to plant structure (growth form and sympodial unit structure), plant defence (glandular trichomes), pollination (corolla shape and colour), and dispersal (fruit colour) are identified as the most evolutionarily labile traits in Solanum. Ten further traits relating to life form (specialised underground organs), defence (prickle type, trichome structure), leaf division, inflorescence position and branching, sexual system, stamen heteromorphism and fruit morphology show signal of evolutionary lability with 50–100 transitions observed across Solanum. Nine traits are more conserved and can be used to assemble combinations of traits that define informally named clades in the genus. Morphological definition of infrageneric clades in the mega-diverse and globally distributed Solanum will provide help with species-level identification as well as enabling us to place unsampled species more confidently into a phylogenetic context.

**AUTHOR CONTRIBUTIONS**

RH, SK and TS planned and led the research; RH led analyses with contributions from EG, SK, XA, EJT, LB, LG, and TS; SK, XA, EJT, LB, LG, YFG, CTO, CIO, IEP and TS generated data; RH and TS led the writing with strong steer from EG, SK, and XA and with significant contributions from all authors. — RH, https://orcid.org/0000-0003-3212-9688, edeline.gagnon@gmail.com; SK, https://orcid.org/0000-0001-7698-3945, s.knapp@nhm.ac.uk; XA, https://orcid.org/0000-0002-8112-0754, xavier.aubriot@universite-paris-naclay.fr; ET, https://orcid.org/0000-0002-8493-0736, eric.tepe@uc.edu; LB, https://orcid.org/0000-0003-2803-2656, bohs@biology.utah.edu; LG, https://orcid.org/0000-0001-8862-4042, giacomin.leandro@gmail.com; YG, https://orcid.org/0000-0002-7162-8458, goueveya.yf@gmail.com; CM, https://orcid.org/0000-0001-5143-1773, ctm015@bucknell.edu; AO, https://orcid.org/0000-0001-6789-3093, tsarkinen@rbge.org.uk.

**ACKNOWLEDGEMENTS**

We thank National Science Foundation (NSF) grant (to LB & SK) “PBI Solanum – a world treatment” DEB-0316614, Sibbald Trust Fellowship (to RH), the Fundación Ceiba and the GEMElab (Agreement 566 from 2014 between the Universidad Nacional de Colombia [https://unal.edu.co] and Colciencias [now called Minciencias https://minciencias.gov.co]) (to AO), and CNPq (427198/2016-0 and 422191/2021-3) and FAPESP/CAPES (Proc. AUXPE 88881.159124/2017-01 to LG) for funding and supporting the research; Rocío Deanna for discussions about character states; and João Renato Stehmann, Richard Olmstead, and Stacey Smith for critical yet insightful comments that helped to enhance the manuscript. We thank the following people for comments: Michael Benedito, Rocío Deanna, Martin Gardner, Paulina Hechenleiter, David Rae, Pedro Acevedo Rodriguez, Mario Vallejo-Marín, and Maria S. Vorontsova.
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