

## Anther Wall Formation in Solanaceae Species

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Anther wall formation was studied in 32 species belonging to 27 genera of Solanaceae. Dicotyledonous and basic types of wall formation were observed, as well as several deviations due to subsequent periclinal divisions in the layers formed (middle layers and sometimes the endothecium). One type of wall formation was observed in each species. Some genera are uniform in their type of wall formation, while others are heterogeneous; a similar situation was observed at the tribal level. Summarizing all reported information on anther wall formation in the Solanaceae, 64 % of species show the basic type, while the remaining 36 % show the dicotyledonous type. Thus, neither type predominates, and no single type characterizes genera, tribes or the entire family.

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**Key words:** Anther ontogeny, anther wall formation, Solanaceae.

### INTRODUCTION

The anther wall is formed by a specific number of cell layers that originate in the earliest developmental stages. Davis (1966) observed different patterns of cell divisions starting in the first two hypodermal layers termed the secondary parietal layers. As a consequence of these divisions, all the wall layers are formed. Four different types of wall formation are recognized: basic, dicotyledonous, monocotyledonous and reduced (Davis, 1966). Many authors have used this classification when describing anther wall ontogeny (Swarajya Lakshmi and Pullaiah, 1989; Hardy and Stevenson, 2000; Strittmatter and Galati, 2000).

Davis (1966) affirmed that dicotyledonous anther wall formation characterized the Solanaceae, with one exception, *Withania somnifera* Dunal, which develops the basic type. The dicotyledonous type was subsequently observed in additional taxa (Bernardello, 1983; Alemany, 1985; Siddiqui and Khan, 1988), but the basic type has also been reported in other species (Prasad and Singh, 1978; Siddiqui and Khan, 1988; Carrizo García, 1998).

In the context of an extensive study of the androecium in the Solanaceae, a diverse group of species was analysed to determine their type of wall formation, as well as the frequency of each type at different hierarchical levels.

### MATERIALS AND METHODS

A total of 32 species belonging to 27 genera was studied (Table 1). All materials examined are deposited at the spirit collection and the herbarium of the Botanical Museum of Córdoba, Argentina (CORD).

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For each species young buds of different sizes were fixed using FAA (formalin, ethilic alcohol and acetic acid), dehydrated, embedded in Paraplast™ and transversely sectioned using a microtome. The sections, 8–12 µm thick, were stained with Cresyl Brilliant Blue (modified from Pérez and Tomasi, 1997) or Cresyl Violet (D'Ambrogio, 1986). Sections were observed under a compound light microscope.

### RESULTS

All the species examined showed the same type of wall formation until the development of the two secondary parietal layers, the outer and the inner. Anther wall formation types are defined on the basis of these two layers and subsequent cell divisions. Only the basic and the dicotyledonous types were observed in the samples analysed.

In the basic type of wall formation, all the cells in the secondary parietal layers divide once periclinally, forming four new layers (Fig. 1A and B). These layers differentiate, from outside to inside, into the endothecium, the two middle layers and the tapetum. The dicotyledonous type differs from the basic type in that only the outer secondary parietal cell layer divides periclinally (Fig. 1C). As a consequence, only three layers are formed: the endothecium, one middle layer and the tapetum. The endothecium and the middle layer are formed from the outer secondary parietal layer, and the tapetum is formed from the inner secondary parietal layer.

In a number of species, regardless of their wall formation type, new periclinal cell divisions may occur when the tapetum differentiates (Fig. 1D–F). These subsequent divisions do not modify the type of wall formation, since they occur at a later stage. However, a distinction is needed between the basic and dicotyledonous types in 'stricto sensu', in which the cell divisions are restricted to those

