

On ‘various contrivances’: pollination, phylogeny and flower form in the Solanaceae

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Members of the euasterid angiosperm family Solanaceae have been characterized as remarkably diverse in terms of flower morphology and pollinator type. In order to test the relative contribution of phylogeny to the pattern of distribution of floral characters related to pollination, flower form and pollinators have been mapped onto a molecular phylogeny of the family. Bilateral flower symmetry (zygomorphy) is prevalent in the basal grades of the family, and more derived clades have flowers that are largely radially symmetric, with some parallel evolution of floral bilateralism. Pollinator types (‘syndromes’) are extremely homoplastic in the family, but members of subfamily Solanoideae are exceptional in being largely bee pollinated. Pollinator relationships in those genera where they have been investigated more fully are not as specific as flower morphology and the classical pollinator syndrome models might suggest, and more detailed studies in some particularly variable genera, such as *Iochroma* and *Nicotiana*, are key to understanding the role of pollinators in floral evolution and adaptive radiation in the family. More studies of pollinators in the field are a priority.

Keywords: adaptive radiation; flower morphology; phylogeny; Solanaceae; pollination syndrome; homoplasy

1. INTRODUCTION

The intricate relationship between flowers and their pollinators has long been considered a key factor in the diversification and radiation of angiosperms (Darwin 1862, 1876; Faegri & van der Pijl 1979; Proctor *et al.* 1996) in part because flowers are so obviously linked to reproductive isolation and thus to speciation (Schemske & Bradshaw 1999; Lorenz-Lemke *et al.* 2006). The incredible intricacy of these relationships, so clearly described for orchids by Darwin (1862) in the first of his many plant books, led to the elaboration of a system of characterizing flowers in terms of ‘pollination syndromes’ as a way of understanding evolution of floral traits and of predicting plant–pollinator relationships (van der Pijl 1960; Faegri & van der Pijl 1979; Proctor *et al.* 1996). Certain morphological or physiological characteristics were assumed to have been evolved in order to facilitate the attraction of specific pollinator types; classic examples are the fleshy, pendant flowers blooming at night to attract bats (Vogel 1969) or long-tubular, fragrant night-blooming flowers that attract sphingid moths (Grant 1983). More recently, it has been suggested that pollination syndromes do not reflect pollinator relationships in nature which are more complex and fluid than the classical syndrome classification might suggest (Herrera 1996;

Waser *et al.* 1996; Valdivia & Niemeyer 2006; Ollerton *et al.* 2009).

The Solanaceae are a medium-sized family of euasterids (*sensu* APG 2003), with 99 currently recognized genera and some 3000 species, almost half of which belong to the hyperdiverse genus *Solanum* (table 1). The family is most diverse in the Neotropics, where all but 21 of these genera are endemic. Members of the family inhabit a wide range of habitats, from the driest deserts of the west coast of South America and of the Tibetan plateau, to the rainforests of the Amazon and southeast Asia. Life form in the family is similarly varied, ranging from tiny annual herbs (*Leptoglossis*) to canopy trees (*Duckeodendron*). Owing to the overwhelming numerical species dominance of *Solanum*, with its mostly radially symmetrical flowers, the family was long considered a classic example of the trend from radial to bilateral symmetry in floral evolution (Hunziker 2000), but mapping floral form onto a phylogeny derived from plastid gene sequences showed that bilateral symmetry was common in the basal grades in the family, and rare in more derived clades such as that containing *Solanum* (Knapp 2002).

Cocucci (1999) characterized floral form and pollination in the family as a classic example of an adaptive radiation in which a lineage diversifies from an original type to occupy a wide range of ecological niches. Adaptive radiations are usually considered to have occurred involving speciation (but see Givnish *et al.* 2009) and to involve colonization of a new, ecologically ‘empty’ space (Linder 2008) and the evolution of key innovations that allow the constituent species of the lineage to interact with the environment in novel ways (Gavrilets & Losos 2009). Adaptations for

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Table 1. Flower morphology, inflorescence type and pollination parameters in the Solanaceae. Scoring is described in the text; states in parentheses are rarer in the genus. Actual pollinators (last column) for each genus are only those specifically reported in the literature (with taxon name of both plant and visitor) or seen by S. Knapp, M. Dillon or T. Mione in the field; speculations as to pollinator owing to flower morphology or unspecified observations of pollinator visits have not been entered here. Genera not included in Olmstead *et al.* (2008) are indicated with asterisks and are placed according to Hunziker (2000), but not included in figure 2.

