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Rebecca Hilgenhof

Edeline Gagnon

Sandra Knapp

Xavier Aubriot

Eric Tepe

See next page for additional authors

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Authors

Rebecca Hilgenhof, Edeline Gagnon, Sandra Knapp, Xavier Aubriot, Eric Tepe, Lynn Bohs, Leandro Giacomini, Yuri Gouvea, Andres Orejuela, Christopher T. Martine, Clara Ines Orozco, Iris E. Peralta, and Tina Sarkinen

RESEARCH ARTICLE

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

Rebecca Hilgenhof,^{1,2} Edeline Gagnon,^{1,3} Sandra Knapp,⁴ Xavier Aubriot,⁵ Eric J. Tepe,⁶ Lynn Bohs,⁷ Leandro L. Giacomini,⁸ Yuri F. Gouvêa,⁹ Christopher T. Martine,¹⁰ Andrés Orejuela,^{1,11} Clara Inés Orozco,¹² Iris E. Peralta,¹³ & Tiina Särkinen¹

1 Royal Botanic Garden Edinburgh, 20a Inverleith Row, Edinburgh EH3 5LR, United Kingdom

2 University of Edinburgh, School of Biological Science, King's Buildings Campus, W Mains Rd, Edinburgh EH9 3JW, United Kingdom

3 TUM School of Life Sciences, Technical University of Munich, Emil-Ramann-Str. 2, 85354 Freising, Germany

4 Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom

5 Université Paris-Saclay, CNRS, AgroParisTech, Écologie, Systématique et Évolution, 91405 Orsay, France

6 University of Cincinnati, Department of Biological Sciences, Cincinnati, Ohio 45221, U.S.A.

7 University of Utah, Department of Biology, 257 South 1400 East, Salt Lake City, Utah 84112, U.S.A.

8 Departamento de Sistemática & Ecología, CCEN, Universidade Federal da Paraíba, Cidade Universitária, João Pessoa 58051-900, Paraíba, Brazil

9 Departamento de Botânica, ICB, Universidade Federal de Minas Gerais, Av. Antônio Carlos 6627, Belo Horizonte 31270-901, Minas Gerais, Brazil

10 Department of Biology, Bucknell University, 1 Dent Drive, Lewisburg, Pennsylvania 17837, U.S.A.

11 Max Planck Tandem Group, Facultad de Ciencias, Universidad Nacional de Colombia, Bogotá D.C., Colombia

12 Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá D.C., Colombia

13 Faculty of Agricultural Sciences, National University of Cuyo, Almirante Brown 500, 5505 Chacras de Coria, Luján, Mendoza, Argentina; and IADIZA CCT CONICET Mendoza, Argentina

Address for correspondence: Tiina Särkinen, tsarkinen@rbge.org.uk

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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 50–100 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).

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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., Tingey & Gibson, 1978; Tingey & Laubengayer, 1981; Avé & Tingey, 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 dioecy 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 poricidally dehiscent anthers (Fig. 1M–R,T,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 monophyletic groups (Fig. 2) (Bohs, 2005; followed by subsequent studies, e.g., Stern & al., 2011; Särkinen & 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 heteromorphism and/or anther 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 *Thelopodium* clade consisting of three species sister to the rest of *Solanum*; (2) Grade I, previously referred to as Clade I (Särkinen & 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, Archaeosolanum, Normania, and African non-spiny), DulMo (Dulcamaroid and Morelloid), Regmandra, and the Potato clade, which includes several economically important minor clades (e.g., Tomato, Petota, Etuberosum, Basarthrum; 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 homoplasy (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. brevifolium* Dunal); **C**, Woody vine (Tomato clade, *S. juglandifolium* Dunal); **D**, Single-stemmed shrub (Pteroides 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. arcanum* Peralta); **J**, Stellate glandular trichomes (Erythrotrichum clade, *S. aciculare* Sw.); **K**, Needle-like prickles on calyx (EHS clade, *S. dasyphyllum* Schumach. & Thonn.); **L**, Broad-based prickles on trunk (Crinitum clade, *S. kioniotrichum* Bitter ex J.F.Macbr.); **M**, Homomorphic stamens, most common state in *Solanum* (Anarrhichomenum clade, *S. appendiculatum* Dunal); **N**, Apical and basal anther modifications (i.e., horn-like projections; Normania clade, *S. trisectum* Dunal); **O**, Apical anther modifications (i.e., appendages; Tomato clade, *S. corneliomulleri* J.F.Macbr.); **P**, Enlarged anther connectives (Pachyphylla clade, *S. betaceum* Cav.); **Q**, Deeply stellate purple corollas (Pachyphylla clade, *S. sycocarpum* Mart. & Sendtn.); **R**, Broadly stellate purple corollas (EHS clade, *S. linnaeanum* Hepper & P.-M.L.Jaeger); **S**, Rotate purple corollas with abundant interpetalar tissue (Herpystichum clade, *S. trifolium* Dunal); **T**, Deeply stellate yellow-green corollas lacking interpetalar tissue (Pteroides clade, *S. anceps* Ruiz & Pav.); **U**, Campanulate pale lilac corollas (Morelloid clade; *S. fiebrigii* Bitter); **V**, Urceolate white-purple corollas (Pachyphylla clade, *S. diversifolium* Dunal); **W**, Bilaterally symmetric corollas with heteromorphic anthers (Normania clade, *S. trisectum* Dunal); **X**, Bilaterally symmetric corollas with heteromorphic anthers (Androceras clade; *S. grayi* Rose var. *grandiflorum* Whalen); **Y**, Obovoid, apically pointed fleshy berries (Thelopodium clade, *S. thelopodium* Sendtn.); **Z**, Globose fleshy berries with colour variation through maturation from yellow (unripe) to red (fully mature; Cyphomandropsis clade, *S. amotapense* Svenson); **AA**, Globose orange berries (Reductum clade, *S. reductum* C.V.Morton); **AB**, Globose black berries (Morelloid clade, *S. longifilamentum* Särkinen & P.González); **AC**, Obovoid, apically pointed brown berries (Herpystichum clade, *S. limoncochaense* Tepe); **AD**, Globose blue berries (Dulcimaroid clade, *S. flaccidum* Vell.). — Photo vouchers: A, Särkinen & al. 4038; B, Tepe & al. 3061; C, Fajardo & al. 3998; D, Särkinen & al. 4822; E, Knapp & al. 10594; F, Tepe & al. 2327; G, Särkinen & al. 4524; H, Knapp & al. 10336; I, Särkinen & al. 4503; J, Gouvêa 280; K, Vorontsova & al. 151; L, Melchor Castro & González 1446; M, Knapp & al. 10156; N, Nijmegen 984750158; O, Knapp & al. 10212; P, Tepe s.n.; Q, Bohs s.n.; R, Knapp s.n.; S, Tepe & al. 2684; T, Fajardo & al. 3982; U, Barboza & al. 3548; V, Bohs 2341 (cult. from seeds of Benítez de Rojas 2744); W, cult. Madeira, no collection voucher; X, Vallejo-Marín 08-s-78; Y, Melchor Castro & González 1454; Z, Särkinen & al. 4508; AA, Barboza & al. 3516; AB, Särkinen s.n.; AC, Tepe & al. 2627; AD, Giacomini & al. 1737. Photographs by S. Knapp (E, H, M, N, R, O, U, AA), T. Särkinen (A, C, D, G, I, T, Z, AB), P. González Arce (L, Y), E. Tepe (B, F, K, P, S, AC), L. Bohs (Q, V), Y.F. Gouvêa (J), M. Vallejo-Marín (X), M. Benedito (W), and L. Giacomini (AD).

