A Summary of Molecular Systematic Research in Solanaceae: 1982–2006

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Abstract

A summary of progress in molecular phylogenetic studies of Solanaceae indicates that with over 50 published studies, more than 90% of genera and 37% of species have been sampled. Circumscription of Solanaceae now includes Nolanaceae, Goetzeaceae, *Duckeodendron*, and *Sclerophylax*. Well-sampled groups include *Capsicum, Lycium, Nicotiana, Nolana*, and *Petunia* and the clades Anthocercideae, Goetzeoideae, and Iochrominae. A major effort currently underway promises extensive sampling of *Solanum*. Groups that remain poorly sampled include *Cestrum, Brunfelsia, Jaltomata, Lycianthes*, and Juanulloeae.

INTRODUCTION

The beginning of modern (DNA-based) molecular plant systematics can be traced to a study of the tomato and its wild relatives (Palmer and Zamir, 1982). In the quarter century since then, the Solanaceae have remained in the forefront of molecular plant systematics, with innovations in the sources of data and analytical approaches used (e.g., chloroplast rflp analysis: Palmer and Zamir, 1982; Hosaka et al., 1984; chloroplast restriction site mapping: Olmstead and Palmer, 1992; Spooner et al., 1993; chloroplast *ndhF* and *rbcL* sequences: Olmstead and Sweere, 1994; Bohs and Olmstead 1997; nuclear ITS and "waxy" sequences: Peralta and Spooner, 2001 Walsh and Hoot, 2001; Levin and Miller, 2005; Whitson and Manos, 2005; Levin et al., 2005; Martine et al., 2006; nuclear SAMT sequences: Martins and Barkman, 2005; AFLP analysis: Mace et al., 1999; Spooner et al., 2005a, b; nuclear retroposon markers: Yuan et al., 2006).

Significant advancements have been made in our understanding of relationships of Solanaceae (Olmstead and Palmer, 1992; Olmstead and Sweere, 1994; Olmstead et al. 1999; Gemeinholzer and Wink, 2004; Martins and Barkman, 2005), including its circumscription to include several small groups previously excluded (e.g., Nolanaceae, Goetzeaceae, *Duckeodendron*, and *Sclerophylax*). A provisional phylogenetic classification presented at the 1994 Solanaceae Conference in Adelaide (Olmstead et al., 1999) has been revised (Fig. 1; Table 1) following expanded sampling in many groups and inclusion of over 90% of all genera in subsequent molecular studies (Olmstead et al., in prep.).

Several clades in Solanaceae have been subject to detailed study, including *Nicotiana* (Aoki and Ito, 2000; Clarkson et al., 2004), *Capsicum* (Walsh and Hoot, 2001; E. Dean and L. Bohs, pers. commun.), *Lycium* (Miller 2002; Levin and Miller, 2005); Goetzeoideae (Santiago-Valentin and Olmstead, 2003), Anthocercideae (Garcia and Olmstead, 2003), Physalinae (Whitson and Manos, 2005), *Petunia* (Ando et al., 2005;

Kulcheski et al., 2006); Iochrominae (Smith and Baum, 2006), *Nolana* (M. Dillon and J. Wen, pers. commun.), and, of course, *Solanum* (e.g., Spooner et al., 1993; Bohs, 2005; Levin et al., 2006; Weese and Bohs, 2007).

RESULTS AND DISCUSSION

In an effort to bring together the accomplishments of the past 25 years and to identify where our knowledge is most complete and where further work is needed, we have compiled a summary of molecular systematic studies in Solanaceae organized in conjunction with the classification in Table 1. In order to quantify the progress, estimates of the number of species in each group were revised from prior compendia (D'Arcy, 1991; Hunziker, 2001) where needed using recent publications and the assistance of authorities in those groups. A new estimate of species number in *Solanum* was calculated from estimates of the ratio of accepted species names to published species names in recently monographed groups and extrapolated to the rest of the genus (S. Knapp and J. Bennett, pers. commun.). Table 1 provides estimated numbers and percentages of species sampled for each genus and of genera sampled for suprageneric clades compiled from all studies. Studies are referenced to each genus or clade for information on phylogeny within that group or on the placement or the genus or clade within the Solanaceae. Clade names in Figure 1 follow Olmstead et al. (1999) with the exceptions of "Salpichroina," "Lyciina," and "Atropina," which are unranked informal names used here for the first time. The "-ina" ending does not denote a formal taxonomic rank, but is used in accordance with other studies coining informal clade names (Kron, 1997).