clade (Olmstead <i>et al.</i> 2008)	genus	approximate number of spp.	flower symmetry	whorl	inflorescence type	pollination syndrome ^a	pollinators (recorded)
Schizanthus	<i>Schizanthus</i> Ruiz & Pav.	12	bilateral	K, C, A	1-flowered	bee; butterfly, moth	bee (Cocucci 1995); butterfly, bee (Pérez <i>et al.</i> 2006)
Goetzeoideae	<i>Metternichia</i> Mikan	1	bilateral	A	1- to few-flowered	moth	
	<i>Tsoala</i> Bosser & D'Arcy	1	radial		1-flowered	moth	
	<i>Coeloneurum</i> Radkl.	1	radial (bilateral)	(A)	1- to few-flowered	insect	
	<i>Henoania</i> Griseb.	1	radial		1- to few-flowered	insect	
	<i>Espadaea</i> A.Rich.	1	bilateral	C, A	1-flowered	bird	
	<i>Goetzea</i> Wycl.	2	radial		1-flowered	bird	
Duckeodendron	<i>Duckeodendron</i> Kuhlms.	1	radial		many-flowered	moth	
Cestreae	<i>Cestrum</i> L.	250	radial		1-flowered; many-flowered	bird; moth	moth (Haber & Frankie 1989)
	<i>Sesaea</i> Ruiz & Pav.	5	radial		1-flowered; many-flowered	bird	
Protoschwenkia	<i>Vestia</i> Willd.	1	bilateral	A	few-flowered	bird	
Browallieae	<i>Protoschwenkia</i> Soler.	1	radial		many-flowered	insect	
	<i>Browallia</i> L.	4	bilateral	C, A	1- to few-flowered	butterfly	butterfly (Cocucci 1995); S. Knapp 2009, personal observation)
	<i>Streptosolen</i> Miers	1	bilateral	C, A	many-flowered	bird	hummingbird (S. Knapp 2009, personal observation)
Salpiglossidae	<i>Salpiglossis</i> Ruiz & Pav.	2	bilateral	C, A	1-flowered	butterfly	no flower visitors (Cocucci 1995)
	* <i>Revesia</i> Gay	2	bilateral	C, A	1-flowered	butterfly	
Benthamielleae	<i>Pantacantha</i> Speg.	1	bilateral	K	1-flowered	moth	
	<i>Combera</i> Sandw.	2	radial		1-flowered	moth	
	<i>Benthamiella</i> Speg.	12	bilateral	A	1-flowered	moth	moth (Arroyo & Squeo 1990)
Petunieae	<i>Fabiana</i> Ruiz & Pav.	15	radial (bilateral)	(A)	1-flowered	moth; insect	
	<i>Calibrachoa</i> La Llave & Lex.	24	bilateral	C, A	1-flowered	bee	bee (Ando <i>et al.</i> 2001; Stehmann & Semir 2001)
	<i>Penunia</i> L.	14	bilateral	K, C, A	1-flowered	bee; moth; bird	bee, moth (Ando <i>et al.</i> 2001; Stuurman <i>et al.</i> 2004; Hoballah <i>et al.</i> 2007); hummingbird (Lorenz-Lemke <i>et al.</i> 2006)
	<i>Brunfelsia</i> L.	50	bilateral	C, A	many-flowered	butterfly; moth	butterfly (Plozman 1998)
	<i>Leptoglossis</i> Benth.	7	bilateral	K, C, A	many-flowered	butterfly	butterfly (Cocucci 1995)

(Continued.)

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clade (Olmstead <i>et al.</i> 2008)	genus	approximate number of spp.	flower symmetry	whorl	inflorescence type	pollination syndrome ^a	pollinators (recorded)
	<i>Nierembergia</i> Ruiz & Pav.	20	bilateral	C, A	1- to few-flowered	bee	oil collecting bee, generalized bee (Cocucci 1991; Cosacov <i>et al.</i> 2008)
	<i>Boucheia</i> Dunal	3	bilateral	C, A	1-flowered	bee	
	<i>Hanzikeria</i> D'Arcy	3	bilateral	C, A	1 or 2-flowered	butterfly	
	<i>Pleomania</i> Hunz. & Subils	1	bilateral	C, A	many-flowered	bird	
Schwenkieae	<i>Melananthus</i> Walp.	6	bilateral	K, (C), A	many-flowered	insect	
	<i>Schwenkia</i> L.	25	bilateral	A	1- to few-flowered	insect	
	* <i>Heteranthis</i> Nees & Mart.	1	bilateral	C, A	many-flowered	insect	
Nicotiana	<i>Nicotiana</i> L.	76	bilateral	C, A	many-flowered	bee; moth; bird; bat	bee; moth (S. Knapp 2009, personal observation); hummingbird, moth (Ippolito <i>et al.</i> 2004; Schueller 2004, 2007; Tadmor-Melamed <i>et al.</i> 2004; Kessler & Baldwin 2006; Kessler <i>et al.</i> 2008)
Anthocercideae	<i>Synonanthus</i> Haegi	2	bilateral	A	1-flowered; few-flowered	insect	
	<i>Anthocercis</i> Labill.	10	radial (bilateral)	(C), A	cyme	insect	many small insects (Stace 1995)
	<i>Grammosolen</i> Haegi	3	bilateral	A	1-flowered; few-flowered	insect	
	<i>Anthotroche</i> Endl.	4	radial		1-flowered; few-flowered	insect	
	<i>Cyphanthera</i> Miers	9	bilateral	A	1-flowered; few-flowered	insect	
	<i>Crenidium</i> Haegi	1	bilateral	A	1-flowered	insect	
	<i>Duboisia</i> R.Br.	4	bilateral	A	many-flowered	insect	
	<i>Lattua</i> Phil.	1	bilateral	A	1-flowered	bird	
	<i>Jaborosa</i> Juss.	25	radial		1-flowered; clustered	insect; moth	moth (Vesprini & Galetto 2000)
	<i>Sclerophylax</i> + <i>Lycieae</i>	<i>Sclerophylax</i> Miers	12	bilateral	K, C, A	1-flowered (rarely few-flowers)	bee
	<i>Nolana</i> L.	90	radial (bilateral)	(A)	1- to few-flowered	insect; bee	bee, many other small insects (M. O. Dillon 2009, personal observation)
	<i>Lycium</i> L.	80	radial (bilateral)	(A)	1-flowered; few-flowered; brachyblasts	insect	bee, fly, butterfly, moth (Galetto <i>et al.</i> 1998)
	<i>Phrodus</i> Miers	1	bilateral	A	1-flowered	insect	
	<i>Gnabowskia</i> Schlttdl.	4	radial		few-flowered	insect	