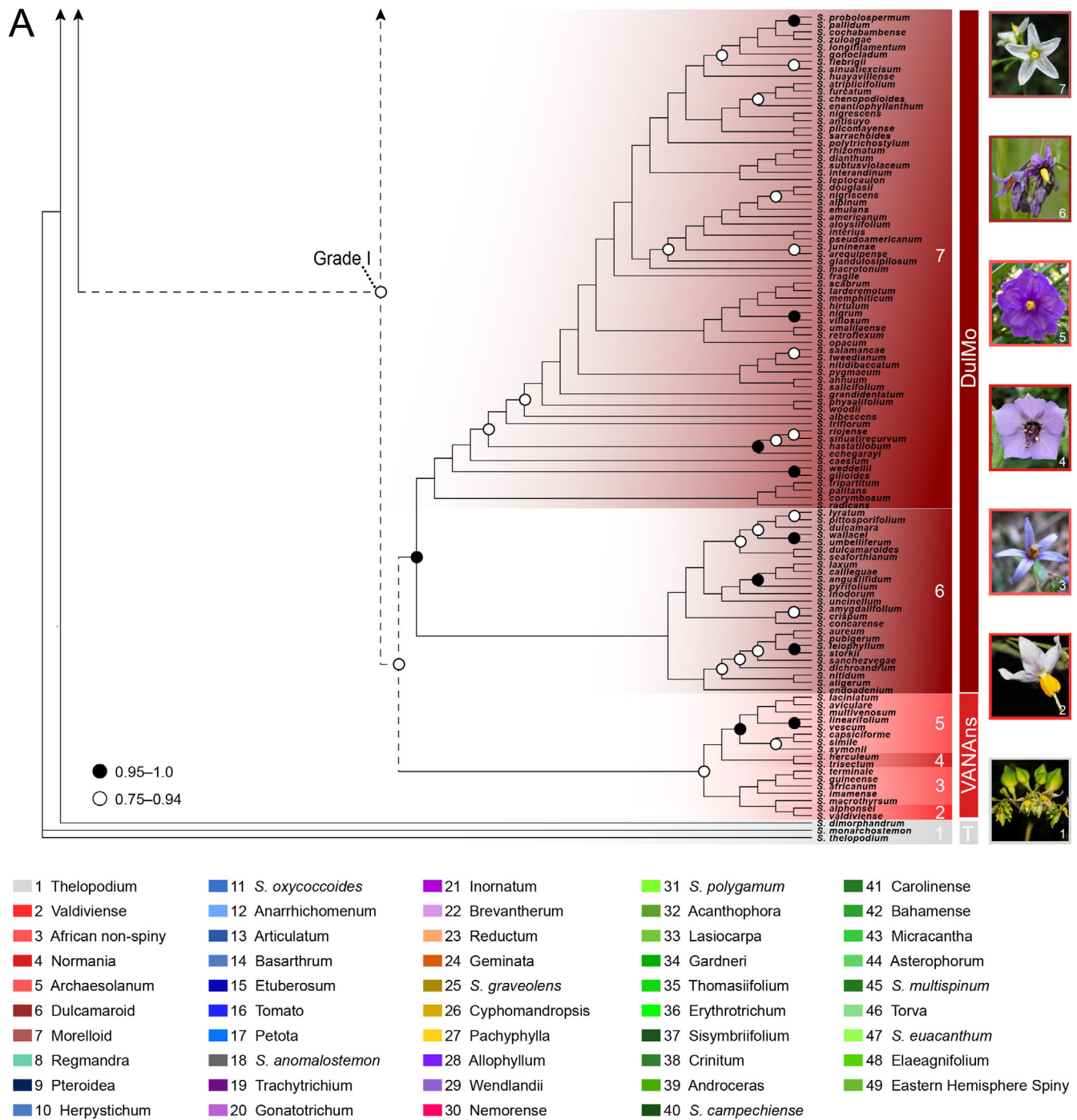


Fig. 2. Phylogeny of *Solanum* highlighting the informally named infrageneric clades based on Bayesian analysis of 742 *Solanum* species (60% of total known diversity) with two nuclear and seven plastid regions by Gagnon & al. (2022). Infrageneric clades are colour-coded and numbered reflecting the currently 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 (Regmandra, Pteroidea, Herpystichum, *S. oxycoccoides*, 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. euacanthum*, 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

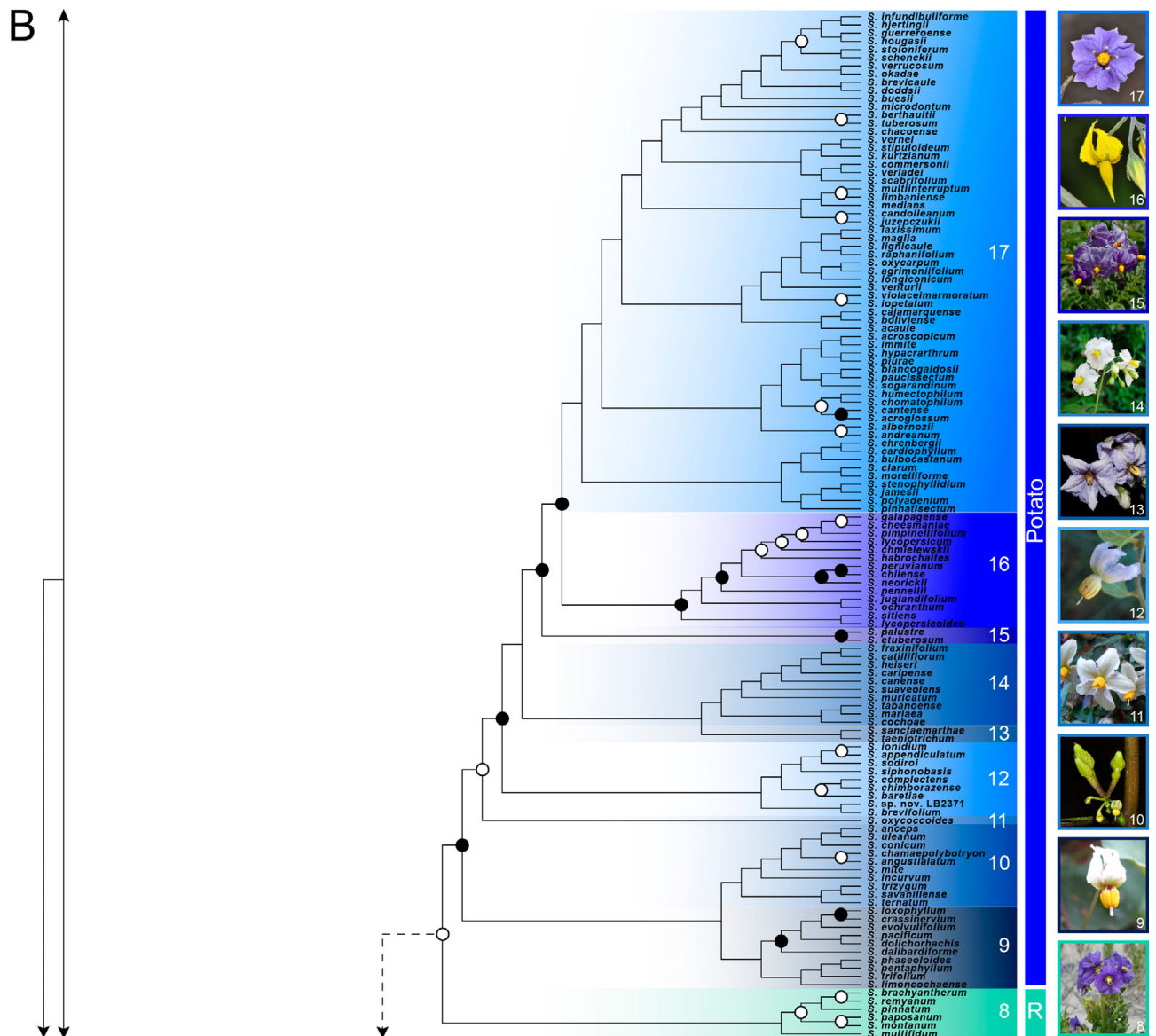


Fig. 2. Continued.

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 & al., 2007). Other reproductive characters that have been suggested as useful for *Solanum* taxonomy are presence of swollen anther connectives (D’Arcy & al., 1990; Bohs, 1994; Cocucci, 1996), anther shape (Knapp, 2001; Bohs, 2005), pedicel insertion and articulation (Knapp, 2001, 2013; Tepe & al., 2016), fruit type (Symon, 1979a, 1984; Whalen, 1984; Knapp, 2001, 2002b; Chiarini & Barboza, 2007), and stone cells (Symon, 1994; Knapp, 2002b;



Fig. 2. Continued.

Särkinen & al., 2018; Knapp & al., 2019, in press). Corolla shape and colour, fruit type and colour, fruiting calyx modifications (e.g., inflated fruiting calyces), and the presence of trichomes on mature fruits have been less frequently used in defining clades but may offer additional characters for unique trait combinations at clade level.