Sampling at the genus level is nearly complete (94%), with only a few hard-to-get taxa remaining to be sampled. However, sampling is uneven at the species level with a total of ca. 37% sampled. Some large clades, including *Cestrum*, *Brunfelsia*, *Lycianthes*, *Jaltomata*, and Juanulloeae remain poorly sampled. *Solanum*, with nearly half the species in the family, is somewhat undersampled at the moment with ca. 31% of species sampled, vs. 37% for the entire Solanaceae (Fig. 2, Table 1). However, there is a major effort underway to understand the global taxonomy and phylogeny of *Solanum* (Knapp et al., 2004; Solanaceae Source: http://www.nhm.ac.uk/solanaceaesource/) and a molecular phylogeny of *Solanum* is progressing at a rapid rate (Bohs, 2004, 2005; Levin et al., 2005, 2006; Martine et al., 2006; Weese and Bohs, 2007; Bohs, in press; L. Bohs and D. Spooner, pers. commun.).

A primary goal of systematics is to discover and describe biodiversity at all levels in the hierarchy of life. Discovery occurs in the field, the herbarium, and in the lab, where molecular phylogenetic studies enable the discovery of clades thoughout that hierarchy. Having a fully sampled and fully resolved phylogeny for Solanaceae will permit interpretation of patterns of character evolution, biogeography, and genome structure resulting in a fully integrated biology of the Solanaceae.

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Table 1. Synoptical, phylogenetic classification of Solanaceae following Olmstead et al., in prep. References provide information about molecular phylogenetic relationships within the group next to which they are placed or information about placement of that group in Solanaceae (taxa used as outgroups not included if uninformative with respect to relationships). Clades in boldface include summary information from groups included in them. Species numbers and sampling percentages are not included for clades in *Solanum* subg. *Leptostemonum* because many unsampled species are not yet assigned to clades.

Indented Classification	Gen./Spp. Sampled	%of group	References
Solanaceae (98 genera/~2716 species)	**92/1000**	**94%/37%**	**15, 24, 29, 30, 32, 33, 34, 41**
Genera of Solanaceae not assigned to a more inclusive clade (2/13)	**2/13**	**100%/100%**	
Duckeodendron (1) Amazonian Brazil	1	100%	12, 34, 41
Schizanthus (12) coastal Chile	12	100%	12, 15, 24, 30, 32, 33, 34, 37, 41
Goetzeoideae (6/7)	**6/7**	**100%/100%**	**33, 34, 41**
Coeloneurum (1) Hispaniola	1	100%	34, 41
Espadaea (1) Cuba	1	100%	34, 41
Goetzea (2) Antilles	2	100%	12, 33, 34, 41
Henoonia (1) Cuba	1	100%	34, 41
Metternichia (1) SE Brazil	1	100%	12, 34, 41
Tsoala (1) Madagascar	1	100%	34
Benthamielleae (3/15)	**3/3**	**100%/20%**	**33**
Benthamiella (12) Patagonia	1	8%	33
Combera (2) Patagonia	1	50%	33
Pantacantha (1) Patagonia	1	100%	33
Cestroideae (8/206)	**7/19**	**87.5%/9%**	**15, 24, 33, 34, 41**
Browallieae (2/7)	**2/4**	**100%/57%**	**15, 24, 30, 33, 34, 41**
Browallia (6) Neotropics to Arizona	3	50%	15, 24, 30, 33, 34, 41
Streptosolen (1) Andes	1	100%	15, 24, 30, 33, 34
Cestreae (3/~192)	**3/13**	**100%/7%**	**15, 24, 30, 33, 34, 41**
Cestrum (~175) Neotropics	10	6%	15, 24, 30, 33, 34, 41
Sessea (16) Andes	2	12.5%	15, 34, 41
Vestia (1) Chile	1	100%	15, 24, 30, 33, 34, 41
Salpiglossideae (2/6)	**1/1**	**50%/17%**	**15, 30, 33, 34, 41**
Reyesia (4) Argentina & Chile	0	0%	
Salpiglossis (2) Argentina & Chile	1	50%	12, 15, 30, 32, 33, 34, 41
Genera of Cestroideae not assigned to a more inclusive clade (1/1)	**1/1**	**100%/100%**	**34**
Protoschwenckia (1) Bolivia, Brazil	1	100%	34