(Continued.)

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clade (Olmstead <i>et al.</i> 2008)	genus	approximate number of spp.	flower symmetry	whorl	inflorescence type	pollination syndrome ^a	pollinators (recorded)
Hyoscyameae	<i>Hyoscyamus</i> L.	25	bilateral	K, C, A	many-flowered	bee	bee (S. Knapp 2009, personal observation)
	<i>Prezalskia</i> Maxim.	1	radial		axillary clusters	insect	
	<i>Scopolia</i> Jacq.	2	bilateral	A	1-flowered	bee	
	<i>Physochlaina</i> G. Don	8	radial		many-flowered	bee	
	<i>Atropanthe</i> Pascher	1	bilateral	C, A	1-flowered	bee	
	<i>Anisodus</i> Link	4	radial		1-flowered	bee	
	<i>Atropa</i> L.	2	bilateral	A	1-flowered	bee	
	<i>Exodeconus</i> Raf.	6	bilateral	C, A	1-flowered	bee	
	<i>Nicandra</i>	1	radial		1–2-flowered	bee	
	<i>Schultesianthus</i> Hunz.	8	bilateral	C, A	few-flowered	bee; bat	
Exodeconus Nicandra Juanulloae + Solandra + Schultesianthus	<i>Solandra</i> Sw.	10	bilateral	C, A	few-flowered cymes	bat	
	<i>Dysochroma</i> Miers	1	radial		1-flowered	bat	bat (Sazima <i>et al.</i> 2003)
	<i>Juanulloa</i> Ruiz & Pav.	10	bilateral	C	many-flowered	bird; bee	hummingbird (S. Knapp 2009, personal observation)
	<i>Merinthopodium</i> Donn.Sm.	3	radial		many-flowered	bat	bat (Voss <i>et al.</i> 1980; Voigt 2004)
	<i>Markea</i> A. Rich.	15	radial (bilateral)	(C)	1-flowered; many-flowered	insect; bird	
	* <i>Trianaea</i> Planch. & Linden	7	radial		1–3-flowered cymes	bat	bat (S. Knapp 2009, personal observation)
	<i>Mandragora</i> L.	2	bilateral	A	1-flowered; few-flowered	bee	bee (S. Knapp 2009, personal observation)
	<i>Brugmansia</i> Pers.	6	radial		1-flowered	moth; bat; bird	hummingbird (Gould 1861)
	<i>Datura</i> L.	11	radial		1-flowered	moth	moth (Grant 1983; Raguso <i>et al.</i> 2003)
	(<i>I. cardenasianum</i>)	1	radial		1-flowered	bird; moth	
[Salpichroina]	<i>Nectouxia</i> Kunth	1	radial		1-flowered	bird; moth	
	<i>Salpichroa</i> Miers	15	radial		1-flowered	bird; moth	
	<i>Cuatresia</i> Hunz.	12	radial		many-flowered	bee; insect	
	<i>Discopodium</i> Hochst.	2	radial		many-flowered	insect	
	<i>Nothocestrum</i> A. Gray	6	bilateral	A	many-flowered	moth; bird	
	<i>Tubocapsicum</i> Makino	1	radial		few-flowered	insect	
	<i>Athenaea</i> Sendtn.	7	radial		many-flowered; 1-flowered	insect	
	<i>Aureliana</i> Sendtn.	5	radial		1– to few-flowered	insect	
	<i>Melissia</i> Hook.f.	1	radial		1–2-flowered	insect	
	<i>Withania</i> Pauq.	10	radial		1– to few-flowered	insect	bee (Anderson <i>et al.</i> 2006)
Iochrominae + Larnax	* <i>Physalistrum</i> Makino	9	radial		1– to few-flowered	insect	
	<i>Larnax</i> Miers	12	radial		1-flowered	insect	
	* <i>Deprea</i> Raf.	7	radial		few-flowered	insect	

(Continued.)