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

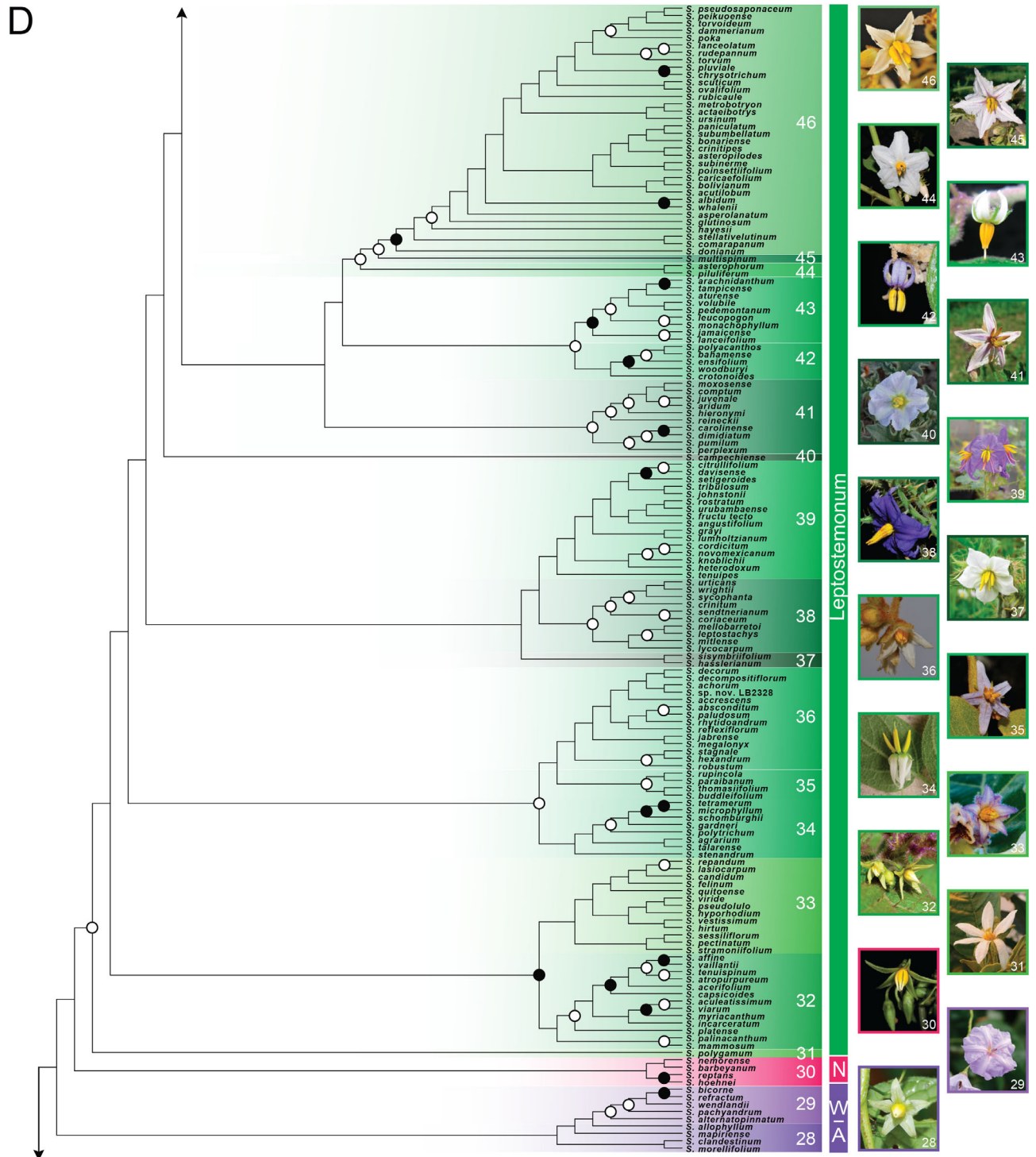


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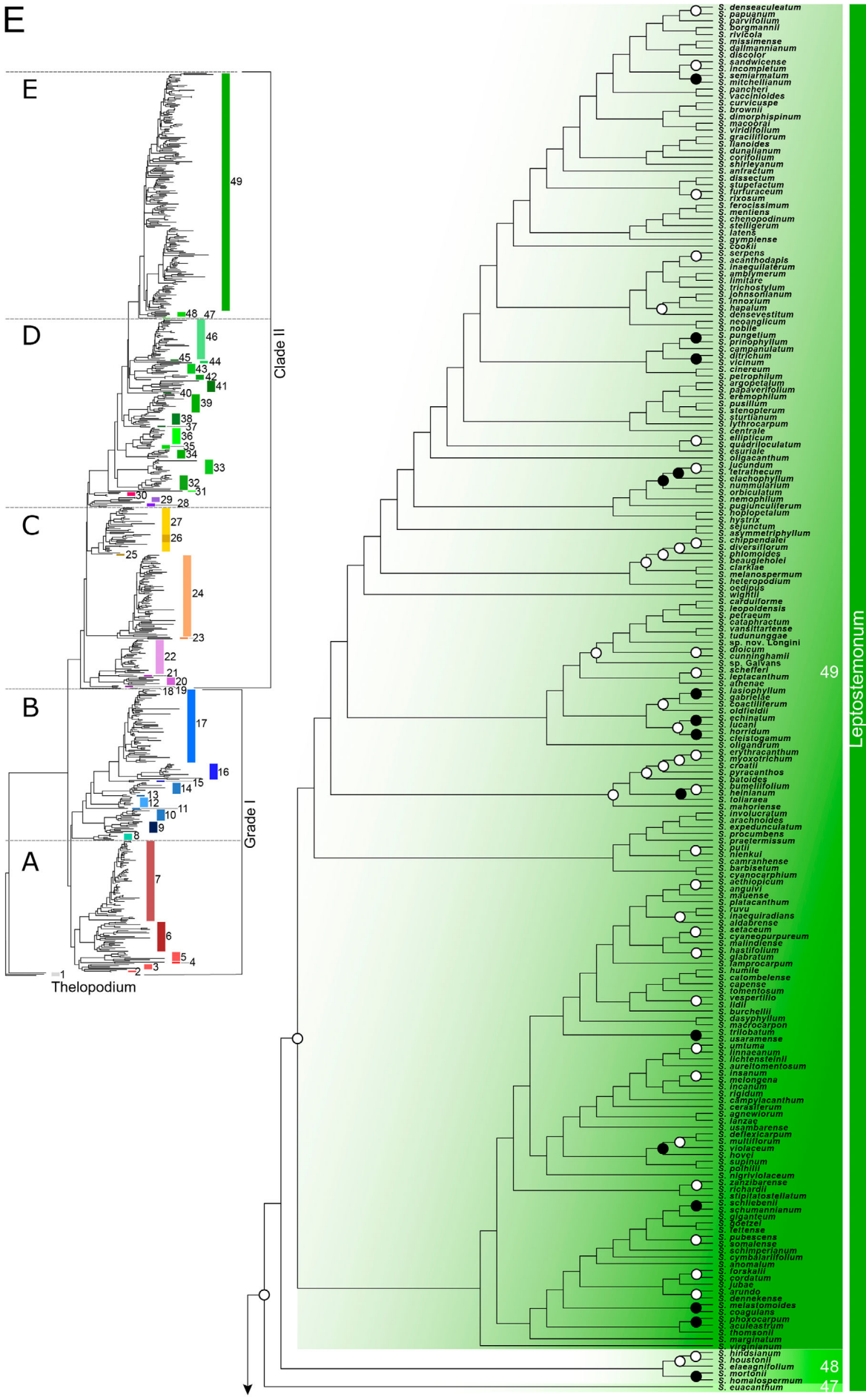