TABLE 1. *Species studied and collection data*

Species	Collection data
<i>Athenaea pereirae</i> Barboza et Hunz.	Brazil, Hunziker 25203
<i>Aureliana fasciculata</i> (Vellozo) Sendtn.	Brazil, Hunziker 25147
<i>Browallia americana</i> L.	Colombia, Barboza 130
<i>Brunfelsia australis</i> Benth.	Argentina, cult. (Cordoba), CORD 318
<i>Cestrum lorentzianum</i> Griseb.	Argentina, Barboza <i>et al.</i> 157
<i>Cyphomandra betacea</i> (Cav.) Sendt.	Argentina, cult. (Buenos Aires), Carrizo García s.n.
<i>Cyphomandra endopogon</i> Bitter	Netherlands, cult. (Nijmegen), Carrizo García s.n.
<i>Datura ceratocaula</i> Ortega	Mexico, CORD 855
<i>Duboisia myoporoides</i> R. Br.	Netherlands, cult. (Nijmegen), Carrizo García s.n.
<i>Dyssochroma viridiflorum</i> (Sims) Miers	Brazil, cult. (Rio do Janeiro), Freire de Carvalho s.n.
<i>Eriolarynx iochromoides</i> (Hunz.) Hunz.	Argentina, Hunziker 25528
<i>Exodeconus prostratus</i> (L'Herit.) Raf.	Peru, Bernardello et Leiva 870
<i>Fabiana patagonica</i> Speg.	Argentina, Luti 9002
<i>Hawkesiophyton panamense</i> (Standl.) Hunz.	England, cult. (Birmingham), Hunziker s.n.
<i>Iochroma</i> sp.	Argentina, cult. (Buenos Aires), Carrizo García s.n.
<i>Leptoglossis linifolia</i> (Miers) Griseb.	Argentina, A. A. Cocucci 243
<i>Nicotiana glauca</i> Graham	Argentina, CORD 582
<i>Nicotiana paa</i> Mart.-Crov.	Argentina, Hunziker <i>et al.</i> 25524
<i>Nierembergia browallioides</i> Griseb.	Argentina, Hunziker 10094
<i>Normania triphylla</i> (Lowe) Lowe	Netherlands, cult. (Nijmegen), Carrizo García s.n.
<i>Petunia axillaris</i> (Lam.) Britton, Stern et Poggenb.	Argentina, CORD 583
<i>Physochlaina orientalis</i> G. Don	Netherlands, cult. (Nijmegen), van der Weerden s.n.
<i>Saracha</i> sp.	Netherlands, cult. (Nijmegen), Carrizo García s.n.
<i>Schizanthus grahamii</i> Gill.	Argentina, A. A. Cocucci 105
<i>Schwenckia americana</i> L.	Argentina, CORD 589
<i>Schwenckia lateriflora</i> (Vahl) Carvalho	Venezuela, Benítez de Rojas 5936
<i>Solanum americanum</i> Mill.	Argentina, CORD 585
<i>Solanum argentinum</i> Bitter et Lillo	Argentina, CORD 581
<i>Solanum glaucophyllum</i> Desf.	Argentina, CORD 588
<i>Streptosolen jamesonii</i> (Benth.) Miers	Argentina, cult. (Capital Federal), CORD 405
<i>Tubocapsicum anomalum</i> (Franch. et Sav.) Makino	Netherlands, cult. (Nijmegen), Carrizo García s.n.
<i>Vestia foetida</i> (Ruiz et Pav.) Hoffmann.	Netherlands, cult. (Nijmegen), Hunziker s.n.

specified for each type, and the basic and dicotyledonous types in which subsequent divisions occur. The subsequent divisions may occur in any of the hypodermal layers, except the tapetum, before they differentiate. In some species these divisions occur in the middle layer(s) (Fig. 1D and F), whereas in others they take place simultaneously in the future endothecium (Fig. 1E). In either case, these divisions usually do not occur in all the cells of every layer. The new cells and layers behave as middle layers.

Anther wall formation may thus be categorized as follows:

#### *Basic type 'stricto sensu'*

*Brunfelsia australis*, *Cestrum lorentzianum*, *Cyphomandra betacea*, *Cyphomandra endopogon*, *Fabiana patagonica*, *Iochroma* sp., *Leptoglossis linifolia*, *Nicotiana glauca* (Fig. 1A), *Nicotiana paa*, *Saracha* sp., *Schizanthus grahamii*, *Streptosolen jamesonii*, *Tubocapsicum anomalum* and *Vestia foetida*.

