The Journal of Plant Reproductive Biology **1**(2) pp. 1-12, 2009

Nectary and Nectar Features: Occurrence, Significance, and Trends in Bignoniaceae[1]

Leonardo Galetto
Instituto Multidisciplinario de Biología Vegetal (Universidad Nacional de Córdoba – CONICET), Casilla de Correo 495, 5000 Córdoba, Argentina
e-mail : leo@imbiv.unc.edu.ar; Fax : 54-0351-433-2104

ABSTRACT

The variety of pollination strategies present in the Bignoniaceae makes the family ideal for comparative studies of the evolution of floral features. Six flower and nectar parameters were recorded from literature for 50 species (nectar concentration, volume per flower, and amount of sucrose, corolla length, and nectary size and stomata number). Comparisons were made between two pollinator guilds and two tribes. Significant differences were not detected between the tribes Tecomeae and Bignonieae (n= 21 and 16 species respectively). On the other hand, bee-pollinated species presented a higher nectar concentration and a lower nectar volume per flower than bird-pollinated species (n=29 and 8 species respectively). Results showed that some nectar features are correlated with the different pollinator guilds and may indicate nectar adaptations by flowers to their pollinators. Floral structural traits seem to be more conservative than nectar features because the lack of significant differences between tribes and pollinator guilds at both the species and the genus level. These patterns suggest that pollinators would be involved in primary changes on nectar traits and later, in a second evolutionary step, on structural floral modifications.

Keywords : pollinator guild, phylogenetic constraint, corolla length, nectar composition

INTRODUCTION

Bignoniaceae is one of the most diverse families of woody plants (Gentry 1988) and its species are well known in the American tropics for their spectacular flowers and as important components of tropical forests (Gentry 1990). In the words of Gentry (1980), “Bignoniaceae may be considered as an appropriate model of the kinds of evolutionary diversification which have given rise to the incredible diversity of tropical plant communities, with the pollinator interaction mode a key determinant of intracommunity bignon diversity”. Although morphological and phenological specializations in Bignoniaceae flowers and flowering are very important in maintaining the within-community diversity of this family, their role in Bignoniaceae specialization is more ambiguous (Gentry 1990).

Interrelated aspects of its pollination biology include floral morphology and type of pollen vector attracted, flowering phenology, and seasonality (Gentry 1974, 1980). Bignoniaceae pollination strategies are extremely diversified but about 75% of the Bignoniaceae species of a given neotropical plant community are pollinated by large and middle-sized bees (Gentry 1980, 1990).

Nectar concentration, volume per flower, the amount of sucrose, and corolla length are related to pollinators and may indicate pollinator specialization (e.g. Baker 1975, Stiles 1976, Baker & Baker 1983, 1990, Opler 1983, Tamm & Gass 1986, Martínez del Río *et al.* 1988, Martínez del Río 1990a, Mitchell & Paton 1990, Stromberg & Johnsen 1990, Downs & Perrin 1996). Nectary size and the number of stomata per nectary may be related with the nectar secretion capacity and, indirectly, with pollinator preferences. Considering that pollinators have their own nectar preferences and nutritional needs (i.e., volume per flower, concentration, sugar composition, etc.; (Baker 1975, Baker & Baker 1975, 1983, 1990, Baker *et al.* 1998), it is reasonable to expect some flower

[1]I am especially grateful to Warren Hauk for encouraging me to write a paper in relation to the Symposium “Bignoniaceae: the post-Gentry era”, XVI International Botanical Congress, Missouri. I am indebted to C. Torres and to two anonymous reviewers for useful suggestions on early versions of the manuscript. This work was supported by funds from CONICET, Agencia Córdoba Ciencia, ANPCYT, and SECYT (UNC).

specialization at this level. In addition to nectar traits, some structural modifications of the nectary may be detected if nectary traits are accompanying nectar specialization.

The general objective of this work is to review the available data on quantitative nectar and nectary traits of Bignoniaceae, determine the general trends, and evaluate if these characters are related to pollinators.

Species may not be independent samples, as is assumed in most comparative statistical analyses. Members of a single clade can be expected to have the same morphological trait because they share recent ancestors, rather than because they share some ecological feature (Armbruster 1996). In order to diminish phylogenetic relatedness, tribe comparisons were also performed at the genera level considering mean values of each genus as independent data points, keeping in mind the following question: Are trait correlations the result of common descent or have they arisen repeatedly as a result of convergent evolution?

MATERIAL AND METHODS

The source of the species examined (50) are in Appendix 1. Six variables were selected in relation to the objectives of the work: nectar volume per flower, nectar concentration (%, mass/mass), amount of sucrose (%), corolla length, nectary volume, and nectary stomata number. The methods to obtain these data can be found in the literature cited in Appendix 1. Data from pollinators were obtained from the references listed in Appendix 1 and from Gentry (1974, 1990). Although there are species pollinated by bats, butterflies, small bees, and hawkmoths (Gentry 1990), statistically comparable data were obtained for species of the two main pollinator guilds, bees and birds. The bird guild includes hummingbird and passerine pollinated species; there are discrepancies related to nectar preferences of these bird groups (Baker 1975, Hainsworth & Wolf 1976, Stiles 1976, Baker & Baker 1983, 1990, Opler 1983, Tamm & Gass 1986, Martínez del Río *et al*. 1988, 1989, Martínez del Río 1990a, 1990b, Mitchell & Paton 1990, Stromberg & Johnsen 1990, Downs & Perrin 1996, Lotz & Nicolson 1996, Downs 1997a, 1997b).