Petunieae (9/145) (Petunioideae in Olmstead et al. 1999)	**9/63**	**100%/43%**	**15, 24, 30, 33, 34, 41**
Bouchetia (3) Neotropics	2	67%	17, 33, 34
Brunfelsia (45) Neotropics	2	4%	15, 24, 30, 33, 34, 41
Calibrachoa (~23 + 9 nom. ined., Ando et al., 2005) Neotropics	32	100%	2, 15, 17, 33, 34
Fabiana (15) Andes	1	7%	15, 30, 33, 34
Hunzikeria (3) SW USA, Mexico	1	33%	33, 34
Leptoglossis (7) W South America	1	14%	34
Nierembergia (21) South America	5	24%	15, 17, 33, 34
Petunia (~17 + 1 nom. ined., Ando et al., 2005) S South America	18	100%	2, 12, 15, 17, 24, 30, 32, 33, 34, 41
Plowmania (1) Mexico, Guatemala	1	100%	34
Schwenckieae (3/28)	**2/3**	**67%/11%**	**24, 33, 34, 41**
Heteranthia (1) Brazil	0	0%	
Melananthus (5) Brazil, Cuba, Guatemala	1	20%	34
Schwenckia (22) Neotropics	2	9%	12, 24, 33, 34, 41
"x = 12" (clade name without rank) (67/~2302)	**62/892**	**93%/39%**	**15, 24, 30, 32, 33, 34, 41**
Nicotianoideae (8/108)	**8/86**	**100%/80%**	**11, 14, 15, 24, 30, 32, 33, 34, 41**
Anthocercideae (7/32)	**7/26**	**100%/81%**	**11, 14, 15, 24, 30, 32, 33, 34, 41**
Anthocercis (10) Australia	7	70%	11, 14, 24, 30, 32, 33, 34, 41
Anthotroche (4) Australia	4	100%	11, 14, 34
Crenidium (1) Australia	1	100%	11, 14, 34
Cyphanthera (9) Australia	7	78%	11, 14, 15, 30, 33, 34
Duboisia (4) Australia	3	75%	11, 14, 15, 30, 33, 34
Grammosolen (2) Australia	2	100%	11, 14, 15, 30, 33, 34
Symonanthus (2) Australia	2	100%	11, 14, 34
Genera of Nicotianoideae not assigned to a more inclusive clade (1/76)	**1/60**	**100%/79%**	
Nicotiana (76) New World (52), Australia (23), Africa (1)	60	79%	3, 11, 12, 14, 15, 24, 29, 30, 32, 33, 34, 41
Solanoideae (59/~2194)	**54/806**	**92%/37%**	**15, 24, 30, 32, 33, 34, 41**
"Atropina" (clade name without rank) (13/252)	**12/171**	**92%/68%**	**15, 24, 30, 32, 33, 34, 54**
Hyoscyameae (8/43)	**7/23**	**87.5%/53%**	**15, 24, 30, 32, 33, 34, 54**
Anisodus (4) China, India, Himalayas	2	50%	15, 33, 34, 54
Archihyoscyamus (1) Turkey	0	0%	
Atropa (3) Eurasia	1	33%	12, 15, 24, 30, 32, 33, 34, 54
Atropanthe (1) China	1	100%	15, 34, 54
Hyoscyamus (~20) Mediterranean to China	14	70%	15, 24, 30, 33, 34, 54
Physochlaina (11) Eurasia	2	18%	15, 33, 34, 54
Przewalskia (1) China	1	100%	15, 34, 54
Scopolia (2) Europe (1) Japan (1)	2	100%	15, 34, 54