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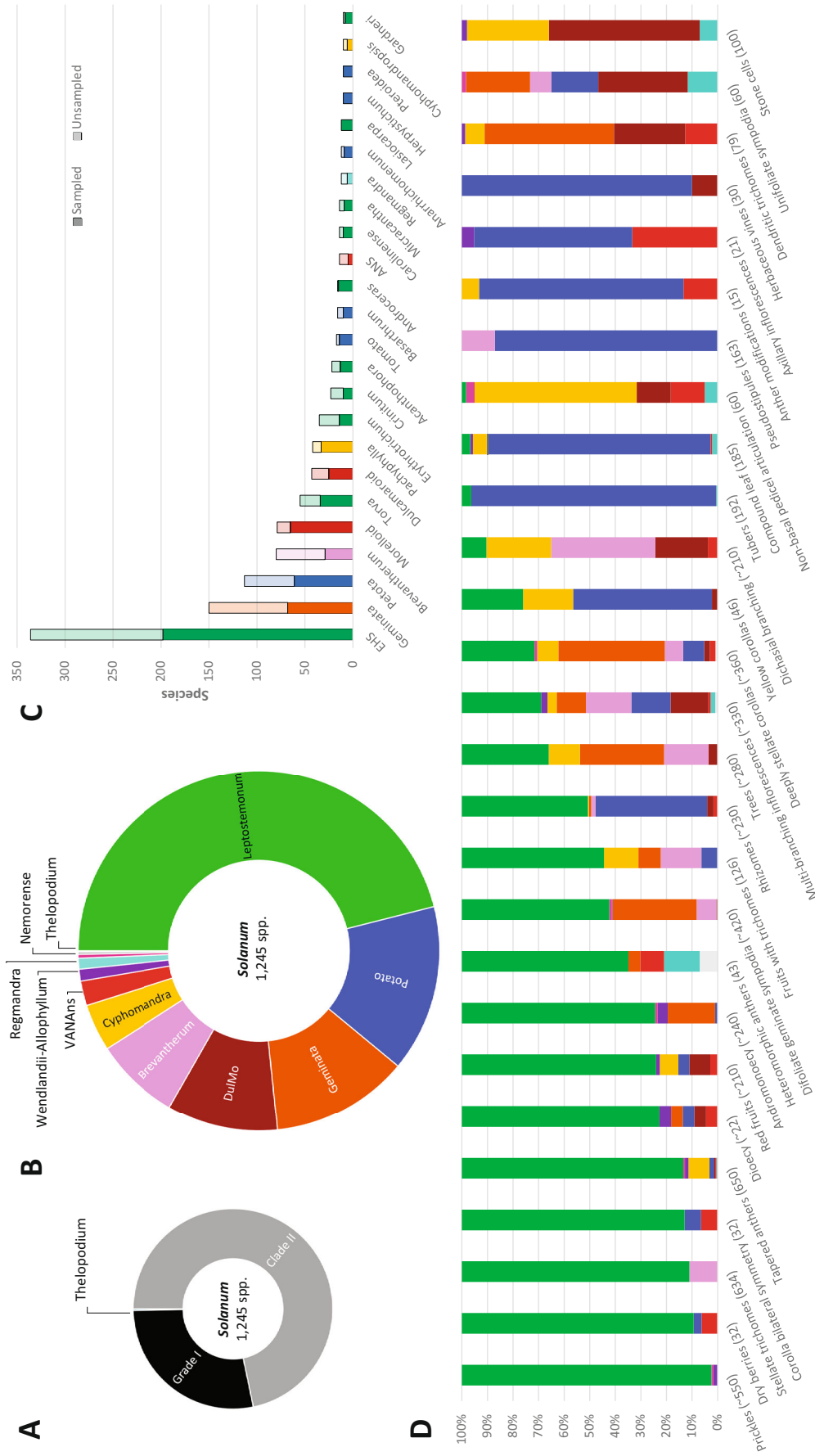


Fig. 3. Overview of morphological diversity across *Solanum* and the informally named infragenetic groups referred to as major and minor clades. **A**, Division of *Solanum* into three main lineages with a graphical summary of species diversity within these large groups; **B**, Species diversity across 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”).

(3) providing morphological descriptions for all *Solanum* clades. Our study is inspired by the dynamic research community working on *Solanum* continuously generating new knowledge on morphological and genotypic diversity as well as unravelling the molecular mechanisms that control the genotype-phenotype interactions across the genus. More than 100 new species have been described in *Solanum* over the past 10 years (e.g., Tepe & Bohs, 2009; Bean, 2014; Giacomini & Stehmann, 2014; Stern & al., 2014; Knapp & al., 2015, 2020; Särkinen & al., 2015a,b,c; Bean, 2016a,b; Martine & al., 2016; Särkinen & Knapp, 2016; Knapp & Särkinen, 2018; Gouvêa & Stehmann, 2019; Aubriot & Knapp, 2022), revealing new traits and trait combinations. This, coupled with the densely sampled molecular phylogeny, provides an ideal opportunity to study the origin and evolution of major vegetative and reproductive traits in this agronomically important genus, and to assess/confirm diagnostic traits for *Solanum* clades using a formal analysis with standardised terminology. Results are discussed in relation to previous evolutionary and developmental hypotheses, and new morphological hypotheses of trait evolution and homology are proposed that could be tested with further studies and new tools.

■ 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).

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 all unbranched trichomes including 2-celled “bayonet” trichomes (Fig. 1G) (Seithe & Anderson, 1982). All branched or forked trichomes and echinoid dendritic 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-angulate 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 cosexual (i.e., hermaphroditic). Three states of corolla shape were recognised reflecting the amount of interpetalar tissue between lobes: deeply stellate corollas without apparent interpetalar tissue (i.e., deeply stellate, Fig. 1P,Q,T), and two states with increasing amount of interpetalar 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

Table 1. Results of the ancestral trait reconstruction analyses (stochastic mapping) of 25 morphological traits across *Solanum*.

Trait	States	Best model based on AIC	Observed mean number of transitions (95% HPD)	Results	Main references used for scoring states (see full list in suppl. Table S2)
1. Growth form	Herb, shrub, single-stemmed shrub, tree, herbaceous vine, woody vine, epiphyte	ARD	110 (65–166)	Highly evolutionarily labile with >100 transitions	
2. Specialised underground organs	Absent, rhizomes, underground storage organs	ARD	64 (51–78)	Evolutionarily labile with 50–100 transitions	Spooner & al., 2004, 2016, 2019; Bennett, 2008; Knapp & al., 2017
3. Prickles	Absent, broad-based, needle-like	ARD	82 (62–100)	Evolutionarily labile with 50–100 transitions	Seithe, 1962, 1979; Clark & al., 2015
4. Trichome structure	Absent, simple, stellate, dendritic	ARD	93 (66–125)	Evolutionarily labile with 50–100 transitions	Seithe, 1962, 1979; Roe, 1971; Seithe & Anderson, 1982; Freire de Carvalho & Machado, 1991; Giacomini & Stehmann, 2011; Stern & Bohs, 2012; Watts & Kariyat, 2022
5. Glandular trichome type	Absent, simple glandular, stellate glandular	ARD	210 (158–265)	Highly evolutionarily labile with >100 transitions	Peralta & al., 2008; Kang & al., 2014; Watts & Kariyat, 2022
6. Pseudostipules	Absent, present (single), present (pair)	SYM	9 (7–11)	Highly conserved with <10 transitions	Spooner & al., 2004, 2016, 2019; Peralta & al., 2008
7. Sympodial unit structure	Plurifoliate, trifoliate, difoliate non-geminate, difoliate geminate, unifoliate	ARD	215 (151–277)	Highly evolutionarily labile with >100 transitions	Danert, 1958; Child, 1979
8. Leaf division (i.e., type)	Simple, lobed, compound	ARD	73 (63–84)	Evolutionarily labile with 50–100 transitions	Geeta & al., 2012
9. Inflorescence position	Terminal, internodal, axillary, leaf-opposed, spur-shoots	SYM	93 (67–118)	Evolutionarily labile with 50–100 transitions	Danert, 1958; Child, 1979
10. Inflorescence branching	Unbranched, forked, multi-branched	ARD	90 (61–116)	Evolutionarily labile with 50–100 transitions	Lippman & al., 2008
11. Sexual system	Cosexual (hermaphroditic), andromonoecious, dioecious	ARD	88 (72–106)	Evolutionarily labile with 50–100 transitions	Symon, 1970, 1979a,b; Levine & Anderson, 1986; Whalen & Costich, 1986; Anderson & Symon, 1989; Knapp & al., 1998; Dupont & Olesen, 2006; Anderson & al., 2015; Ndem-Galbert & al., 2021
12. Corolla shape	Deeply stellate, broadly stellate, rotate	SYM	271 (214–334)	Highly evolutionarily labile with >100 transitions	
13. Corolla bilateral symmetry	Present, absent	ARD	15 (12–21)	Conserved with 10–49 transitions	Bohs & al., 2007
14. Corolla colour	White, green, purple, yellow	ARD	180 (120–234)	Highly evolutionarily labile with >100 transitions	Passarelli & Bruzzone, 2004
15. Stamen heteromorphism	Absent, anther, filament	ARD	51 (24–71)	Evolutionarily labile with 50–100 transitions	Bohs & al., 2007

(Continues)

Table 1. Continued.