#### *Basic type 'with subsequent divisions'*

*Aureliana fasciculata*, *Datura ceratocaula*, *Dyssochroma viridiflorum*, *Nierembergia browallioides* and *Solanum glaucophyllum*: only one subsequent division in cells of

the outer middle layer. More unusual in *Aureliana fasciculata*, *Datura ceratocaula* and *Solanum glaucophyllum*. Up to three middle layers will be formed.

*Solanum argentinum*: subsequent divisions are observed in the outer middle layer and/or the endothecium (Fig. 1D). Three or four middle layers are formed.

*Hawkesiophyton panamense* and *Normania triphylla*: the subsequent divisions may occur simultaneously in the two middle layers and in the endothecium. Up to six middle layers may be formed in *Normania triphylla* and nine in *Hawkesiophyton panamense* (Fig. 1E).

#### *Dicotyledonous type 'stricto sensu'*

*Browallia americana*, *Schwenckia americana* (Fig. 1C) and *Schwenckia lateriflora*.

#### *Dicotyledonous type 'with subsequent divisions'*

*Athenaea pereirae* (Fig. 1F), *Duboisia myoporoides*, *Eriolarynx iochromoides*, *Exodeconus prostratus*, *Petunia axillaris*, *Physochlaina orientalis* and *Solanum americanum*: subsequent divisions are observed in the middle layer. Eventually, other divisions occur in some endothecial cells, except in *Athenaea pereirae*. In general, two middle layers, rarely three, are formed.