STATISTICAL ANALYSIS — Although mean values are reported in Appendix 1, all available data for each species were used in statistical analyses. All variables were log-transformed to met assumptions. Comparisons between tribes (Bignonieae vs. Tecomeae) and between pollinator guilds (bees vs. birds) were done with *t*-test. Not enough data were available from Eccremocarpeae and Crescenctieae to be compared together with Bignonieae and Tecomeae. Correlation analyses were done using Pearson's coefficient. The statistical program package SPSS (1992) was used for these analyses.

The phylogenetic relationship due to a common ancestry may confer some dependence among samples. Thus, it would be interesting to analyze the patterns of the different variables considering different levels of taxonomic units. First, the taxonomic unit of comparison was species and, in order to diminish the potential effects of common ancestry, an additional correlation analysis was made using genus as the taxonomic unit of comparison.

RESULTS

The general description of nectary types and nectar characteristics in the family is not detailed here because it can be found elsewhere (Elias & Gelband 1975, 1976; Gentry 1980, Baker & Baker 1983, Rudramuniyappa & Mahajan 1991, Belmonte *et al*. 1994, Galetto 1995 and references therein, Rivera 1996, 2000, Baker *et al*. 1998).

After the bibliographic review, partial data for 50 species on nectar, nectary, and flower traits, and pollinators were available (Appendix 1). When the variables were compared between pollinator guilds, some differences could be evidenced. Bee-pollinated species showed a lower nectar volume per flower but with a higher concentration than nectar of bird-pollinated flowers (Table 1). Although bird-flowers showed a higher mean nectary volume and stomata number, these differences were not significant (Table 1).

Considering the available data base on Bignoniaceae nectar and nectaries, some genera are represented by many species while others by only one species (Appendix 1). In order to diminish the effects of phylogenetic relatedness, a new analysis was done using the mean traits for each genus. The results obtained showed the same pattern described above (Table 1).

Bignonieae species showed a higher nectar volume per flower with a similar concentration but with a higher amount of sucrose in their sugar composition than Tecomeae species (Table 2). The nectaries of Bignonieae species showed a higher volume and a lower stomata number compared to nectaries from Tecomeae species (Table 2). Nevertheless, significant differences could not be detected when comparing nectar and nectary traits at both the species and the tribe level (Table 2).

CORRELATION ANALYSIS — Some of the pairs of variables showed significant correlations (Table 3). Nectar volume per flower was negatively correlated with nectar concentration (Fig. 1), while the nectary size was positively correlated with the number of stomata (Fig. 2) at both the species and the genera level. The other significant positive correlation was between nectary size and the nectar volume per flower (Fig. 3). The latter

Table 1 — Nectar and nectary trends of the Bignoniaceae flowers grouped by the pollinator guild. The analysis of the data was done at both the species and the genus level in order to remove the potential effects of common ancestry.

Variables	**species level**		**Statistical analysis**	**genus level**		**Statistical analysis**
	Bee-pollinated	**Bird-pollinated**		**Bee-pollinated**	**Bird-pollinated**	
Nectar concentration (%, mass/mass)	37.49 ± 9.38 (n = 29)	24.98 ± 9.25 (n = 8)	$t = 2.29$, $P < 0.04$	36.11 ± 7.99 (n = 15)	28.07 ± 5.60 (n = 7)	$t = 2.46$, $P < 0.03$
Nectar volume per flower (µl)	8.31 ± 6.53 (n = 17)	37.30 ± 36.31 (n = 7)	$t = -2.78$, $P < 0.03$	9.32 ± 6.08 (n = 10)	22.76 ± 7.91 (n = 6)	$t = -3.50$, $P < 0.005$
Nectar sucrose (%)	39.95 ± 32.93 (n = 28)	43.92 ± 25.28 (n = 10)	$t = -0.68$, $P = 0.53$	40.93 ± 33.71 (n = 14)	50.28 ± 20.16 (n = 8)	$t = -1.75$, $P = 0.10$
Corolla length (mm)	46.24 ± 11.23 (n = 26)	45.72 ± 11.62 (n = 6)	$t = 0.09$, $P = 0.93$	43.62 ± 10.03 (n = 13)	46.01 ± 12.95 (n = 5)	$t = -0.31$, $P = 0.77$
Nectary volume (mm^3)	5.67 ± 6.53 (n = 24)	7.61 ± 8.81 (n = 6)	$t = -0.39$, $P = 0.71$	6.65 ± 8.11 (n = 12)	8.91 ± 9.19 (n = 5)	$t = -0.58$, $P = 0.58$
Stomata number per nectary	97.76 ± 74.70 (n = 9)	252.98 ± 451.40 (n = 4)	$t = 0.04$, $P = 0.97$	95.14 ± 66.47 (n = 8)	252.98 ± 451.40 (n = 4)	$t = 0.05$, $P = 0.96$

Abbreviations: n= number of taxonomic units (species or genera respectively).

Table 2 — Nectar and nectary trends of the Bignoniaceae flowers grouped by tribe. The analysis of the data was done at both the species and the genus level in order to remove the potential effects of common ancestry.