Trait	States	Best model based on AIC	Observed mean number of transitions (95% HPD)	Results	Main references used for scoring states (see full list in suppl. Table S2)
16. Anther connectives	Enlarged, not enlarged	ARD	8 (7–11)	Highly conserved with <10 transitions	D’Arcy & al., 1990; Bohs, 1994; Cocucci, 1996
17. Anther modifications	Absent, appendage, horn, beak, sack	ER	7 (5–9)	Highly conserved with <10 transitions	Francisco-Ortega & al., 1993; Peralta & al., 2008; Knapp & Nee, 2009; Barboza, 2013
18. Anther shape	Cylindrical, tapered, cordate	SYM	12 (11–14)	Conserved with 10–49 transitions	
19. Pedicel insertion	Flat, cup-shaped	ER	2 (2–2)	Highly conserved with <10 transitions	
20. Pedicel articulation	Basal, near-basal, basal 1/4–1/2, distal 1/2, absent	ER	10 (8–12)	Conserved with 10–49 transitions	
21. Fruit type	Fleshy, dry	ER	14 (13–15)	Conserved with 10–49 transitions	Symon, 1979a, 1984; Whalen, 1984; Knapp, 2002b; Chiarini & Barboza, 2007
22. Fruit colour	Green, white, purple, yellow, orange, red	ARD	286 (166–298)	Highly evolutionarily labile with >100 transitions	Peralta & al., 2008; Dhar & al., 2015
23. Fruit trichomes	Absent, present	ARD	68 (45–88)	Evolutionarily labile with 50–100 transitions	
24. Fruiting calyx modifications	Absent, appressed, inflated, swollen	ARD	62 (53–73)	Evolutionarily labile with 50–100 transitions	
25. Stone cells	Absent, present	ARD	42 (36–49)	Conserved with 10–49 transitions	Bitter, 1911, 1914; Symon, 1994; Knapp, 2002b; Särkinen & al., 2018; Knapp & al., 2019, in press

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.

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 rhachis. 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, intermediately mature fruits

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 clades 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) in *phytools*. The root state was treated as equally likely for all characters ($\pi = \text{equal}$), as this is the best approach here because full nuclear genome sequences show strong gene discordance with respect to the sister relationship of *Jaltomata* and *Solanum* (Wu & al., 2018b): These data resolve the sister lineage to *Solanum* as ambiguous, either tribe Capsiceae (c. 20% gene trees), *Jaltomata* (c. 38% gene trees), or Capsiceae + *Jaltomata* (c. 42% gene trees). Stochastic mapping was simulated with 200 generations to obtain a posterior probability distribution of ancestral states across the tree. The mean number of transitions per trait was determined based on the best-fitting model.

Evolutionary lability was measured based on mean number of transitions (i.e., shifts) modelled across the phylogeny, where traits with >100 transitions were considered highly labile, traits with 50–100 transitions as labile, traits with 10–49 as conserved, and traits with <10 as highly conserved. We focused on the mean number of transitions because we found these results stable for rare terminal states under the ARD model, compared to evolutionary rates that appeared highly elevated in some of these rare terminal states.

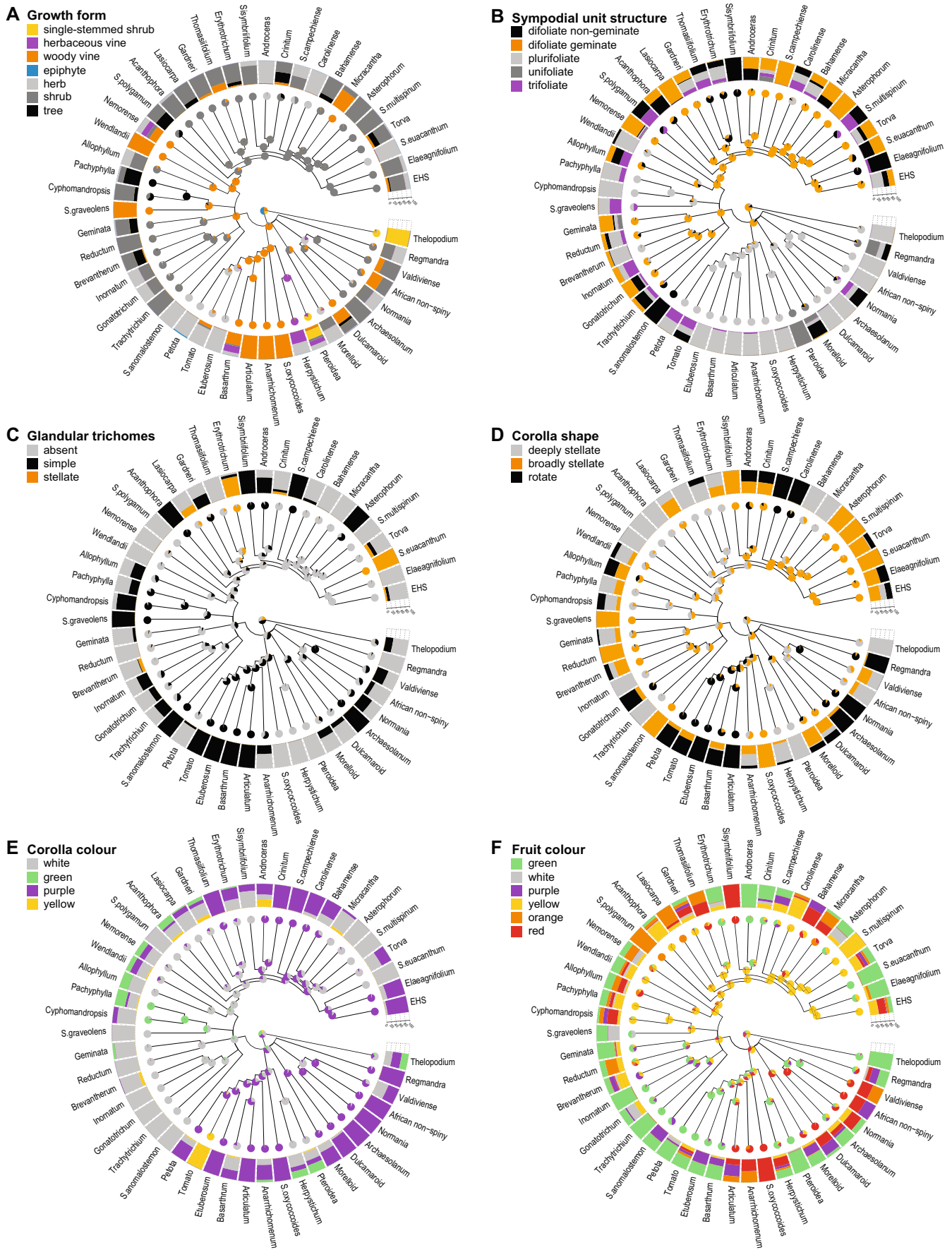
■ RESULTS

Our results show large variation in the evolutionary lability of the 25 traits we explored. Six traits were recognised as highly evolutionarily labile, ten as labile, five as conserved, and four as highly conserved based on the mean number of transitions (Table 1). We carefully inspected our results for state reconstruction artefacts relating to rare terminal states, and detected no artefacts in the mean number of transitions but elevated evolutionary rates in some (e.g., epiphyte and single-stem shrub states under growth form, unifoliate sympodial units state under sympodial unit structure, and stellate state under glandular trichome type); hence, our results section focuses on the mean number of transitions as a measure of evolutionary lability/conservatism, and we highlight that evolutionary rate results for rare

terminal states should be interpreted with caution (suppl. Table S4).

Six traits show >100 mean shifts across *Solanum* indicating high evolutionary lability. These relate to plant structure (growth form and sympodial unit structure), herbivore defence (glandular trichomes), pollination (corolla shape and colour), and dispersal (fruit colour) (Table 1; suppl. Table S4; Fig. 4). Shifts between herbaceous and woody growth forms (shrubs, woody vines, and trees) are frequent 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 difoliate geminate structure being modelled as ancestral in *Solanum* (Fig. 4B). Plurifoliate sympodial units dominate in Grade I and difoliate (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 interpetalar tissue present (Fig. 4D). Colour in both corollas and fruits shows high evolutionary lability, with 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 *Nemorense* 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 I 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 regains. 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 cordate anthers have two independent origins (Fig. 7B; suppl. Table S4). Fruiting pedicels abscise at the basal junction between pedicel and inflorescence rhachis 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; Bogarín & 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

Fig. 4. Evolution of the most highly labile morphological traits in *Solanum* with >100 transitions based on species-level analysis using stochastic character mapping. **A**, Growth form; **B**, Sympodial unit structure; **C**, Glandular trichomes; **D**, Corolla shape; **E**, Corolla colour; **F**, Fruit colour. 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.

defining particular clades when rare states are expressed and if used in combination (e.g., axillary inflorescences in Pterioidea 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 Nemorensis clade (*S. hoehnei* C.V.Morton, Fig. 4A), while woody growth forms predominate in