"Lyciina" (clade name without rank) (3/185)	**3/143**	**100%/77%**	**15, 24, 30, 32, 33, 34**
Lycium (87[3]) World-wide (incl. *Grabowskia*, 3 spp.; *Phrodus* 1 sp.)	72[3]	83%	12, 13, 15, 18, 24, 25, 26, 30, 32, 33, 34, 41, 54
Nolana (86[2])W South America	68[2]	79%	12, 13, 15, 18, 24, 25, 26, 30, 32, 33, 34, 49
Sclerophylax (12) Andes	3	25%	15, 18, 34
Genera of Atropina not assigned to a more inclusive clade (2/24)	**2/5**	**100%/21%**	
Jaborosa (23) South America	4	17%	15, 33, 34,
Latua (1) S Chile	1	100%	34
Capsiceae (2/~231)	**2/57**	**100%/25%**	**15, 24, 30, 31, 32, 33, 34, 42, 51, 52, 53, 54**
Capsicum (31[5]) Neotropics	18[1]	58%	12, 15, 24, 30, 31, 32, 33, 34, 42, 51, 52, 53, 54
Lycianthes (~200) Neotropics, Asia	39[1]	19.5%	15, 30, 31, 33, 34, 42, 51, 52, 53, 54
Datureae (~2/18)	**2/15**	**100%/83%**	**15, 21, 24, 30, 32, 33, 34**
Brugmansia (6) Andes	6	100%	15, 21, 24, 30, 33, 34
Datura (11) Mexico, Neotropics	8	73%	12, 15, 21, 24, 30, 32, 33, 34
Iochroma cardeniasianum (Bolivia)	1	100%	34, 42
Physaleae (28/~240)	**25/116**	**89%/48%**	**15, 24, 30,** 31, **32, 33, 34, 42, 53**
Iochrominae (6/37)	**6/36**	**100%/97%**	**15, 30, 31, 33, 34, 42, 53**
Acnistus (1) Neotropics	1	100%	15, 34, 42
Dunalia (5) Andes	5	100%	33, 34, 42
Eriolarynx (3) Argentina & Bolivia	2	67%	34, 42
Iochroma (24) Andes	24	100%	15, 33, 34, 42, 53
Saracha (2) Andes	2	100%	28, 30, 31, 33, 34, 42
Vassobia (2) South America	2	100%	15, 33, 34, 42, 53
Physalinae (10/~122)	**9/51**	**90%/42%**	**15, 24, 30, 31, 33, 34, 42, 53**
Brachistus (3) Mexico & Central America	1	33%	34, 53
Chamaesaracha (10) Mexico & Central America	2	20%	28, 30, 33, 34, 53
Darcyanthus (1) (= *Physalis spruceanus*) Bolivia & Peru	0	0%	
Leucophysalis (3) SW USA, Mexico	3	100%	28, 33, 34, 42, 53
Margaranthus (1) Mexico	1	100%	28, 30, 31, 33, 34, 53
Oryctes (1) SW US	1	100%	33, 34, 53
Quincula (1) SW US, Mexico	1	100%	34, 53
Physalis (~85) Neotropics and China (1)	35	41%	12, 15, 24, 28, 30, 31, 32, 33, 34, 42, 53
Tzeltalia (2) Mexico, Guatemala	2	100%	53
Witheringia (~15) Neotropics	5	33%	15, 33, 34, 42, 53
Withaninae (9/42)	**7/9**	**78%/21%**	**15, 30, 31, 33, 34, 42**
Archiphysalis (3) China, Japan	0	0%	
Athenaea (7) Brazil	1	14%	34