Variables	species level		Statistical analysis	genus level		Statistical analysis
	Bignonieae	**Tecomeae**		**Bignonieae**	**Tecomeae**	
Nectar concentration (%, mass/mass)	34.06 ± 11.51 (n = 21)	35.25 ± 9.57 (n = 16)	t = -0.68, P = 0.50	34.99 ± 8.59 (n = 12)	31.40 ± 7.29 (n = 10)	t = 0.93, P = 0.37
Nectar volume per flower (µl)	18.86 ± 28.86 (n = 12)	7.12 ± 4.93 (n = 10)	t = 1.85, P = 0.11	16.18 ± 10.48 (n = 8)	8.00 ± 4.83 (n = 7)	t = 1.74, P = 0.11
Nectar sucrose (%)	47.76 ± 34.69 (n = 19)	32.90 ± 25.49 (n = 19)	t = 1.06, P = 0.30	55.59 ± 29.84 (n = 12)	31.17 ± 26.20 (n = 10)	t = 1.39, P = 0.18
Corolla length (mm)	42.26 ± 10.42 (n = 16)	51.43 ± 9.28 (n = 15)	t = -1.49, P = 0.15	43.89 ± 10.20 (n = 10)	47.26 ± 10.50 (n = 7)	t = -0.70, P = 0.49
Nectary volume (mm^3)	7.67 ± 7.52 (n = 16)	4.31 ± 6.12 (n = 13)	t = 1.67, P = 0.13	8.82 ± 8.43 (n = 10)	5.54 ± 8.70 (n = 6)	t = 1.13, P = 0.29
Stomata number per nectary	99.88 ± 79.62 (n = 8)	218.54 ± 398.42 (n = 5)	t = 0.02, P = 0.98	97.19 ± 71.59 (n = 7)	258.99 ± 447.70 (n = 4)	t = -0.5, P = 0.96

Abbreviations: n= number of taxonomic units (species or genera respectively).

Table 3 — Correlation analyses of nectary and nectar traits of the Bignoniaceae flowers. The analysis of the data was done at both the species and the genus level in order to remove the potential effects of common ancestry.

	nectar concentration (%, mass/mass)	**nectar volume per flower (µl)**	**sucrose (%) (mm)**	**corolla length (mm^3)**	**nectary volume**
nectar volume per flower (µl)	*r* = -0.63, *P*<0.001 (n = 23)				
	***r* = -0.71, *P*<0.001 (n = 17)**				
sucrose (%)	*r* = 0.05, *P*=0.78 (n = 32)	*r* = 0.14, *P*=0.58 (n = 18)			
	***r* = 0.07, *P*=0.77 (n = 19)**	***r* = 0.35, *P*=0.22 (n = 14)**			
corolla length (mm)	*r* = -0.15, *P*=0.41 (n = 31)	*r* = 0.13, *P*=0.61 (n = 18)	*r* = 0.17, *P*=0.35 (n = 32)		
	***r* = -0.39, *P*=0.11 (n = 18)**	***r* = 0.35, *P*=0.24 (n = 13)**	***r* = -0.006, *P*=0.98 (n = 19)**		
nectary volume (mm^3)	*r* = -0.11, *P*=0.56 (n = 30)	*r* = 0.69, *P*<0.004 (n = 15)	*r* = 0.36, *P*=0.07 (n = 30)	*r* = 0.34, *P*=0.07 (n = 30)	
	***r* = -0.02, *P*=0.93 (n = 17)**	***r* = 0.45, *P*=0.17 (n = 11)**	***r* = 0.31, *P*=0.23 (n = 17)**	***r* = 0.45, *P*=0.07 (n = 17)**	
stomata number per nectary	*r* = 0.22, *P*=0.46 (n = 13)	*r* = 0.11, *P*=0.77 (n = 9)	*r* = -0.30, *P*=0.32 (n = 13)	*r* = 0.46, *P*=0.12 (n = 13)	*r* = 0.64, *P*<0.02 (n = 13)
	***r* = -0.09, *P*=0.79 (n = 12)**	***r* = 0.07, *P*=0.85 (n = 9)**	***r* = -0.11, *P*=0.73 (n = 12)**	***r* = 0.48, *P*=0.11 (n = 12)**	***r* = 0.62, *P*<0.03 (n = 12)**

Abbreviations: n= number of taxonomic units (species or genera respectively).

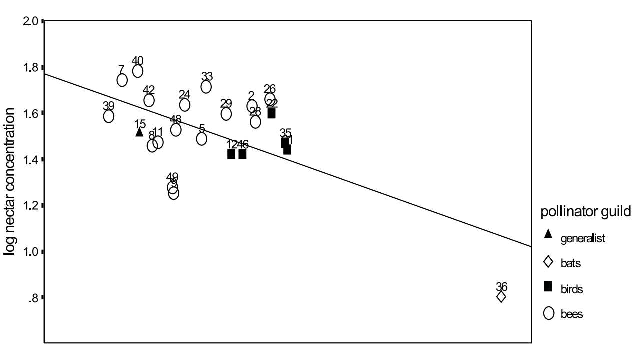

Fig. 1 — Dispersion diagram based on the significant correlation between nectar concentration (%, mass/mass) and nectar volume (µl) per flower of Bignoniaceae species visited by different pollinator guilds. Values represent the mean (log transformed) for each trait. Plotted numbers correspond to species identification codes of Appendix 1.

correlation was found at the species level but not at the genus level (Table 3). Pollinator guild of each species was plotted for all significant correlations (Figs. 1—3). Nectar traits discriminate between bird- and bee-pollinated species (Fig. 1) but not when nectary traits are considered (Figs. 2—3).