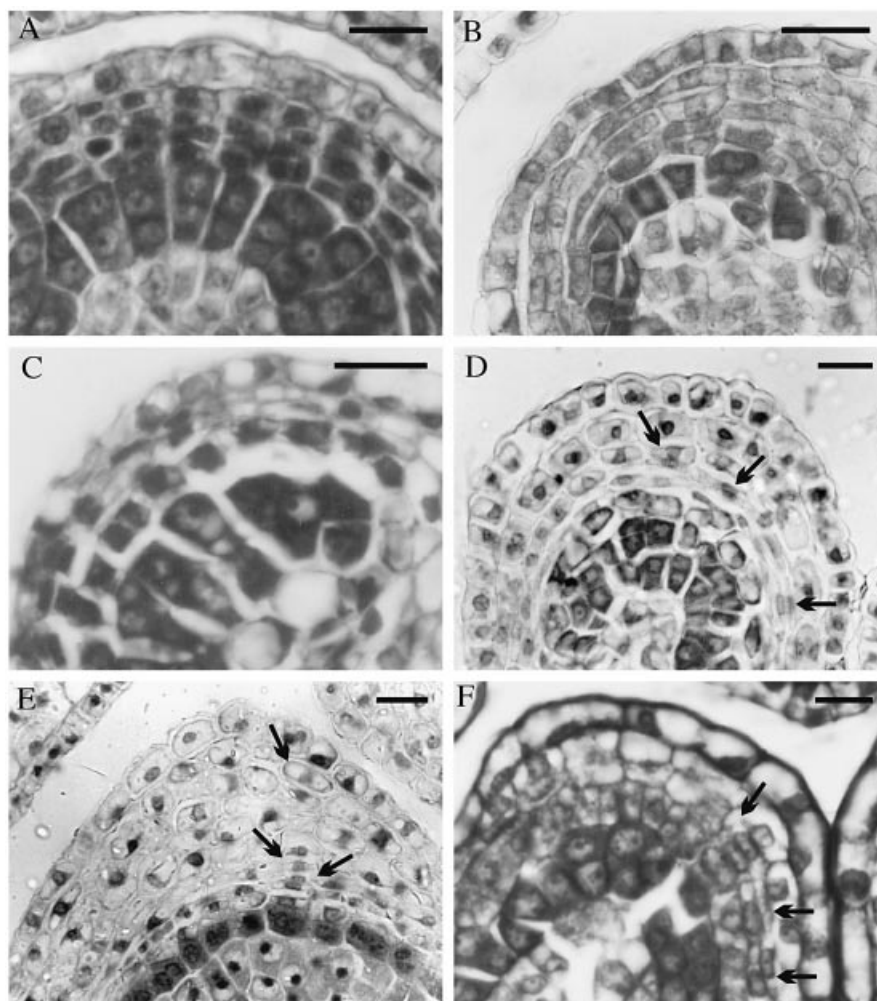


FIG. 1. Anther wall formation in Solanaceae. A and B, Basic type; C, dicotyledonous type; D and E, basic type with posterior divisions in the middle layers and/or endothecium (arrows); F, dicotyledonous type with posterior divisions in the middle layers (arrows). A, *Nicotiana glauca*; B and D, *Solanum argentinum*; C, *Schwenckia americana*; E, *Hawkesiophyton panamense*; F, *Athenaea pereirae*. Bar = 20  $\mu$ m.

## DISCUSSION

Wall formation usually receives little attention in the study of anther ontogeny. With regard to the Solanaceae, wall formation has been studied in a few genera (Table 2). Data in this paper are reported for the first time for many genera (e.g. *Streptosolen*, *Dyssochroma*, *Schizanthus*, *Normania*, *Tubocapsicum*).

Davis (1966) defined wall formation types on the basis that 'discontinuous variation, however, is apparent in the behaviour of the secondary parietal layers and, although the final product is an anther wall, it is achieved by a precise series of periclinal cell divisions'. This series of cell divisions (dicotyledonous and basic types '*stricto sensu*') was observed in several of the species analysed (e.g. *Schwenckia americana* and *Brunfelsia australis*, respectively). However, irregular divisions subsequent to that series could be observed in other species.

Davis (1966) did consider the subsequent divisions, but these divisions are generally overlooked in descriptions of

wall development, even when it can be deduced that they have occurred. For example, two middle layers are mentioned in the wall of *Nierembergia linariaefolia* Graham (syn = *Nierembergia hippomanica* Miers; Alemany, 1985), as well as in *Atropa* spp. (Sharma *et al.*, 1987), although the dicotyledonous type is reported in both cases. In contrast, Prasad and Singh (1978) mentioned the subsequent divisions in *Nicandra physalodes* (L.) Gaertn. and reported that both secondary parietal layers divide, and the outer derivative continues dividing to form a five to six-layered wall. These subsequent divisions cannot be ignored for several reasons. First, they highlight the different properties of the cells, such as the ability to divide. Secondly, the cell divisions determine the number of wall layers formed and, consequently, the wall structure (e.g. up to three middle layers in *Nierembergia browallioides*, and nine in *Hawkesiophyton panamense*). Finally, they show the difficulty in interpreting wall formation type because subsequent divisions may obscure the analysis and lead to incorrect conclusions. For instance, four layers are formed

TABLE 2. Types of wall formation in Solanaceae (species arranged according to Hunziker, 2001).