Table 1. (Continued.)

clade (Olmstead <i>et al.</i> 2008)	genus	approximate number of spp.	flower symmetry	whorl	inflorescence type	pollination syndrome ^a	pollinators (recorded)
Physalinae	<i>Dunalia</i> Kunth	5	radial (bilateral)	(A)	many-flowered	bird	
	<i>Iochroma</i> Benth.	25	radial (bilateral)	(A)	many-flowered	bird; bee; butterfly	hummingbird, fly, bee, butterfly (Smith <i>et al.</i> 2008a,b)
	<i>Saracha</i> Ruiz & Pav.	2	radial		few-flowered	insect	
	<i>Vassobia</i> Rusby	2	radial		many-flowered	bee	
	<i>Eriolarynx</i> Hunz.	3	radial		many-flowered	bee	
	<i>Acinisus</i> Schott	2	radial		many-flowered	bee	
	* <i>Darcyanthus</i> Hunz.	1	radial		many-flowered	bee	bee (Bohs 2000; Sousa-Peña 2001; Stone <i>et al.</i> 2006; Stone & Jenkins 2008)
	<i>Witheringia</i> LHer.	25	radial		many-flowered	bee	
	<i>Brachistus</i> Miers	3	radial		many-flowered	bee	
	* <i>Tzeltalia</i> E. Estrada & M. Martínez	2	radial		few-flowered	bee	
Capsiceae	<i>Leucophysalis</i> Rydb.	3	radial		few-flowered	bee	
	<i>Physalis</i> L.	90	radial		1-flowered; few-flowered	bee	bee (Sullivan 1984; Roulston 2005)
	<i>Oryctes</i> S. Watson	1	bilateral	K, A	few-flowered	insect	
	<i>Quincula</i> Raf.	1	radial		1-flowered	bee	
	<i>Chamaesaracha</i> (A. Gray) Benth.	10	radial (bilateral)	(A)	1-flowered	bee	
	<i>Margaranthus</i>	1	radial		1- to few-flowered	insect	
	<i>Lycianthes</i> Bitter	200	radial (bilateral)	A	many-flowered	bee	bee-vibratile (Dean 2001; S. Knapp 2009, personal observation)
	<i>Capsicum</i> L.	25	radial		few-flowered	bee; insect	bee (Cauich <i>et al.</i> 2006; Cruz & Oliveira de Campos 2007; Palma <i>et al.</i> 2008)
	<i>Falcomata</i> Schltdl.	50	radial		few-flowered	bee	bee, hummingbird (T. Mione 2009, personal observation)
	<i>Solanum</i> L.	1400	radial (bilateral)	C, A	many-flowered	bee	bee-vibratile (Knapp 1986; Soares <i>et al.</i> 1989; Sazima <i>et al.</i> 1993; Gracie 1993; Barreto <i>et al.</i> 2006)

^aPollination syndromes—insect (entomophily)—flowers small and open, usually cream or white or purple, with nectar, diurnal, fragrance limited or strong; bee (melittophily)—flowers usually yellow or blue with obvious nectar guides, open or broad-tubular, with nectar or with poricidal anthers and/or other rewards, diurnal, fragrance limited; butterfly (psychophily)—flowers usually blue or purple, the tube narrow and constricted, nectar present, diurnal, fragrance limited; moth (phalaenophily)—flowers white, tube long, wide or narrow, nectar present, nocturnal, fragrance strong at night; bird (ornithophily)—flowers red or orange, tubular, thick, nectar present, diurnal, fragrance not conspicuous; bat (chiropterophily)—flowers large and tough, cup-shaped, hanging free of leaves, greenish or cream, nectar copious, nocturnal, fragrance musky. After Faegri & van der Pijl (1979).

pollination by different animals are indeed ways in which species partition ecological space, but several recent studies have shown that pollination is apparently less important in radiations than other characteristics (Tripp & Manos 2008; Givnish *et al.* 2009). If pollinator relationships are important in the speciation processes generating diversity at the family level in the Solanaceae, then one might expect the most species-rich genera to be concomitantly richer in pollinator relationships.

Distribution of morphological characters associated with pollination on an independently derived phylogeny is one way to examine the pattern of evolution of floral form in the Solanaceae and compare this with putative pollinator relationships. Such an analysis will not resolve the question of whether or not the diversity seen is indeed an adaptive radiation, but it allows insights into the degree of homoplasy in these pollinator-related traits, and can reveal genera in which more detailed studies of flower development in relation to pollination can be undertaken in the future. These more targeted studies may indeed reveal adaptive radiations in pollinator relationships in the family. My aim here is to explore some general aspects of floral form and pollinator types in the genera of the Solanaceae in a phylogenetic context and to use these results to suggest areas for further investigation into the evolution of floral form in relation to pollinators in this florally diverse group.