DISCUSSION

The process of coevolution is one of the major driving forces influencing the structure of biological communities and the worldwide organization of biodiversity. It can produce mutualistic alliances among phylogenetically distant taxa (Thompson 1998). Although some other evolutionary constraints not related to pollination may also be operating and conducting nectar and nectary traits evolution, studies

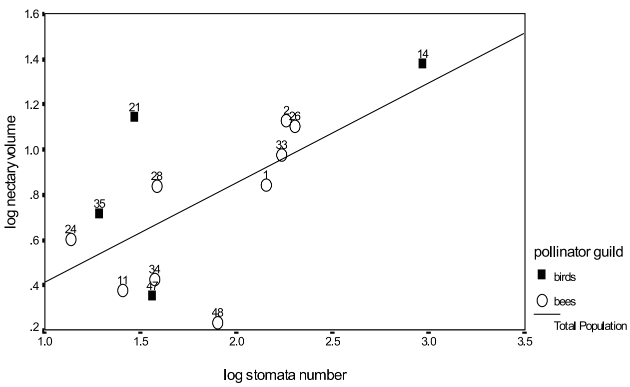

Fig. 2 — Dispersion diagram based on the significant correlation between nectary volume (mm^3) and stomata number per nectary of Bignoniaceae species visited by different pollinator guilds. Values represent the mean (log transformed) for each trait. Plotted numbers correspond to species identification codes of Appendix 1.

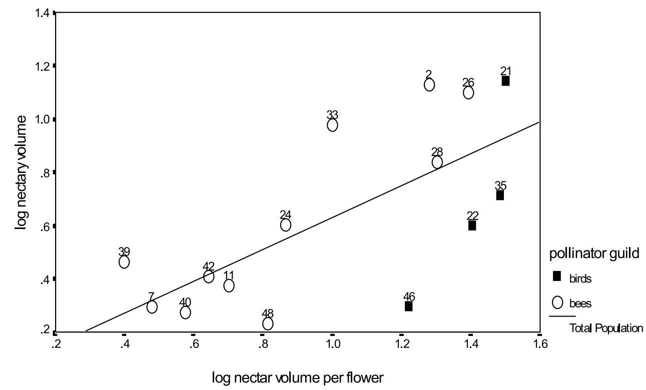

Fig. 3 — Dispersion diagram based on the significant correlation between nectary volume (mm^3) and nectar volume (µl) per flower of Bignoniaceae species visited by different pollinator guilds. Values represent the mean (log transformed) for each trait. Plotted numbers correspond to species identification codes of Appendix 1.

on flowers and their animal visitors have led to the assumption that there are coevolutionary relationships between nectar traits and pollinator type. Several authors have discussed volume and nectar concentration of flowers attracting different guilds of pollinators. In general, they found that hummingbird and honeyeater flowers present large amounts of dilute nectar, especially compared to nectars of bee flowers (e.g. Baker 1975, Pyke & Waser 1981, Cruden *et al.* 1983, Opler, 1983). However, under laboratory conditions, birds given a choice of sugar solutions have been found to prefer the highest concentrations offered at an equal volume presentation (Hainsworth & Wolf 1976, Stiles 1976, Tamm & Gass 1986, Mitchell & Paton 1990), while bees feed in a manner that tends to maximize their rate of net energy intake (Waddington 1983) on a broad range of concentrations, especially when nectar is available in large volumes (Harder 1986). Nectar specialization (volume and concentration) of flowers to different pollinator guilds was previously reported for species belonging to different plant families (e.g. Pyke & Waser 1981, Cruden *et al.* 1983), as was found here for Bignoniaceae.

On the other hand, studies on the sugar composition of nectar showed that long-tongued bees visit flowers of species that secrete nectar of a wide range of sugar compositions, hummingbird flowers produce sucrose-dominated nectars, and passerine bird flowers produce nectars dominated by glucose and fructose (Baker & Baker 1983, 1990). Sugar preferences of hummingbirds have been examined in previous studies with preferences on sucrose solutions instead of equivalent monosaccharides solutions (Stiles 1976, Martínez del Río 1990a, Stromberg & Johnsen 1990). Physiological studies on New World nectarivores passerine birds showed a correlation between sucrose aversion and a relative lack of activity of the enzyme sucrase (Martínez del Río *et al.* 1988, 1989, Martínez del Río 1990b). However, studies on Old World passerine demonstrated that these birds possess high efficiency in sucrose absorption and do not reject sucrose in favor of hexose sugars (Downs & Perrin 1996, Lotz & Nicolson 1996, Downs 1997a, 1997b). It is therefore not surprising to find a diversity of nectar sugar composition in Bignoniaceae species, and the lack of significant differences between the species visited by different pollinator guilds it is not unexpected.