Aureliana (5) S South America	1	29%	33, 34
Discopodium (2) East African mtns	1	100%	34
Mellissia (1) St. Helena	1	100%	34
Nothocestrum (4^{8}) Hawaii	2	50%	34
Physaliastrum (9) Asia	0	0%	
Tubocapsicum (1) China	1	100%	15, 31, 33, 34, 42
Withania (10) Canary Is., Africa to Nepal	2	20%	15, 30, 33, 34
Genera of Physaleae not assigned to a more inclusive clade (3/39)	**3/20**	**100%/51%**	
Cuatresia (11) Neotropics	3	27%	34, 42
Deprea (6^{6}) Neotropics	3	50%	(unpubl. sequences in GenBanK)
Larnax (22^{6}) Andes	14	64%	34, 42, 53, (unpubl. sequences in GenBanK)
"Salpichroina" (2/16) (clade name without rank; Salpichroinae in Olmstead et al. 1999)	**2/2**	**100%/12.5%**	**15, 31, 33, 34, 42**
Nectouxia (1) Mexico	1	100%	34
Salpichroa (15) Andes	1	7%	15, 31, 33, 34, 42
Solaneae (2/~1378)	**2/431**	**100%/31%**	**15, 30, 31, 32, 33, 34, 42, 52**
Jaltomata (~50^{4}) Neotropics	16	32%	15, 28, 30, 31, 33, 34, 52
***Solanum* (~1,328) World-wide**	**415** [1,7,9]	**31%**	**1, 4, 5, 6, 7, 8, 9, 10, 12, 15, 16, 19, 20, 22 23, 24, 27, 29, 30, 31, 32, 33, 34, 35, 36, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 50, 52, 54**
Clades within *Solanum* (following Bohs, 2005 and Weese & Bohs, in press)			
Thelopodium (3) South America	1	33%	
Regmandra (11) South America	2	18%	
Potato (203) New World	130	64%	
African non-spiny (38) Africa	3	8%	
Archaesolanum (8) Australia, South Pacific	2	25%	
Normania (3) Macaronesia, Spain, NW Africa	2	67%	
Morelloid (135) Worldwide	28	21%	
Dulcamaroid (67) Worldwide	11	16%	
S. mapiriense/clandestinum (3) South America	3	100%	
S. wendlandii/allophyllum (8) Neotropics	4	50%	
S. nemorense/hoehnei (4) South America	3	75%	
Cyphomandra (50) Neotropics	36	72%	
Geminata (145) Neotropics & Asia/Australia (1 sp.)	50	34%	
Brevantherum (89) Neotropics	10	11%	
Leptostemonum (561) Worldwide	**130**	**23%**	

Clades within Leptostemonum (Levin et al, 2006)			
Robustum	6		
Lasiocarpa	12		
Acanthophora	14		
Androceras/Crinitum	5		
Torva	5		
Carolinense	3		
Bahamense	2		
Micracantha	3		
Elaeagnifolium	3		
Old World	71		
miscellaneous unplaced	6		
Juanulloeae (5/32) Treatment follows Knapp et al, 1997	**4/5**	**80%/16%**	**15, 24, 30, 32, 33, 34**
Dyssochroma (2) SE Brazil	1	50%	30, 33, 34
Juanulloa (11) South and Central America	1	12.5%	12, 15, 24, 30, 32, 33, 34
Markea (9) South and Central America	2	22%	30, 33, 34
Merinthopodium (3) South America	1	50%	34
Trianaea (~6) South America	0	0%	
Markea lopezii incertae sedis	0	0%	
Genera of Solanoideae not assigned to a more inclusive clade (5/27)	**5/9**	**100%/33%**	
Exodeconus (6) W South America	1	17%	24, 30, 33, 34
Mandragora (2) Eurasia	2	100%	12, 15, 30, 32, 33, 34, 54
Nicandra (1) Neotropics	1	100%	12, 15, 24, 30, 32, 33, 34
Schultesianthus (8) Neotropics	2	25%	34
Solandra (10) Neotropics	3	30%	12, 15, 24, 30, 32, 33, 34

References (group for which primary evidence for phylogeny is presented; for *Solanum* unitalicized names denote clades sensu Weese and Bohs, 2007).