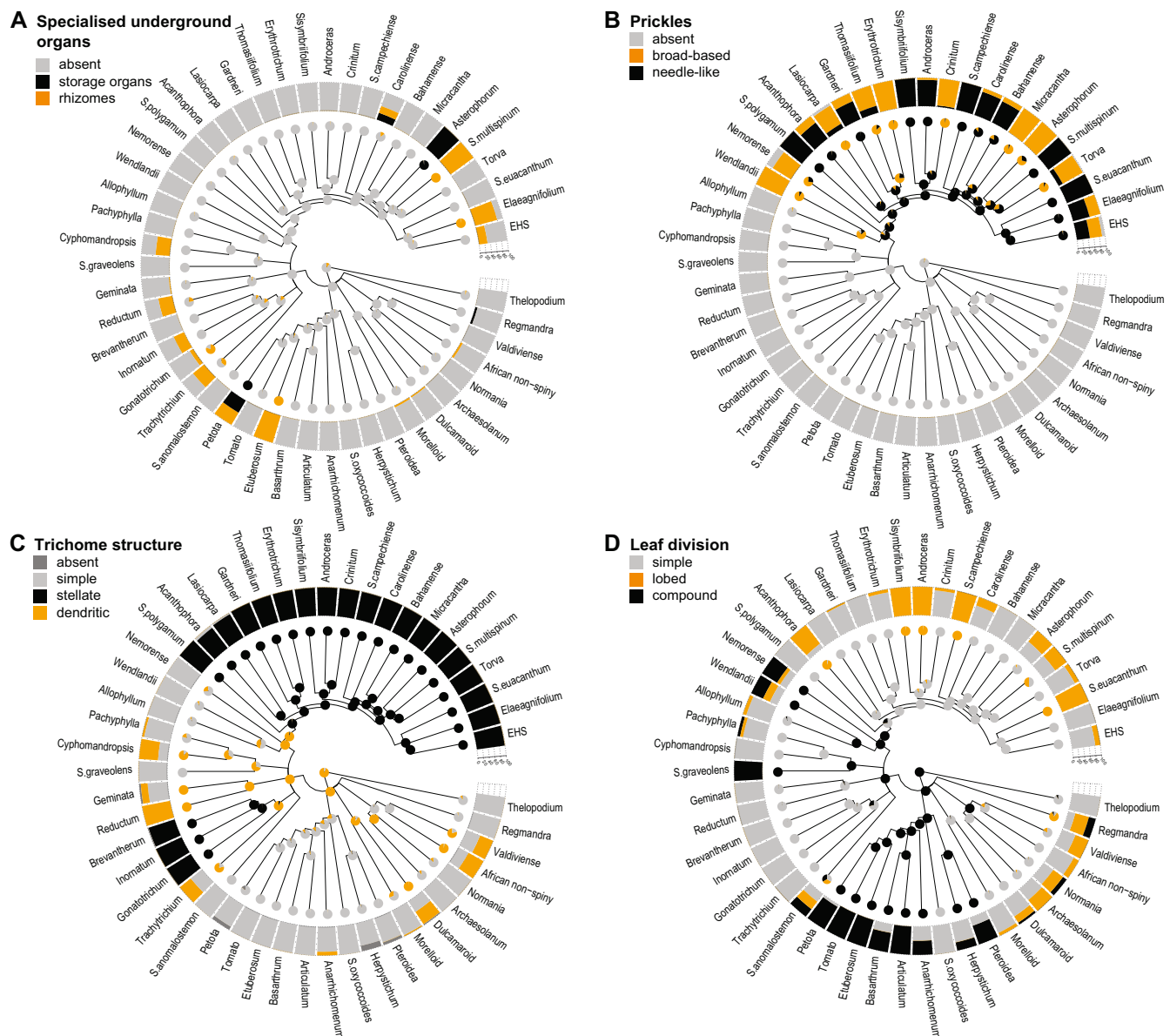


Fig. 5. Evolution of labile morphological traits (vegetative) in *Solanum* with 50–100 transitions based on species-level analysis using stochastic character mapping. **A**, Specialised underground organs; **B**, Prickles; **C**, Trichome structure; **D**, Leaf division. Results from the best model are 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*. Sympodial 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 above-ground 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; Särkinen & 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 (Schillmiller & 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 prickly-like with an apical stellate trichome (Vorontsova & Knapp, 2016; Aubriot & Knapp, 2022). Previous studies have proposed glandular trichomes to be involved in prickly 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 prickly type and density observed within species and individuals shows that prickly 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. elaeagnifolium* 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 prickly 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., *Herpystichum*, *Pterioidea*, *Anarrhichome-num*, *Basarthrum*, 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 & 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 *Pachyphylla* 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 documented 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 & 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 phylogenomic sampling (Gagnon & 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 & al., 2002; Efroni & al., 2010).

Floral traits. — Two traits linked to pollinator attraction, corolla shape and colour (Møller, 1995; Gómez & al., 2008, 2016; Muchhala & al., 2014; Reverte & al., 2016; Moré & 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 interpetalar tissue present between lobes, and changes seem frequent throughout the genus highlighting the need to explore pollinator-linked trait variation in buzz-pollinated plant groups.

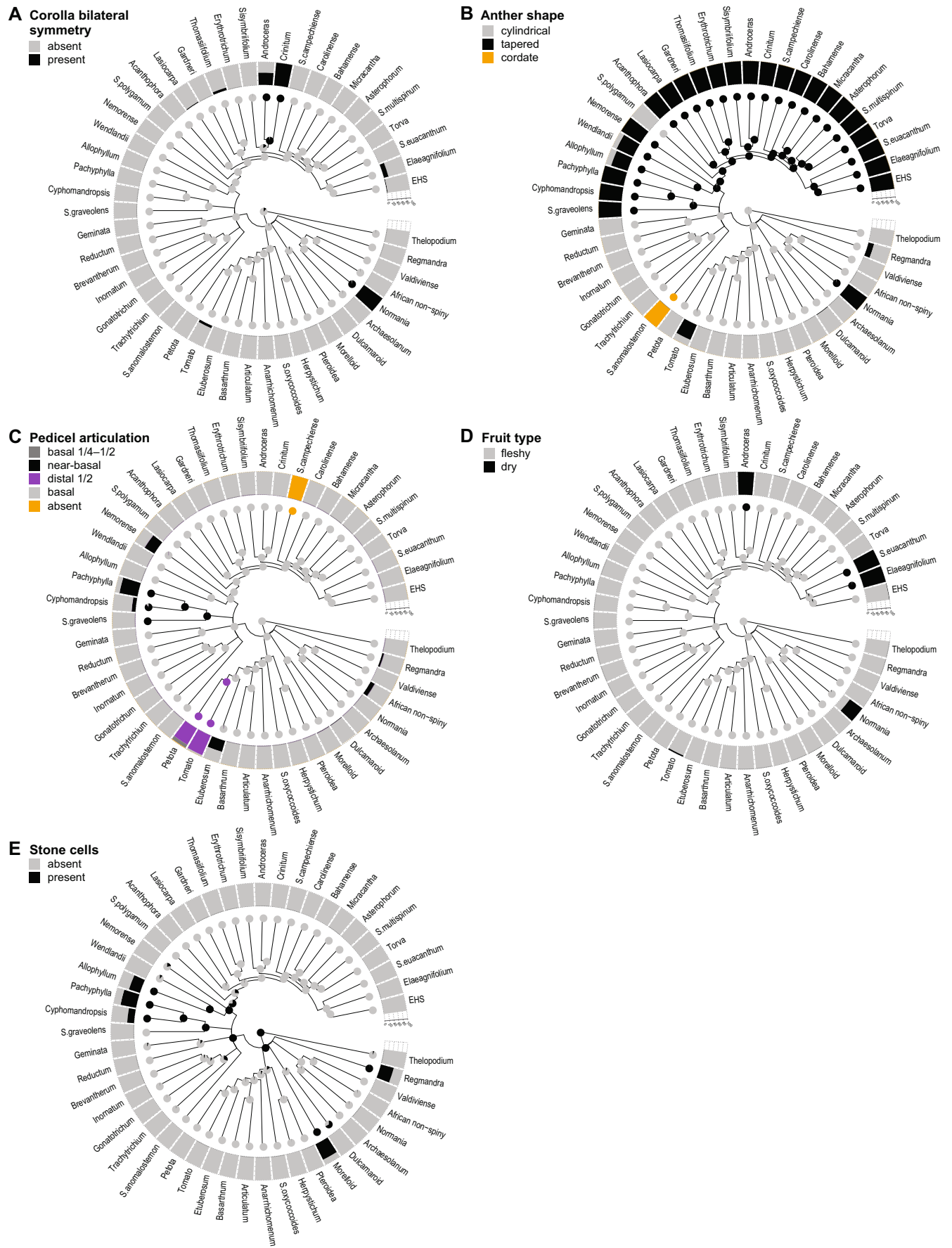
Shifts between purple and white dominate in *Solanum* with >66 gains of purple corollas (Fig. 4E). Transitions to yellow are rare with a minimum of five independent origins of yellow corollas, twice from white ancestors. A similar pattern has been found in tribe *Antirrhineae* (*Plantaginaceae*), where transitions from purple to yellow have been found to have occurred 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 control of corolla colouration (e.g., Gates & al., 2018) has not been studied in *Solanum*, but flavonoids (anthocyanins: purple; flavones: yellow) and carotenoids (yellow) are components of corolla colouration in other genera of *Solanaceae* (*Iochroma* Benth.: Berardi & al., 2016; Larter & al., 2019; *Nicotiana* L.: McCarthy & al., 2017; *Petunia* Juss.: Berardi & al., 2021). We did not record the presence of multiple colours 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 & al., 2000; Dyer & al., 2006, 2007).