Pollinators may provide a set of discrete opportunities that plants take advantage of, in which case floral differences could represent adaptations to different pollinators. Nevertheless, patterns of phenotypic variation of flowers and pollinator assemblage in a temporal and regional scale are not consistent with the idea of generalized selection by pollinators on floral traits (e.g. Herrera 1988, 1996, Waser *et al.* 1996, Wilson & Thompson 1996; but see Johnson & Steiner 2000). Plant interactions with animals for reproduction may successfully persist even in the absence of mutual adaptation and a shared history of interaction between counterparts (Herrera 1996).

Regardless of selection, some traits may change more easily than others (Thompson 1999). This would be the case when comparing nectar and nectary trait patterns within Bignoniaceae. Independent of the time-period necessary to produce a trait change, the diversity of nectars would reflect the selective pressures to which the Bignoniaceaous flowers have been exposed to different pollinator guilds and their relative more malleability compared to nectary traits. On the other hand, some phylogenetic constraints may be responsible

Appendix 1 — Quantitative traits from Bignoniaceae species after a bibliographic survey. References: code = species code of Figs. 1-3; Conc. = nectar concentration. Values are means. Blank spaces = no data.

Species	code	Tribe	Nectar			Corolla length (mm)	Nectary		Polli-nator guild	Bibliographic source
			Conc. (%)	Volume (µl)	Sucrose (%)		Volume (mm^3)	Stomata number		
Adenocalymma marginatum (Cham.) DC.	1	Bignonieae	41.5	–	0.7	48.3	6.0	140.5	Bees	Galetto, 1995; Rivera, 1999
Amphilophium paniculatum (L.) Kunth	2	Bignonieae	42.0	18.0	73.4	39.6	12.5	180.0	Bees	Galetto, 1995; Rivera, 1999
Anemopaegma laevis DC.	3	Bignonieae	–	–	42.0	–	–	–	Bees	Gottsberger *et al*., 1984
Anemopaegma orbiculatum (Jaqc.) DC.	4	Bignonieae	–	–	99.0	–	–	–	Bees	Baker, 1977
Argylia robusta Sandw.	5	Tecomeae	30.0	8.3	0.4	39.7	–	–	Bees	Galetto, unpublished
Arrabidaea corallina (Jacq.) Sandwith	6	Bignonieae	36.0	–	18.9	33.0	4.5	–	Bees	Rivera, 1999
Arrabidaea chica (Humb. & Bonpl.) B. Verl.	7	Bignonieae	55.0	2.0	9.5	30.0	1.0	–	Bees	Galetto, 1995
Arrabidaea mollisima (Kunth) Bureau & K. Schum.	8	Bignonieae	28.0	3.6	–	–	–	–	Bees	Frankie *et al*., 1983
Arrabidaea patellifera (Schlidl.) Sandwith	9	Bignonieae	17.0	5.3	–	–	–	–	Bees	Frankie *et al*., 1983
Arrabidaea selloi (Sprengel) Sandwith	10	Bignonieae	38.0	–	2.8	28.0	3.6	–	Bees	Rivera, 1999
Arrabidaea truncata (Sprague) Sandwith	11	Bignonieae	29.0	4.0	11.9	38.9	1.4	24.5	Bees	Galetto, 1995
Campsidium valdivianum (Philip.) Skottsb.	12	Tecomeae	25.6	13.4	42.8	–	–	–	Birds	Galetto & Aizen, unpublished
Campsis grandiflora (Thunb.) K. Schum.	13	Tecomeae	–	–	1.6	–	–	–	Birds	Baker & Baker, 1983, Baker *et al*., 1998
Campsis radicans (L.) Seeman	14	Tecomeae	25.6	21.0	35.2	64.6	23.2	930.0	Birds	Elias & Gelband, 1975; Bertin, 1982; Baker & Baker, 1982; Galetto, 1995; Baker *et al*., 1998

Appendix 1 — Continued ....

Species	code	Tribe	Nectar			Corolla length (mm)	Nectary		Polli-nator guild	Bibliographic source
			Conc. (%)	Volume (μl)	Sucrose (%)		Volume (mm^3)	Stomata number		
Catalpa speciosa Warder ex Engelm.	15	Tecomeae	31.4	2.0	–	–	–	–	gener-alist	Stephenson & Thomas, 1977
Crescentia alata Knuth	16	Crescentieae	–	110.0	20.0	55.0	–	–	Bats	Opler, 1983; Baker *et al*., 1998
Crescentia cujete L.	17	Crescentieae	–	–	26.0	–	–	–	Bats	Baker *et al*., 1998
Crescentia sp.	18	Crescentieae	–	–	28.0	–	–	–	Bats	Baker *et al*., 1998
Cuspidaria convoluta (Vell.) A.H. Gentry	19	Bignonieae	32.5	–	60.9	32.7	0.4	–	Bees	Rivera, 1999
Distictella elongata (Vahl) Urban	20	Bignonieae	–	–	85.8	–	–	–	Bees	Gottsberger *et al*., 1984
Dolichandra cynanchoides Cham.	21	Bignonieae	26.7	30.7	49.7	42.9	12.9	28.3	Birds	Galetto, 1995; Morales & Galetto, unpublished
Eccremocarpus scaber Ruíz & Pav.	22	Eccremo-carpeae	39.0	24.5	47.3	28.9	3.0	–	Birds	Belmonte *et al*., 1994; Bernardello *et al*., 1999; Galetto & Aizen, unpublished
Fridericia speciosa Mart.	23	Tecomeae	–	–	69.0	–	–	–	Birds	Gottsberger *et al*., 1984
Jacaranda mimosifolia D. Don	24	Tecomeae	42.8	6.3	36.5	33.6	3.0	12.7	Bees	Galetto, 1995
Kigelia sp.	25	Coleeae	–	–	40.0	–	–	–	Bats	Baker *et al*., 1998
Macfadyena dentata K. Schum.	26	Bignonieae	45.0	23.7	62.3	57.2	11.7	200.0	Bees	Galetto, 1995
Macfadyena uncata (Andrews) Sprague & Sandwith	27	Bignonieae	42.3	–	6.3	43.0	2.8	–	Bees	Rivera, 1999
Macfadyena unguis-cati (L.) A.H. Gentry	28	Bignonieae	35.9	19.0	14.4	44.1	5.9	37.4	Bees	Galetto, 1995