Taxon	Type of anther wall formation	Reference
Subfamily Anthocercidoideae		
Tribe Anthocercideae		
<i>Duboisia myoporoides</i>	Dicotyledonous*	This paper
Subfamily Cestroideae		
Tribe Cestreae		
<i>Cestrum lorentzianum</i>	Basic	This paper
<i>Vestia foetida</i>	Basic	This paper
Tribe Nicotianeae		
<i>Fabiana patagonica</i>	Basic	This paper
<i>Leptoglossis linifolia</i>	Basic	This paper
<i>Nicotiana tabacum</i> , <i>N. rustica</i>	Basic	Jagannadham, 1988
<i>Nicotiana glauca</i> , <i>N. paa</i>	Basic	This paper
<i>Nierembergia linariaefolia</i>	Dicotyledonous*	Aleman, 1985
<i>Nierembergia browallioides</i>	Basic*	This paper
<i>Petunia axillaris</i>	Dicotyledonous*	This paper
Tribe Francisceae		
<i>Brunfelsia australis</i>	Basic	This paper
Tribe Browallieae		
<i>Browallia americana</i>	Dicotyledonous	This paper
<i>Streptosolen jamesonii</i>	Basic	This paper
Tribe Schwenckieae		
<i>Schwenckia americana</i> , <i>S. lateriflora</i>	Dicotyledonous	This paper
Subfamily Juanulloideae		
Tribe Juanulloae		
<i>Dyssochroma viridiflorum</i>	Basic*	This paper
<i>Hawkesiophyton panamense</i>	Basic*	This paper
Subfamily Schizanthoideae		
Tribe Schizanthaeae		
<i>Schizanthus grahami</i>	Basic	This paper
Subfamily Solanoideae		
Tribe Nicandreae		
<i>Nicandra physalodes</i>	Basic*	Prasad and Singh, 1978
Tribe Datureae		
<i>Brugmansia candida</i> , <i>B. suaveolens</i>	Basic*	Carrizo García, 1998
<i>Datura metel</i>	Basic*	Thiagarajan, 1986
<i>Datura discolor</i> , <i>D. ferox</i> , <i>D. inoxia</i> , <i>D. kimatocarpa</i> , <i>D. leichhardtii</i> , <i>D. stramonium</i>	Basic*	Carrizo García, 1998
<i>Datura fastuosa</i> , <i>D. metel</i> , <i>D. stramonium</i>	Dicotyledonous	Sharma, 1984
<i>Datura ceratocaula</i>	Basic*	This paper
Tribe Lycieae		
<i>Lycium cestroides</i>	Dicotyledonous	Bernardello, 1983
Tribe Hyoscyameae		
<i>Hyoscyamus niger</i>	Dicotyledonous*	Sharma <i>et al.</i> , 1987
<i>Physochlaina orientalis</i>	Dicotyledonous*	This paper
Tribe Atropeae		
<i>Atropa belladonna</i> , <i>A. acuminata</i>	Dicotyledonous*	Sharma <i>et al.</i> , 1987
Tribe Solaneae		
<i>Athenaea pereirae</i>	Dicotyledonous*	This paper
<i>Aureliana fasciculata</i>	Basic*	This paper
<i>Cyphomandra betacea</i> , <i>C. endopogon</i>	Basic	This paper
<i>Cyphomandra sciadostylis</i>	Dicotyledonous*	Sazima <i>et al.</i> , 1993
<i>Eriolarynx iochromoides</i>	Dicotyledonous*	This paper
<i>Exodeconus prostratus</i>	Dicotyledonous*	This paper
<i>Iochroma</i> sp.	Basic	This paper
<i>Normania triphylla</i>	Basic*	This paper
<i>Saracha</i> sp.	Basic	This paper
<i>Solanum cornutum</i> , <i>S. citrullifolium</i> , <i>S. integrifolium</i> , <i>S. aethiopicum</i> , <i>S. opacum</i> , <i>S. sisymbriifolium</i> , <i>S. torvum</i>	Dicotyledonous (some species*)	Siddiqui and Khan, 1988
<i>Solanum americanum</i>	Dicotyledonous*	This paper
<i>Solanum argentinum</i> , <i>S. glaucophyllum</i>	Basic*	This paper
<i>Solanum bonariense</i> , <i>S. pseudocapsicum</i> , <i>S. surattense</i>	Basic	Siddiqui and Khan, 1988
<i>Solanum nigrum</i>	Basic and dicotyledonous	Bhandari and Sharma, 1987
<i>Tubocapsicum anomalum</i>	Basic	This paper
<i>Withania somnifera</i>	Basic	Davis, 1966
Tribe Jaboroseae		
<i>Jaborosa sativa</i> , <i>J. bergii</i> , <i>J. integrifolia</i>	Basic	Barboza, 1991