Our results indicate that the general floral “bauplan” in *Solanum* has changed several times independently despite the relative morphological homogeneity in *Solanum* flowers based on the buzz-pollination syndrome with poricidally dehiscent anthers arranged in a central cone. Changes include a minimum of 13 origins of heteromorphic anthers, 8 origins of heteromorphic filaments (Fig. 6D), 7 origins of bilaterally symmetric corollas (Fig. 7A), and 5 independent origins of anther modifications (Fig. 8C). Bilaterally symmetric corollas have evolved largely in clades with heteromorphic anthers (*Leptostemonum*; Figs. 6D, 7A; Lester & al., 1999; Knapp, 2002b, 2010; Bohs & 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 bilaterally symmetric corollas (Zhang & al., 2017). Genes controlling corolla bilateral symmetry (and heteromorphic anthers) in *Solanum* have not yet been identified, but the trait is likely to affect pollination by increasing pollinator specificity and efficiency (Jesson & Barrett, 2002, 2005; Fenster & 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 & al., 1993; Bohs, 1994; Cocucci, 1996, 1999; Falcão & Stehmann, 2018). Taken together, our results indicate continuous shifts in pollination-related floral traits in a buzz-pollinated genus.

Fruit morphology. — *Solanum* is well-known for variation 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 & 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 & 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.



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-acrescent to acrescent (appressed) and inflated fruiting calyces but also indicate a second path from non-acrescent directly to inflated (suppl. Table S4). Fruiting calyx modifications (Table 1; Fig. 6F) enable physical dispersal mechanisms, for example where prickly acrescent fruiting calyces around dry berries act as trample-burrs or censer fruits where seeds shake out of the open end of the acrescent calyx with plant movement (e.g., *S. euacanthum* Phil., *Elaeagnifolium*, *Androceras* 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. sycophanta* Dunal), and explosively dehiscent fleshy berries (e.g., all species of the Gonatotrichum clade; Knapp, 2001, 2002c; Stern & al., 2013; *S. mellobarretoii* Agra & 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 (Anarrichomenum 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 staminate flowers and pistillate flowers in more or less equal proportions to strongly andromonoecious species with

Fig. 7. Evolution of conserved morphological traits in *Solanum* with 10–49 transitions based on species-level analysis using stochastic character mapping. **A**, Corolla bilateral symmetry; **B**, Anther shape; **C**, Pedicel articulation; **D**, Fruit type; **E**, Stone cells. 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.

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

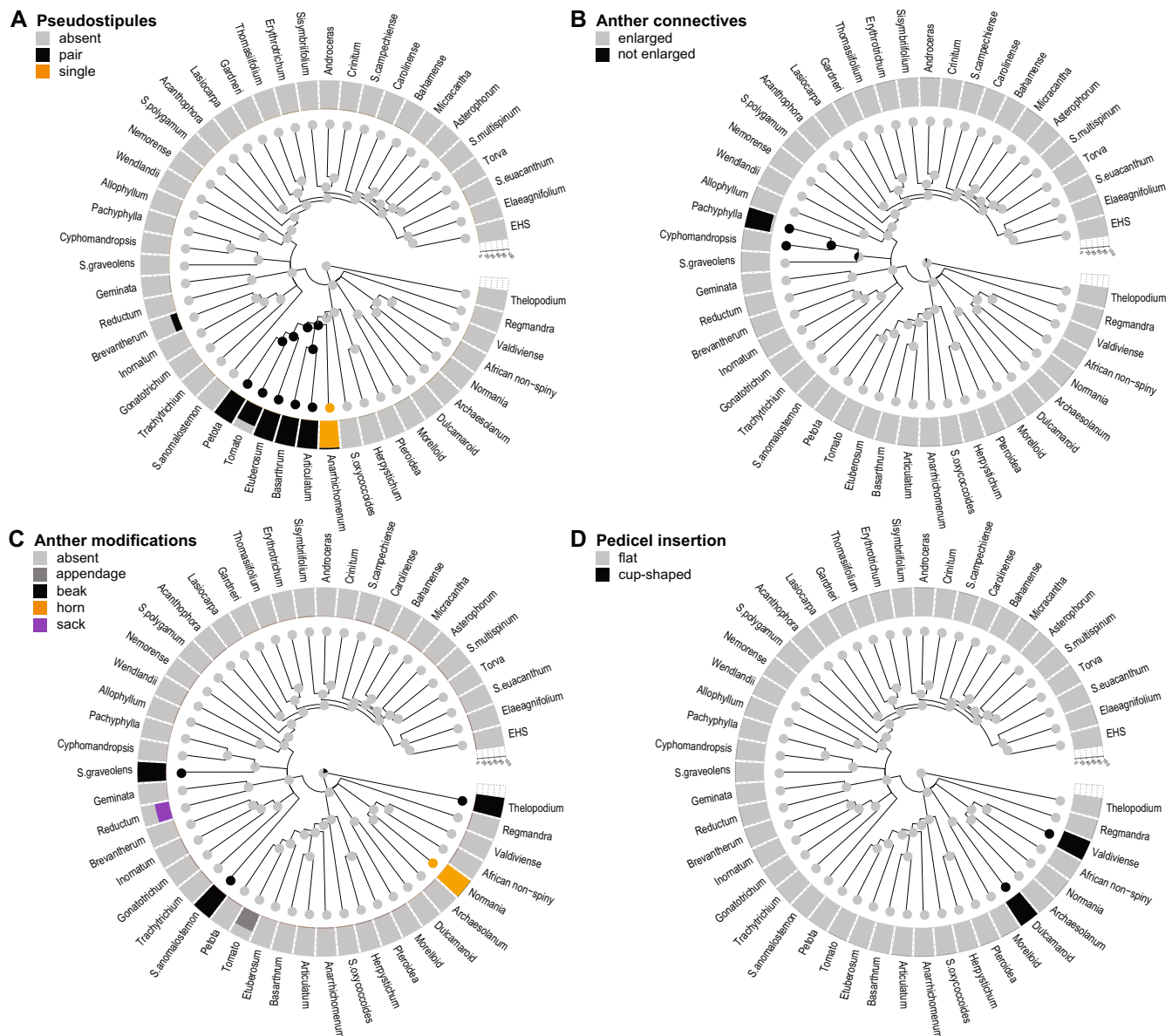


Fig. 8. Evolution of the most conserved morphological traits in *Solanum* with <10 transitions based on species-level analysis using stochastic character mapping. **A**, Pseudostipules; **B**, Enlarged anther connectives; **C**, Anther modifications; **D**, Pedicel insertion. Results from the best model are shown for each character (see Table 1 and 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.

Table 2. Definition/description of *Solanum* clades based on morphology, geography, and broad-scale ecology.

Main group	Description	Major clade	Description	Minor clade	Description	Geography	
Thelopodium (3)					Single-stemmed (unbranched) shrubs with heteromorphic anthers and filaments and beak-like anther modifications, fruits apically pointed onion dome shaped and pointing upwards	Lowland and pre-montane South America	
Grade I	Non-prickly herbs, shrubs or herbaceous or woody vines that lack stellate trichomes; mostly plurifoliate sympodial unit structure, many compound-leaved species	Regmandra (12)			Herbs and shrubs, leaves mostly deeply lobed to compound, thick and somewhat succulent, corollas mostly rotate, stigmas expanded and clavate, stone cells present	Pacific coastal deserts and dry habitats (incl. lomas) of Peru and Chile	
					Woody plant with cup-shaped pedicel bases (insertion), berries red at maturity	Chile	
		VANAns			Valdiviense (2)	Woody shrubs or vines, mostly climbing, many species with branched dendritic trichomes, plurifoliate sympodial units, terminal inflorescences, and mostly deeply stellate purple corollas	Africa & Madagascar
					African non-spiny (ANS, 14)	Herbs and shrubs with inflated calyces, bilaterally symmetric purple corollas, heteromorphic anthers with basal modifications (horn-like projections), unbranched intermodal inflorescences	Macaronesia, southern Spain and Mediterranean North Africa
					Normania (3)	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	Australia and the South Pacific (New Guinea, Australia, Tasmania, New Zealand)
DulMo			Archaeosolanum (8)	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	Global		
			Dulcamaroid (43)	Herbs to shrubs, with intermodal or leaf-opposed inflorescences, stone cells absent	Global		

(Continues)

Table 2. Continued.