Appendix 1 — Continued ....

Species	code	Tribe	Nectar			Corolla length (mm)	Nectary		Polli-nator guild	Bibliographic source
			Conc. (%)	Volume (µl)	Sucrose (%)		Volume (mm^3)	Stomata number		
Mansoa hymenaea (DC.) A.H. Gentry	29	Bignonieae	39.0	12.2	–	–	–	–	Bees	Frankie *et al.*, 1983
Melloa quadrivalvis (Jacq.) A.H. Gentry	30	Bignonieae	38.0	–	34.6	46.0	1.6	–	Bees	Rivera, 1999
Parabignonia chodatii (Hassler) A.H. Gentry	31	Bignonieae	29.0	–	98.2	65.0	29.1	–	Bees	Rivera, 1999
Pithecoctenium crucigerum (L.) A. Gentry	32	Bignonieae	37.5	–	98.6	46.0	16.5	–	Bees	Rivera, 1999
Pithecoctenium cynanchoides DC.	33	Bignonieae	50.9	9.0	78.3	31.3	8.5	170.0	Bees	Galetto, 1995; Morales & Galetto, unpublished
Podranea ricasoliana (Tanfani) Sprague	34	Tecomeae	28.0	–	12.6	49.1	1.7	36.5	Bees	Galetto, 1995
Pyrostegia venusta (Kerr-Gawl.) Miers	35	Bignonieae	28.6	29.6	69.3	50.1	4.2	18.3	Birds	Gobatto-Rodrigues & Stort, 1992; Galetto *et al.*, 1994; Galetto, 1995; Gusman & Gottsberger, 1996
Spathodea campanulata P. Beauv.	36	Tecomeae	5.4	651.0	–	–	–	–	Birds	Cruden *et al.*, 1983
Tabebuia aurea (Silva Manso) Benth. & Hook. f. ex S. Moure	37	Tecomeae	38.0	–	63.3	58.0	7.7	–	Bees	Rivera, 1999
Tabebuia chrysantha (Jacq.) G. Nicholson	38	Tecomeae	41.0	–	39.7	53.0	2.6	–	Bees	Rivera, 1999
Tabebuia heptaphylla (Vell.) Toledo	39	Tecomeae	38.0	1.5	68.7	52.3	1.9	–	Bees	Galetto, 1995
Tabebuia impetiginosa (Mart. ex DC.) Standl.	40	Tecomeae	60.0	2.8	52.2	56.0	0.9	–	Bees	Frankie *et al.*, 1983; Rivera, 1999
Tabebuia lapacho (K. Schum.) Sandwith	41	Tecomeae	35.0	–	12.5	66.0	7.6	–	Bees	Frankie *et al.*, 1983; Rivera, 1999

Appendix 1 — Continued ....

Species	code	Tribe	Nectar			Corolla length (mm)	Nectary		Pollinator guild	Bibliographic source
			Conc. (%)	Volume (µl)	Sucrose (%)		Volume (mm³)	Stomata number		
Tabebuia ochracea (Cham.) Standl.	42	Tecomeae	44.8	3.4	39.6	57.5	1.6	–	Bees	Frankie *et al.*, 1983; Rivera, 1999
Tabebuia pulcherrima Sandwith	43	Tecomeae	42.0	–	3.2	54.0	2.8	–	Bees	Frankie *et al.*, 1983; Rivera, 1999
Tabebuia rosea (Bertol.) A. DC	44	Tecomeae	–	11.5	–	58.0	–	–	Bees	Baker, 1977; Opler, 1983; Frankie *et al.*, 1983
Tabebuia serratifolia (Vahl) G. Nicholson	45	Tecomeae	–	–	22.0	–	–	–	generalist	Thomas & Dave, 1992
Tecoma capensis (Thunb.) Lindl.	46	Tecomeae	25.5	15.7	4.8	45.0	0.9	–	Birds	Beutler, 1952; Cruden *et al.*, 1983; Subramanian & Inamdar, 1989; Rivera, 1999
Tecoma garrocha Hieron.	47	Tecomeae	23.5	–	43.5	42.8	1.3	35.3	Birds	Galetto, 1995
Tecoma stans (L.) Juss. ex Kunth	48	Tecomeae	32.9	5.5	1.6	42.0	0.7	78.2	Bees	Freeman *et al.*, 1985; Galetto, 1995
Xylophragma seemannianum (Kuntze) Sandwith	49	Bignonieae	18.0	5.2	–	–	–	–	Bees	Frankie *et al.*, 1983
Zeyheria montana Mart.	50	Tecomeae	–	–	76.1	–	–	–	Birds	Gottsberger *et al.*, 1984

for nectary trait stability, as well as other evolutionary forces that were not analyzed here. Anyway, structural traits seem to be more conservative than nectar features because the lack of significant differences between tribes and pollinator guilds at both the species and the genus level. These correlations suggest that pollinators would be involved in primary changes on nectar traits and later, in a second evolutionary step, on structural floral modifications.