1. Anderson et al., 1996. (*Solanum*: Potato: sect. *Basarthrum*)
2. Ando et al., 2005. (*Petunia*, *Calibrachoa*)
3. Aoki and Ito, 2000. (*Nicotiana*)
4. Bohs, 2004. (*Solanum*: Leptostemonum: sect. *Lasiocarpa*)
5. Bohs, 2005. (*Solanum*)
6. Bohs, 2007. (*Solanum*: Cyphomandra)

7. Bohs and Olmstead, 1997. (*Solanum*)
8. Bohs and Olmstead, 1999. (*Solanum*)
9. Bohs and Olmstead, 2001. (*Solanum*: Normania)
10. Castillo and Spooner, 1997. (*Solanum*: Potato)
11. Clarkson et al., 2004. (*Nicotiana*, Anthocercideae)
12. Fay et al., 1998. (*Duckeodendron*, Goetzeoideae)
13. Fukuda et al., 2001. (*Lycium*)
14. Garcia and Olmstead, 2003. (Anthocercideae)
15. Gemeinholzer and Wink, 2004. (Solanaceae)
16. Hosaka et al., 1984. (*Solanum*: Potato)
17. Kulcheski et al., 2006. (*Petunia*)
18. Levin and Miller, 2005. (*Lycium*)
19. Levin et al., 2005. (*Solanum*: Leptostemonum: sect. *Acanthophora*)
20. Levin et al., 2006. (*Solanum*: Leptostemonum)
21. Mace et al., 1999a (*Datura*)
22. Mace et al., 1999b (*Solanum*: Leptostemonum: sect. *Melongena*)
23. Martine et al., 2006. (*Solanum*: Leptostemonum: sect. *Melongena*)
24. Martins and Barkman, 2005. (Solanaceae)
25. Miller, 2002. (*Lycium*)
26. Miller and Venable, 2000. (*Lycium*)
27. Miller and Spooner, 1999. (*Solanum*: Potato)
28. Mione et al., 1994. (*Jaltomata*)
29. Olmstead and Palmer, 1991. (Solanaceae, *Nicotiana*)
30. Olmstead and Palmer, 1992. (Solanaceae)
31. Olmstead and Palmer, 1997. (*Solanum*)
32. Olmstead and Sweere, 1994. (Solanaceae)
33. Olmstead et al., 1999. (Solanaceae)
34. Olmstead et al., in prep. (Solanaceae)
35. Palmer and Zamir, 1982. (*Solanum*: Potato: sect. *Lycopersicon*)
36. Peralta and Spooner, 2001. (*Solanum*: Potato: sect. *Lycopersicon*)
37. Perez et al., 2006. (*Schizanthus*)

38. Prohens et al., 2006. (*Solanum*: Potato: sect. *Basarthrum*)
39. Rodriguez and Spooner, 1997. (*Solanum*: Potato)
40. Sakata and Lester, 1997. (*Solanum*: Leptostemonum: sect. *Melongena*)
41. Santiago-Valentin and Olmstead, 2003. (Goetzeoideae, *Duckeodendron*)
42. Smith and Baum, 2006. Physaleae: Iochrominae)
43. Spooner and Castillo, 1997. (*Solanum*: Potato)
44. Spooner and Sytsma, 1992. (*Solanum*: Potato)
45. Spooner et al., 1991. (*Solanum*: Potato)
46. Spooner et al., 1993. (*Solanum*)
47. Spooner et al., 2005a. (*Solanum*: Potato)
48. Spooner et al., 2005b. (*Solanum*: Potato: sect. *Lycopersicon*)
49. Tago-Nakazawa and Dillon, 1999. (*Nolana*)
50. Volkov et al., 2003. (*Solanum*: Potato)
51. Walsh and Hoot, 2001. (Capsiceae: *Capsicum*)
52. Weese and Bohs, 2007. (*Solanum*)
53. Whitson and Manos, 2005. (Physaleae: Physalinae: *Physalis*)
54. Yuan et al., 2006. (Hyoscyameae)