2. MATERIAL AND METHODS

In order to examine the pattern of character distribution in relation to phylogeny, I took a recently published (Olmstead *et al.* 2008) molecular phylogeny based on two plastid genes (*trnLF* and *ndhF*; see Olmstead *et al.* 2008) and 'pruned' it so that genera were terminal taxa (see figure 2). Enigmatic taxa of very uncertain taxonomy were excluded (e.g. *Iochroma cardenasianum*, that resolves as sister to *Datura* and *Brugmansia*; see Smith & Baum 2006; Olmstead *et al.* 2008). In order to test the pattern in floral form seen in the analysis of Knapp (2002), I scored not only flower symmetry as was done in that study, but also recorded symmetry in each floral whorl (calyx, corolla and androecium). I scored characters considered important in pollinator relationships for all genera, including those not included in the phylogenetic analysis (these genera are marked with asterisks in table 1), and putative pollination syndromes were scored based on flower morphology (table 1, figure 1). I scored the syndromes as insect (generalized insect, including flies and beetles) ('entomophilous', figure 1a,b), bee ('melittophilous', figure 1c,d), butterfly ('psychophilous', figure 1e), moth ('phalaenophilous', figure 1f), bird ('ornithophilous', figure 1g) or bat ('chiropterophilous', figure 1h) using the types defined in Faegri & van der Pijl (1979; see footnote to table 1). Pollination syndromes were scored both as multi-state and single-state characters (see electronic supplementary material). It is clear that pollination syndromes are not necessarily the most biologically informative way in which to view plant–animal interactions involved with pollination

(Ollerton *et al.* 2009), but they are a first step (see below). Inflorescence morphology was scored as a simple one- to few-flowered versus many-flowered state, despite this being rather arbitrary; the inflorescence morphology of Solanaceae is very complex and is only beginning to be understood (Lippman *et al.* 2008). Species numbers in each genus were recorded from the most recent revision or in the absence of a modern taxonomic treatment taken from estimates provided by Hunziker (2000).

3. RESULTS

There is no simple correlation between species number and number of pollination syndromes in a genus ($r^2 = 0.1$, results not shown), despite the tempting observation that two of the largest genera (*Solanum* and *Lycianthes*) have single pollinator types (table 1). Bilaterally symmetrical (zygomorphic) flowers are found in the basal grades of the family (figure 2, right-hand side), with several independent losses and gains of this characteristic in the rest of the family (confirming results of Knapp 2002). The most common bilaterally symmetrical whorl is the androecium (table 1), followed by the corolla; many genera exhibit zygomorphy in the corolla and androecium, while other clades (e.g. the Anthocercidae; see electronic supplementary material, figure S1) are only bilaterally symmetrical in the androecium (usually with reduced anther numbers or insertion point differences). Different pollination syndromes have evolved many times in the family (figure 2, left-hand side); bird-type flowers have apparently evolved 10 times independently (see electronic supplementary material, figure S6). Bee flowers predominate in the more derived clades (see dark blue in figure 2), with the bee pollination syndrome being a synapomorphy of the largest subclade of the subfamily Solanoideae as defined by Olmstead *et al.* (2008). This group corresponds with that having little zygomorphy in most floral whorls (compare the topmost clades in the two sides of figure 2). Individual pollination syndromes have extensive parallel evolution in the family (for details of distribution of individual pollinator syndromes on the phylogeny of Olmstead *et al.* (2008), see electronic supplementary material, figures S2–S7). Generalized insect pollination is common (electronic supplementary material, figure S1), but much of this may be due to the difficulty of scoring pollination syndromes, for these sorts of flowers may be pollinated by bees and other insects. Butterfly pollination (electronic supplementary material, figure S4) is largely confined to the Petunieae + Benthamielleae + Salpiglossideae + Browallieae (with some exceptions, figure 2); these complex mechanisms have been described in detail by Cocucci (1995). Moth pollination has evolved at least eight times in the family, including in the most basal grade (figure 2, left-hand side, and electronic supplementary material, figure S5); bat pollination syndromes have two independent origins (*Datura* and the *Markea* clade, see electronic supplementary material, figure S7), and as mentioned earlier, bee pollination appears to be a synapomorphy of the Solanoideae as defined by Olmstead *et al.* (2008; see electronic