LITERATURE CITED

Armbruster WS 1996 Evolution of floral morphology and function: an integrative approach to adaptation, constraint, and compromise in *Dalechampia* (Euphorbiaceae). In DG Lloydt & Barrett SCH (Eds.), *Floral biology. Studies of floral evolution in animal-pollinated plants*, Chapman & Hall, New York, 241-272.

Baker HG 1975 Sugar concentrations in nectars from hummingbird flowers. *Biotropica* **7** 37-41.

Baker HG 1977 Chemical aspects of the pollination biology of woody plants in the tropics. In PB Tomlinson & Zimmermann MH (Eds.). *Tropical trees as living systems*, Cambridge University Press, New York, 57-82.

Baker HG & Baker I 1975 Studies of nectar-constitution and pollinator-plant coevolution. In LE Gilbert & Raven PH (Eds.). *Coevolution of animals and plants*. Columbia Univ. Press, New York, 126-152.

Baker HG & Baker I 1982 Some chemical constituents of floral nectars of *Erythrina* in relation to pollinators and systematic. *Allertonia* **3** 25-37.

Baker HG & Baker I 1983 A brief historical review of the chemistry of floral nectar. In B Bentley & Elias TS (Eds.). *The biology of nectaries*, Columbia Univ. Press., New York, 127-152

Baker HG & Baker I 1990 The predictive value of nectar chemistry to the recognition of pollinator types. *Israel J. Bot.* **39** 157-166

Baker HG, Baker I & Hodges SA 1998 Sugar composition of nectars and fruits consumed by birds and bats in the tropics and subtropics. *Biotropica* **30** 559-586

Belmonte E, Cardemil L & Kalin Arroyo MJ 1994 Floral nectary structure and nectar composition in *Eccremocarpus scaber* (Bignoniaceae), a hummingbird-pollinated plant of central Chile. *Amer. J. Bot.* **81** 493-503

Bernardello G, Galetto L & Forcone A 1999 Floral nectar chemical composition of some species from Patagonia. II. *Biochem. Syst. Ecol.* **27** 779-790

Bertin RI 1982 Floral biology, hummingbird pollination and fruit production of trumpet creeper (*Campsis radicans*, Bignoniaceae). *Amer. J. Bot.* **69** 122-134

Beutler R 1952 Nectar. *Bee World* **24** 128-136

Cruden RWS, Hermann M & Peterson S 1983 Patterns of nectar production and plant -pollinator coevolution. In B Bentley & Elias TS (Eds.), *The biology of nectaries*, Columbia Univ. Press., New York, 80-125

Downs CT 1997a Sugar digestion efficiencies of Gurney's sugarbirds, malachite sunbirds, and black sunbirds. *Physiol. Zool.* **70** 93-99

Downs CT 1997b Sugar preferences and apparent sugar assimilation in the red lory. *Austral. J. Zool.* **45** 613-619

Downs CT & Perrin MR 1996 Sugar preferences of some southern African nectarivorous birds. *Ibis* **138** 455-459

Elias TS & Gelband H 1975 Nectar: its production and functions in trumpet creeper. *Science* **189** 289-291

Elias TS & Gelband H 1976 Morphology and anatomy of floral and extrafloral nectaries in *Campsis* (Bignoniaceae). *Amer. J. Bot.* **63** 1349-1353

Frankie GW, Haber WA, Opler PA & Bawa KS 1983 Characteristics and organization of the large bee pollination system in the Cota Rican dry forest. In CE Jones & Little RJ (Eds.) *Handbook of experimental pollination biology*. Van Nostrand Reinhold Company Inc., New York, 411-447

Freeman CE, Worthington RD & Corral RD 1985 Some floral nectar-sugar compositions from Durango and Sinaloa, Mexico. *Biotropica* **17** 309-313

Galetto L 1995 Nectary structure and nectar characteristics in some Bignoniaceae. *Pl. Syst. Evol.* **196** 99-121

Galetto L, Bernardello LM & Juliani HR 1994 Characteristics of secretion of nectar in *Pyrostegia venusta* (Ker-Gawl.) Miers (Bignoniaceae). *New Phytol.* **127** 465-471

Gentry AH 1974 Co-evolutionary patterns in Central America Bignoniaceae. *Ann. Missouri Bot. Gard.* **61** 728-759

Gentry AH 1980 Bignoniaceae-Part I (Crescentieae and Tourrettieae). *Flora Neotropica Monograph* **25** 1-131

Gentry AH 1988 Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Missouri Bot. Gard.* **75** 1-34

Gentry AH 1990 Evolutionary patterns in neotropical Bignoniaceae. *Mem. New York Bot. Gard.* **55** 118-129

Gobatto-Rodrigues A & Stort MNS 1992 Biologia floral e reproduçao de *Pyrostegia venusta* (Ker-Gawl) Miers (Bignoniaceae). *Revista Brasil. Bot.* **15** 37-41