TABLE 2. Continued

Taxon	Type of anther wall formation	Reference
<i>Jaborosa runcinata</i> , <i>J. odonelliana</i> , <i>J. oxipetala</i> , <i>J. leucotricha</i> , <i>J. laciniata</i> , <i>J. kurtzii</i> , <i>J. rotacea</i> , <i>J. lanigera</i> , <i>J. reflexa</i>	Basic*	Carrizo García, 2000
<i>Salpichroa organifolia</i> , <i>S. tristis</i>	Dicotyledonous	Carrizo García, 2000

Asterisks indicate cases in which subsequent divisions occur in the middle layers and/or endothecium (some inferred from the reference cited).

in the basic type '*stricto sensu*'; however, wall formation is not always of the basic type in all species with four layers since the four layers may have originated from the dicotyledonous type with one subsequent division. When summarizing all available information regarding anther wall formation in the Solanaceae, it is apparent that subsequent divisions are frequent within the family (asterisks in Table 2) although there is no apparent consistency within taxonomical groups.

It is worth mentioning that a single type of anther wall formation was observed in each species. The only exception reported in the Solanaceae to date is in *Solanum nigrum* L., in which basic and dicotyledonous types develop simultaneously in the same anther (Bhandari and Sharma, 1987).

With regard to the distribution of the types of wall formation in supraspecific taxa (Hunziker, 2001), several generalizations can be made (Table 2). Of the genera in which more than one species has been studied, *Nicotiana* seems to be relatively constant, although only four of the approx. 60 species have been examined (Jagannadham, 1988). The two *Schwenckia* species share the dicotyledonous type, being the first records for the genera. Other genera which to date have a uniform wall formation type include *Brugmansia* (Carrizo García, 1998) and *Jaborosa* (Barboza, 1991; Carrizo García, 2000) with the basic type, and *Atropa* (Sharma *et al.*, 1987) and *Salpichroa* (Carrizo García, 2000) with the dicotyledonous type.

In contrast, other genera are heterogeneous (Table 1). The dicotyledonous type is reported in *Cyphomandra sciadostylis* Sendt. (Sazima *et al.*, 1993), but the basic type occurs in *C. betacea* and *C. endopogon*. A similar situation is found in *Nierembergia*, where the basic type was observed in *N. browalliioides*, whereas *N. linariaefolia* develops the dicotyledonous type (Alemany, 1985). Both types have been reported in species of *Solanum* (Siddiqui and Khan, 1988), and both types were found in the three species examined in this research.

The genus *Datura* is exceptional. Only one species was included in this study, *Datura ceratocaula*, whose wall formation type (basic) is the same as that of another six *Datura* species reported previously (Carrizo García, 1998). However, the dicotyledonous type (Sharma, 1984) and the basic type are reported in *Datura stramonium* L. and *Datura metel* L. [Carrizo García (1998) and Thiagarajan (1986), respectively]. Research is needed to resolve this problem.

At the tribal level, among non-monotypic tribes, Nicotianeae, Browallieae and Solaneae appear to be heterogeneous, and contain both the dicotyledonous and the basic types (Table 2). The same situation has been reported previously in two other tribes, Datureae (Sharma, 1984; Thiagarajan, 1986; Carrizo García, 1998) and Jaboroseae (Carrizo García, 2000). In contrast, in the tribes Cestreae, Juanulloae and Hyoscyameae the same type was found in the two genera analysed for each tribe (Table 2).

Of all the species studied to date (including data in the literature), and ignoring the subsequent divisions, 64 % show the basic type of anther wall formation, while the remaining 36 % develop the dicotyledonous type. In contrast to Davis' suggestion (1966), the dicotyledonous type is less frequent than the basic type indicating that the dicotyledonous type does not characterize the family. In agreement with previous reports, the presence of both the basic and the dicotyledonous types of wall formation is confirmed in the Solanaceae. Neither type predominates, and no single type characterizes genera, tribes or the entire family.

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