Species estimates based on personal communications.
[1]L. Bohs – *Capsicum*, *Lycianthes*, and *Solanum*
[2]M. Dillon and J. Wen – *Nolana*
[3]R. Levin – *Lycium*
[4]T. Mione – *Jaltomata*
[5]E. Moscone – *Capsicum*
[6]N. Sawyer – *Deprea* and *Larnax*
[7]D. Spooner – *Solanum*
[8]W. Wagner – *Nothocestrum*
[9]G. van der Weerden and M. Manoko – *Solanum*

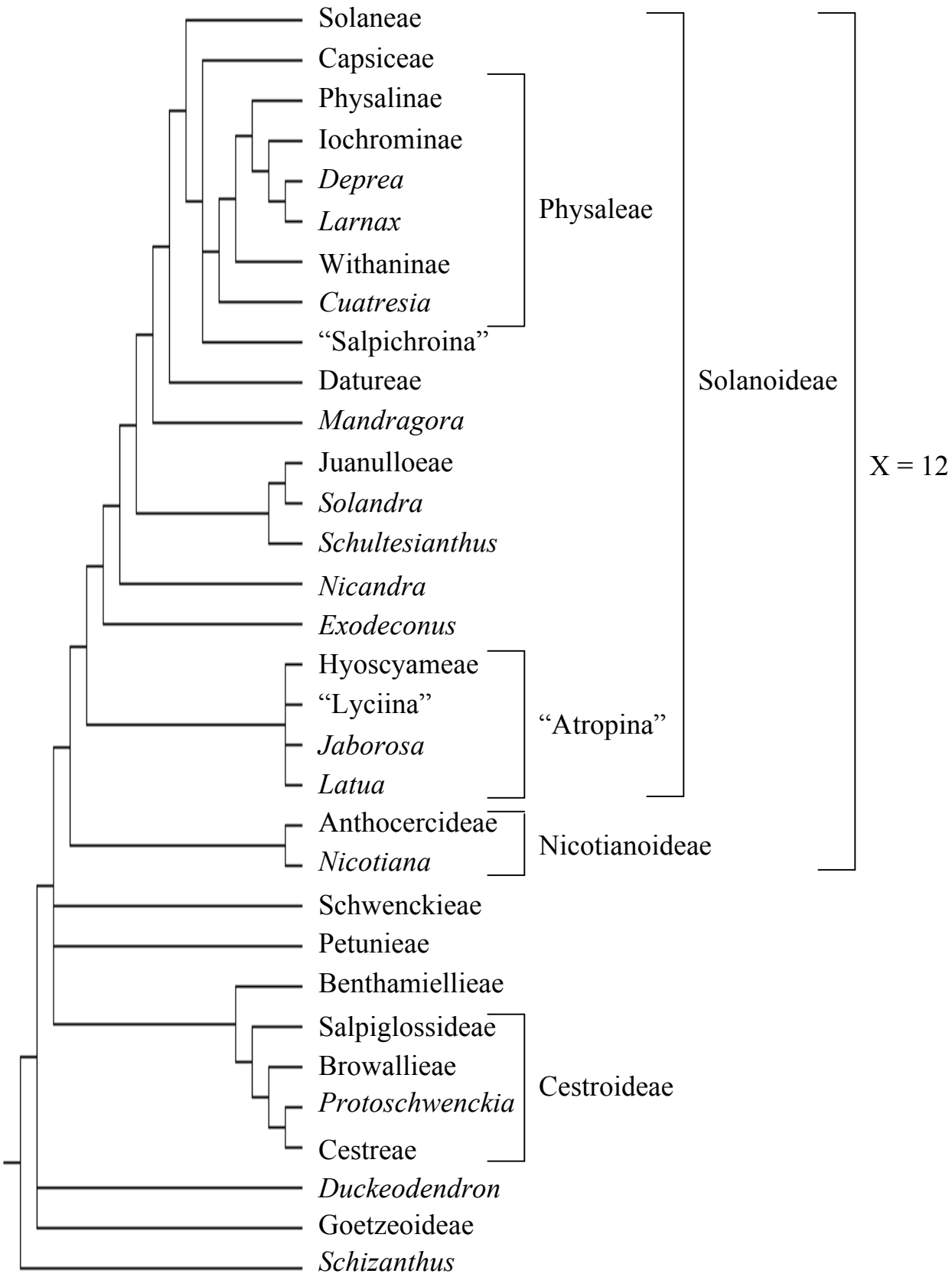

Fig. 1. Major clades of Solanaceae following Olmstead et al., in prep.

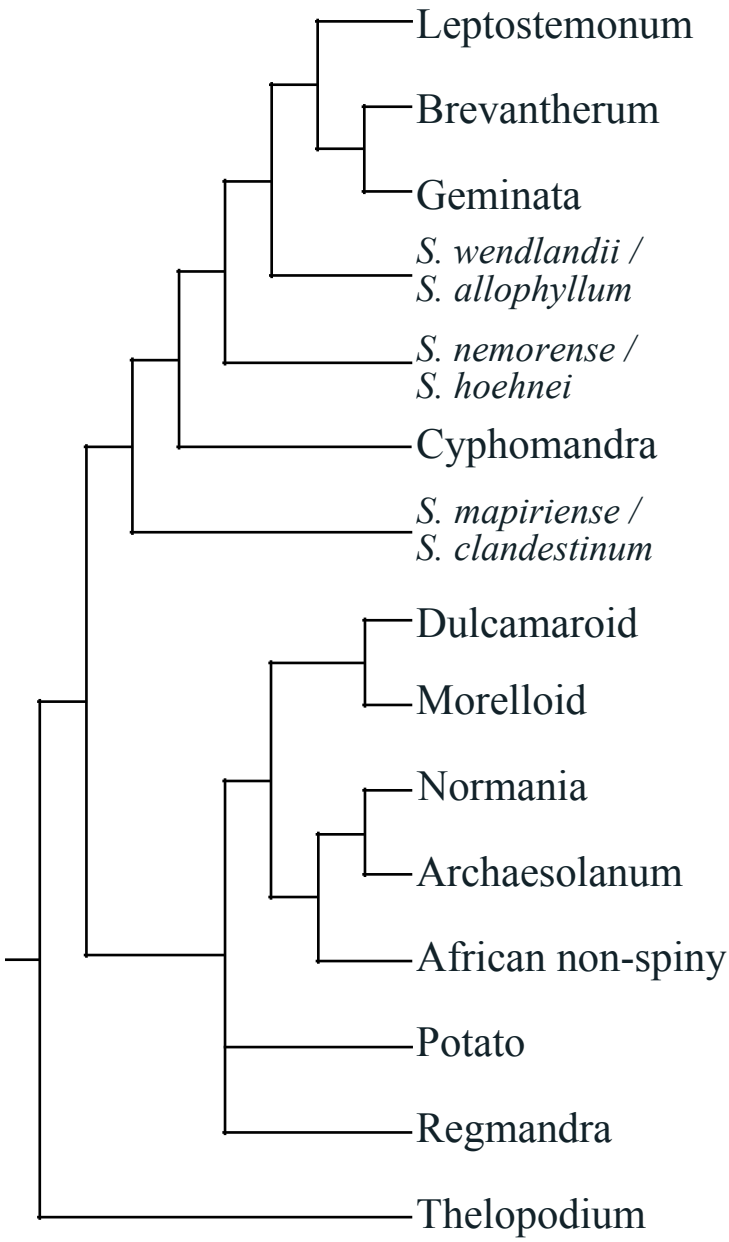

Fig. 2. Major clades of *Solanum* following Weese and Bohs, 2007.