Gottsberger G, Schrauwen J & Linskens HF 1984 Amino acids and sugars in nectar, and their putative evolutionary significance. *Pl. Syst. Evol.* **145** 55-77

Gusman AB & Gottsberger G 1996 Differences in floral morphology, floral nectar constituents, carotenoids, and flavonoids in petals of orange and yellow *Pyrostegia venusta* (Bignoniaceae) flowers. *Phyton* (Austria) **36** 161-171

Hainsworth FR & Wolf LL 1976 Nectar characteristics and food selection by hummingbirds. *Oecologia* **25** 101-113

Harder LD 1986 Effects of nectar concentration and flower depth on flower handling efficiency of bumble bees. *Oecologia* **69** 309-315

Herrera CM 1988 Variation in mutualisms: the spatio-temporal mosaic of a pollinator assemblage. *Biol. J. Linn. Soc.* **35** 95-125

Herrera CM 1996 Floral traits and plant adaptation to insect pollinators: a devil's advocate approach. In DG Lloydt & Barrett SCH (Eds.). *Floral biology. Studies of floral evolution in animal-pollinated plants*. Chapman & Hall, New York, 65-87

Johnson SD & Steiner KE 2000 Generalization versus specialization in plant pollinator systems. *Trends Ecol. Evol.* **15** 140-143

Lotz CN & Nicolson SW 1996 Sugar preferences of a nectarivorous passerine bird, the lesser double-collared sunbird (*Nectarinia chalybea*). *Funct. Ecol.* **10** 360-365

Martínez del Río C 1990a Sugar preferences in hummingbirds: the influence of subtle chemical differences on food choice. *Condor* **92** 1022-1030

Martínez del Río C 1990b Dietary, phylogenetic, and ecological correlates of intestinal sucrase and maltase activity in birds. *Physiol. Zool.* **63** 987-1011

Martínez del Río C, Stevens BR, Daneke DE & Andreadis PT 1988 Physiological correlates of preference and aversion for sugars in three species of birds. *Physiol. Zool.* **61** 222-229

Martínez del Río C, Karasov WH & Levey DJ 1989 Physiological basis and ecological consequences of sugar preferences in cedar waxwings. *Auk* **106** 64-71

Mitchell RJ & Paton DC 1990 Effects of nectar volume and concentration on sugar intake rates of Australian honeyeaters (Meliphagidae). *Oecologia* **83** 238-246

Opler P 1983 Nectar production in a tropical ecosytem. In B Bentley & Elias TS (Eds.), *The biology of nectaries*. Columbia Univ. Press., New York, 30-79

Pyke GH & Waser NM 1981 The production of dilute nectars by hummingbird and honeyeater flowers. *Biotropica* **13** 260-270

Rivera GL 1996 Nectarios y tricomas florales en cuatro especies de Tecomeae (Bignoniaceae). *Darwiniana* **34** 19-26

Rivera GL 1999 Estudios fenéticos de las especies argentinas de la familia Bignoniaceae. *Anales Inst. Biol. Univ. Nac. Autón. Mexico, Bot.* **70** 141-158

Rivera GL 2000 Nuptial nectary structure of Bignoniaceae from Argentina. *Darwiniana* **38** 227-239

Rudramuniyappa CK & Mahajan PB 1991 Morphogenesis and histochemistry of ovarial nectaries in *Spathodea campanulata* Beauv. *J. Indian Bot. Soc.* **70** 169-174

SPSS Inc 1992 *SPSS for Windows: base system user's guide*. Release 5.0, SPSS Inc., Chicago

Stephenson AG & Thomas WW 1977 Diurnal and nocturnal pollination of *Catalpa speciosa* (Bignoniaceae). *Syst. Bot.* **2** 191-198

Stiles FG 1976 Taste preferences, color preferences, and flower choice in hummingbirds. *Condor* **78** 10-26

Stromberg MR & Johnsen PB 1990 Hummingbird sweetness preferences: taste or viscosity? *Condor* **92** 606-612

Subramanian RB & Inamdar JA 1989 The structure, secretion and biology of nectaries in *Tecomaria capensis* Thunb. (Bignoniaceae). *Phytomorphology* **39** 69-74

Tamm S & Gass CL 1986 Energy intake rates and nectar concentration preferences by hummingbirds. *Oecologia* **70** 20-23

Thomas V & Dave Y 1992 Structure and biology of nectaries in *Tabebuia serratifolia* Nichols (Bignoniaceae). *Bot. J. Linn. Soc.* **109** 395-400

Thompson JN 1998 The population biology of coevolution. *Res. Popul. Ecol.* **40** 159-166

Thompson JN 1999 The raw material for coevolution. *Oikos* **84** 5-16

Waddington KD 1983 Foraging behavior of pollinators. In. Real L (Ed.), *Pollination biology*. Academic Press, New York, 213-239

Waser NM, Chittka L, Price MV, Williams N & Ollerton J 1996 Generalization in pollination systems, and why it matters. *Ecology* **77** 279-296

Wilson P & Thompson JD 1996 How flowers diverge? In DG Lloydt & Barrett SCH (Eds.). *Floral biology. Studies of floral evolution in animal-pollinated plants*. Chapman & Hall, New York, 88-111