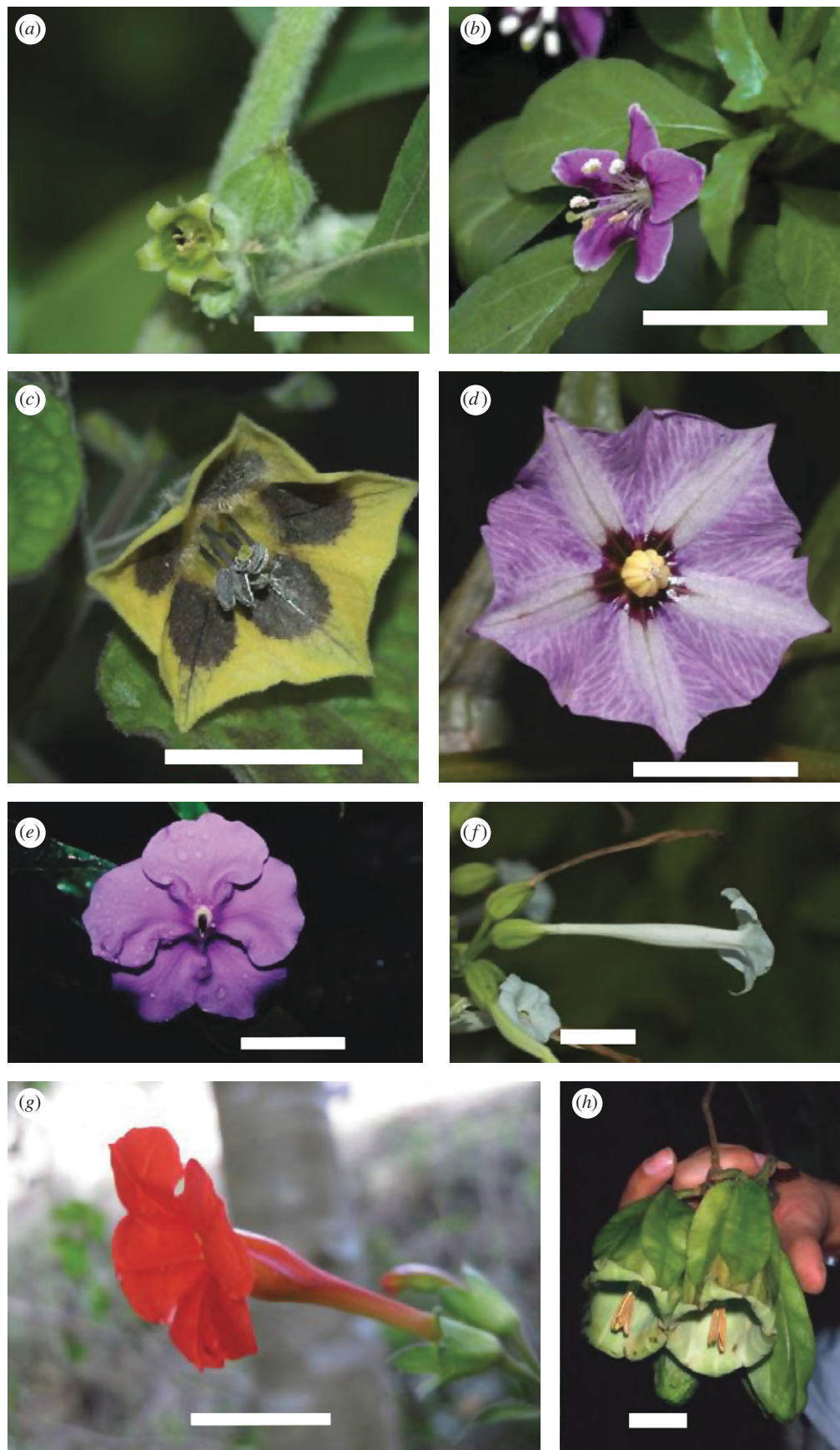


Figure 1. Flower forms in the Solanaceae: (a) insect flower of *Withania somnifera* L. (MPIZ, Cologne, Germany), (b) insect flower of *Lycium barbarum* L. (Knapp IM-10134, China), (c) bee flower of *Physalis pubescens* L. (MPIZ, Cologne, Germany), (d) buzz-pollinated bee flower of *Lycianthes* sp. (Monro et al. 5301, Panama, photo A. Monro), (e) butterfly flower of *B. grandiflora* D. Don (Knapp et al. 9161, Panama), (f) moth flower of *N. sylvestris* Speg. & S. Comes (MPIZ, Cologne, Germany), (g) bird flower of *Plowmania nyctaginoides* (Standl.) Hunz. & Subils (Christenhusz et al. 5355, Guatemala, photo M. Vorontsova), (h) bat flower of *Merinthopodium neuranthum* (Hemsl.) Donn. Sm. (Monro et al. 260, Costa Rica). All scale bars, 1 cm; photos S. Knapp except where indicated.