Main group	Description	Major clade	Description	Minor clade	Description	Geography
Grade I continued		Potato	Mostly herbs, herbaceous vines, or weakly woody vines	Herpystichum (10)	Small herbs or herbaceous vines commonly rooting along nodes with simple to 3–5-foliolate leaves, flower buds distinctly onion-shaped and fruits mostly flattened along base to tip axis	Lowland rain forest and pre-montane forests from southern Mexico to northern Peru
				Pteroiidea (10)	Understory herbs, herbaceous vines with adventitious roots and unbranched shrubs with unifoliolate sympodial units, simple or pinnate leaves, and axillary inflorescences with small, deeply stellate corollas, fruits often pointed and warty	Lowland rain forest and pre-montane forests from Mexico to tropical South America
				S. oxycoccooides (1)	Somewhat woody vine with simple leaves lacking pseudostipules, and small red fruits with only a few seeds	Peruvian Andes >3000 m
				Articulatum (2)	Somewhat woody vines with paired pseudostipules, with large, often branched inflorescences and winged seeds, resembling <i>Basarthurum</i> clade but lacking bayonet hairs (2-celled hairs with a short apical cell)	Montane forests >2500 m in Costa Rica, Panama, and northern Colombia
				Basarthurum (16)	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	Dry to moist mid-elevation habitats in Central & South America
				Anarrichomenum (12)	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	Mid-elevation habitats in Central & South America
				Etuberosum (3)	Rhizomatous herbs with pinnately compound leaves with frequent interjected leaflets subtended by paired pseudostipules, with many-branched terminal inflorescences, morphologically similar to <i>Petota</i> clade members that have tubers, pedicels articulated at or near the base (unlike <i>Petota</i> clade)	Argentina and Chile

(Continues)

Table 2. Continued.

Main group	Description	Major clade	Description	Minor clade	Description	Geography		
Grade I continued		Potato continued		Tomato (17)	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	Colombia, Ecuador, Peru and Chile		
Clade II		<i>S. anomalostemon</i> (1)		Petota (113)	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	North, Central & South America		
					Small herb with glandular trichomes, simple to 3-foliolate leaves, distinct cordate shaped anthers with apical modification (beak)	Dry forests in southern Peru		
				Brevantherum	Non-prickly, shrubs or trees (herbs) with cylindrical anthers, some with stellate hairs	Trachytrichium (2)	Shrubs with simple entire leaves, simple trichomes and unbranched inflorescences with deeply stellate white corollas, heteromorphic filaments in some species, fruits dull green, many-seeded	Argentina, Brazil and Paraguay
						Inornatum (5)	Herbs to small shrubs with simple entire leaves, simple trichomes, and unbranched inflorescences with deeply stellate white corollas, fruits translucent or dull green to red, with few large seeds	Brazilian Atlantic Forest and Cerrado
						Gonatotrichium (7)	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	Southern United States to southern South America
				Brevantherum (80)	Trees or shrubs, some species with distinct branching pattern where stem forks have an inflorescence or a leaf arising from it (dichasial 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	Native to Central and South America with many species now found globally		

(Continues)

Table 2. Continued.

Main group	Description	Major clade	Description	Minor clade	Description	Geography
Clade II continued		Geminata	Non-prickly shrubs or trees with simple entire leaves and sometimes a rank vegetative odour (burning smell), anthers cylindrical	Reductum (2)	Small shrubs with dendritic hairs, broadly stellate white corollas, and one species with basal anther modifications (sack)	Argentina
				Geminata (150)	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	Moist lowland or montane forests from Central to South America
		Cyphomandra	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	S. graveolens (1)	Woody vine with pinnately compound leaves, white broadly stellate corollas, anthers with apical modification (beaks)	Brazilian Atlantic Forest
				Cyphomandropsis (11)	Shrubs or small trees with simple entire leaves, many with dendritic trichomes, mostly white corollas, some with stone cells	Mostly dry habitats across South America
				Pachyphylla (42)	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	Lowland and pre-montane moist forests from Mexico to South America
		Wendlandii-Allophyllum	Prickly to non-prickly shrubs, herbs and woody vines with tapered anthers	Allophyllum (4)	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	Lowland and montane moist forests of Central and South America
				Wendlandii (9)	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	Mexico, and Central and South America

(Continues)

Table 2. Continued.

Main group	Description	Major clade	Description	Minor clade	Description	Geography
Clade II continued		Nemorense	Prickly vines, shrubs or herbs, andromonoecious, with tapered anthers	Nemorense (4)	Woody or herbaceous vines or herbs with mostly broad-based recurved prickles, sympodial units mostly difoliolate geminate, leaves usually lobed or compound, inflorescences unbranched and leaf-opposed with flowers with deeply stellate corollas	South America
		Leptostemonum	Prickly shrubs, trees, woody vines or herbs with stellate trichomes, difoliolate (geminate or non-geminate) sympodial units dominate, leaves simple or lobed, mostly andromonoecious, simple inflorescences dominate, anthers tapered	<i>S. polygamum</i> (1)	Diocious 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	Caribbean
				Lasiocarpa (12)	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	Global (mostly Central America and northern and western South America, with two species in Asia and the Pacific)
				Acanthophora (22)	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	Disturbed and open habitats from Mexico to South America (mostly eastern Brazil); introduced and naturalized elsewhere
				Gardneri (10)	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	Dry habitats of eastern to central Brazil, Caribbean, Mexico and Central America, and northern Peru
				Thomasiifolium (9)	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	Eastern Brazil

(Continues)

Table 2. Continued.

Main group	Description	Major clade	Description	Minor clade	Description	Geography
Clade II continued		Leptostemonum continued		Erythrotrichum (35)	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	Tropical South America
				Sisymbriifolium (2)	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	Dry habitats of South America
				Crinitum (23)	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	Mexico and South America
				Androcera (16)	Herbs densely covered in needle-like prickles, with bilaterally symmetric corollas with heteromorphic anthers, dry fruits surrounded by accrescent spiny calyces	Southern U.S.A. and Mexico
				S. campechiense (1)	Small shrub covered in needle-like prickles, corollas rotate, fruits with appressed calyces lacking pedicel articulation	Dry forests of Mexico, and Central and South America
				Carolinense (14)	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	Open habitats of southeastern U.S.A. and Bolivia, Argentina and Paraguay
				Bahamense (6)	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	Caribbean
				Micracantha (14)	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	Florida to Bolivia, including the Caribbean

(Continues)

Table 2. Continued.

Main group	Description	Major clade	Description	Minor clade	Description	Geography
Clade II continued		Leptostemonum continued		Asterophorum (4)	Tuber-bearing shrubs with difoliolate 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	Brazilian Atlantic Forest
				<i>S. multispinum</i> (1)	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	Dry habitats of Argentina, Brazil and Paraguay
				Torva (55)	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	Global (mostly tropical Americas, with a few members in Asia)
				<i>S. euacanthum</i> (1)	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	Dry habitats of subtropical Argentina
				Elaeagnifolium (5)	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	Deserts and dry habitats in North and South America
				Eastern Hemisphere Spiny (EHS, 336)	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 <i>Solanum</i> species outside the Americas are members of this clade	Africa, Madagascar, Asia, Australia, Pacific

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., *Dulcimaroids*) 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*, *Dulcimaroid*, *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, 2002b,c; 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 hetermorphism 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, LLG, and TS; SK, XA, EJT, LB, LLG, YFG, CTM, AO, 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/0000-0002-3940-4710>, rhilgenhof@rbge.org.uk; EG, <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-saclay.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>, giacomini.leandro@gmail.com; YG, <https://orcid.org/0000-0002-7162-8458>, gouvea.yf@gmail.com; CM, <https://orcid.org/0000-0001-5143-1773>, ctm015@bucknell.edu; AO, <https://orcid.org/0000-0002-3511-1478>, aorejuela@rbge.org.uk; CIO, <https://orcid.org/0000-0001-5639-2558>, ciorozcop@unal.edu.co; IEP, <https://orcid.org/0000-0002-0526-3606>, iperalta@fca.uncu.edu.ar; TS, <https://orcid.org/0000-0002-6956-3093>, tsarkinen@rbge.org.uk

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