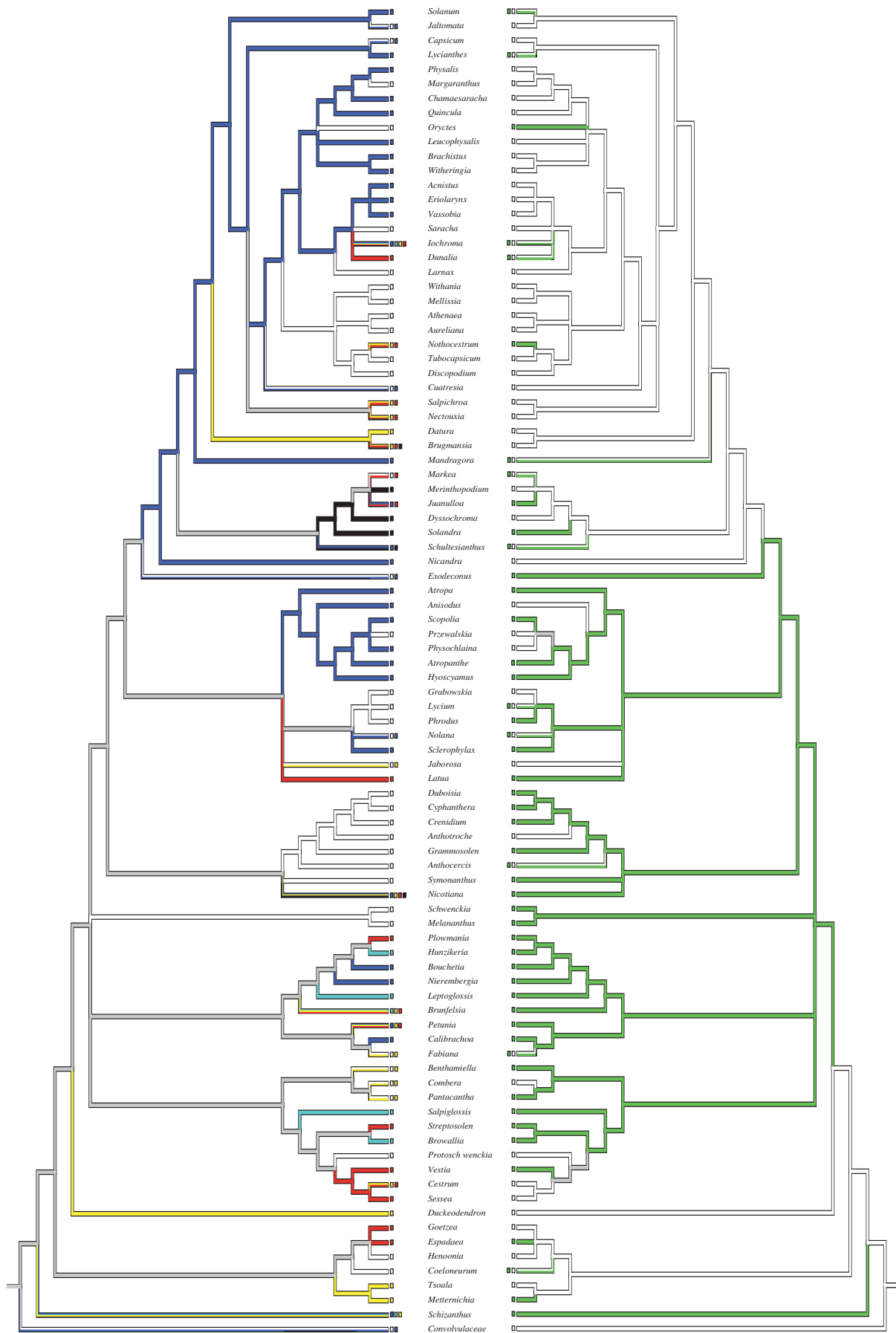


Figure 2. Distribution of flower form (right-hand cladogram) and pollination syndromes (left-hand cladogram; see table 1 for definitions). In the right-hand cladogram, radial flower symmetry is indicated with white, bilateral flower symmetry with green. In the left-hand cladogram, pollination syndromes are indicated as follows: insect flower, white; bee flower, dark blue; butterfly flower, turquoise; moth flower, yellow; bird flower, red; bat flower, black. Boxes associated with each terminal indicate the different syndromes or forms with their respective colours.

supplementary material, figure S3). Vibratile pollination, in which bees actively 'buzz' poricidal anthers to extract pollen (e.g. Michener 1962; Buchmann 1983), has independently evolved in both *Solanum* and *Lycianthes* (electronic supplementary material, figure S3). The possession of this complex pollination system has previously been seen as evidence of the close relationship of these two taxa (Hunziker 2000). Oil-collecting bees pollinate some species of *Nierembergia* (Cocucci 1991; Tate *et al.* 2009); this is unique in the family, although similar trichomes on the corolla of *Boucheitia* suggest pollination of this type might occur there as well (Cocucci 1991).

4. DISCUSSION

Pollinators are indeed diverse in the Solanaceae, and while floral zygomorphy is more common in the basal grade, it is not only these groups that exhibit great diversity in pollinator syndromes (and indeed in pollinators, see table 1). There is a great deal of homoplasy in pollinator syndrome at the generic level, as evidenced by the equivocal status of deep branches (figure 2). This indicates that at the generic level at least, the Solanaceae have not adaptively radiated in terms of pollinators, but certain clades and/or genera have clearly exploited pollinator space extensively. The genera of the Petunieae have five different pollinator syndromes, and *Brunfelsia* alone has three (moth, butterfly and bird). In *Brunfelsia*, the South American species have either moth (e.g. *Brunfelsia guianensis*) or butterfly (e.g. *Brunfelsia grandiflora*, figure 1e) flowers, while the Caribbean taxa (thought to be monophyletic by Plowman 1998) are all long-tubed (e.g. *Brunfelsia americana*) and probably pollinated by sphingid moths, except for the Cuban endemic *Brunfelsia cestroides*, which has bright red, presumably hummingbird-pollinated flowers. *Petunia* exhibits a similar range of flower types (Stehmann *et al.* 2009), and developmental studies on species pairs have revealed the genetics behind these differences (Stuurman *et al.* 2004; Hoballah *et al.* 2007; Gübitz *et al.* 2009). *Schizanthus*, sister to the rest of the family (Olmstead *et al.* 2008) and with the most zygomorphic flowers in the family (Knapp 2002), has a range of pollinators (Pérez *et al.* 2006), and combinations of floral traits related to pollination have been shown to have evolved in a concerted fashion (Pérez *et al.* 2007).

Two clear candidates for adaptive radiation owing to pollinators are the relatively distantly related *Iochroma* and *Nicotiana*, each of which contains flowers of four pollination syndromes (figure 2). The amazing diversity of form and colour in flowers of the *Iochroma* lineage (Smith & Baum 2006, fig. 3) does not correlate with pollinator shift (Smith *et al.* 2008a) and, when growing in sympatry, species with quite different flower morphologies share pollinators (Smith *et al.* 2008b). Thus, in this lineage, floral diversification is not an adaptive response to pollinators, but may instead be due to factors such as selection against nectar robbers or various community-related effects (Smith *et al.* 2008a). *Nicotiana* species have a similar wide array of flower types (Knapp *et al.* 2004).

In the widespread, bird-pollinated *Nicotiana glauca*, Nattero & Cocucci (2007) correlated geographical variation in floral tube length with bill length in hummingbird communities, suggesting adaptation to pollinators, but observations in the field on pollinator preferences for variable populations of *N. glauca* showed no such partitioning (Schueller 2007). Species of section *Alatae* with bird and moth-type flowers asymmetrically shared pollinators, with hawkmoths visiting both floral types (Ippolito *et al.* 2004); a similar pattern has been shown in *Petunia* (Lorenz-Lemke *et al.* 2006). Kaczorowski *et al.* (2005) have suggested that nectar traits, rather than floral form *per se*, have shaped pollinator preferences in the *Alatae*. The bat-pollinated *Nicotiana otophora* (Vogel 1969) was visited by hawkmoths when in sympatry with the classically moth-pollinated *Nicotiana sylvestris* (Nattero *et al.* 2003; figure 2f). *Nicotiana attenuata* has typical moth flowers, but in a series of elegant field experiments, a complex trade-off between scent and nectar chemistry was shown to mediate pollination by both hawkmoths and hummingbirds, with differences occurring seasonally (Kessler & Baldwin 2006; Kessler *et al.* 2008). As in the *Iochroma* lineage, pollinator relationships in *Nicotiana* are clearly complex and not simply the result of the interaction of floral form and pollinator-mediated selection, but new data on floral form and phylogeny (E. W. McCarthy 2009, personal communication) will shed light on these relationships.

It is clear from this preliminary and broad-brush look at floral form and pollination in the Solanaceae that simple adaptive evolution between flowers and their pollinators does not adequately explain the great variety in floral form and broad homoplasy in pollinator types in the family. Even if pollinator syndromes are not truly a reflection of plant–pollinator relationships in the field (Herrera 1996; Ollerton 1996; Ollerton *et al.* 2009), they do serve to alert us to potentially interesting areas in which to investigate the intersection of ecology and evolution and to further delve into these complex relationships. There may be a lot of phylogenetic 'inertia' in flower form, so its analysis in the light of a well-supported phylogeny (molecular or morphological) is critical (Tripp & Manos 2008). It is clear too that species richness at the generic level has not been accompanied by radiation in pollinator systems (see Ricklefs & Renner 1994 for an angiosperm-wide analysis). The more than 1000 species of *Solanum* are all manipulated similarly by bees, so here diversification is clearly the result of other factors such as habitat shifts (e.g. van der Niet *et al.* 2006) or other morphological features such as architecture (e.g. Miller & Diggle 2003; Diggle & Miller 2004). Bridging the gaps between large-scale phylogenetic patterns, local ecological factors and comparison of finer scale developmental processes between individual species or populations in order to test the universality of fine scale changes in flower form across the grand scope of angiosperm diversity is one of the next great challenges in our understanding of the evolution of flowers. The Solanaceae, with emerging genomic tools (Mueller *et al.* 2009) and great floral diversity, represents an excellent group in which to further explore these patterns.

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