DARWINIANA ISSN 0011-6793

38(3-4): 227-239. 2000

NUPTIAL NECTARY STRUCTURE OF BIGNONIACEAE FROM ARGENTINA

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ABSTRACT: Rivera, G. L. 2000. Nuptial nectary structure of Bignoniaceae from Argentina. *Darwiniana* 38(3-4): 227-239.

Nuptial nectary characteristics were investigated in 37 taxa of Bignoniaceae. A nuptial nectary associated to the floral axis was found in all species. Two main types can be distinguished according to their degree of development and functionality: 1) vestigial and non-secretory and 2) well-developed and secretory. The former is characteristic of *Clytostoma* spp., while the latter is found in the remaining species. Two subvarieties of the secretory type of nectary can be discerned according to their position and shape: 1) annular, found in *Adenocalymma, Amphilophium, Anemopaegma, Arrabidaea, Dolichandra, Eccremocarpus, Macfadyena, Melloa, Pithecoctenium, Tabebuia,* and *Tecoma*, and 2) cylindrical, found in *Argylia, Cuspidaria, Jacaranda, Mansoa, Parabignonia, Pyrostegia,* and *Tynnanthus*. Anatomically, two tissues are distinguished: 1) a single-layered epidermis covered by a cuticle and a variable number of stomata, and 2) a secretory tissue composed of compactly arranged parenchyma cells. Both nectary size and nectary/ovary ratio were usually larger in lianas (Bignonieae) than in trees (Tecomeae). Nectary type proved to be consistent among species of same genus but not among genera of same tribe. Nectary features such as vascularization, presence of trichomes and nectary type were constant within the analyzed species and therefore have a reliable taxonomic value.

Key words: Anatomy, Bignoniaceae, Flower, Nectary, Stomata

RESUMEN: Rivera, G. L. 2000. Estructura de nectarios nupciales en Bignoniaceae de Argentina. *Darwiniana* 38(3-4): 227-239.

Se investigaron las características de los nectarios florales en 37 especies de Bignoniaceae. Se encontró un nectario nupcial asociado al eje floral en todas las especies, pudiéndose distinguir dos tipos principales de acuerdo a su grado de desarrollo y funcionalidad: 1) vestigial y no secretor y 2) bien desarrollado y secretor. El primero es característico de las especies de *Clytostoma* mientras que el segundo está presente en el resto de las especies estudiadas. Dos variedades del tipo secretor pueden discernirse de acuerdo a su posición y forma: 1) anular, encontrado en *Adenocalymma, Amphilophium, Anemopaegma, Arrabidaea, Dolichandra, Eccremocarpus, Macfadyena, Melloa, Pithecoctenium, Tabebuia,* y *Tecoma* y 2) cilíndrico, presente en *Argylia, Cuspidaria, Jacaranda, Mansoa, Parabignonia, Pyrostegia,* y *Tynnanthus*. Anatómicamente se distinguen dos tejidos: 1) una epidermis monoestratificada, cubierta por una cutícula y con un número variable de estomas y 2) un tejido secretor compuesto por células parenquimáticas dispuestas en forma compacta. Tanto el tamaño del nectario como la relación nectario/ovario fue usualmente más grande en lianas (Bignoniaceae) que en árboles (Tecomeae). El tipo de nectario fue invariable entre las especies de un mismo género, pero no así entre los géneros de una misma tribu. Las características de los nectarios analizados en este estudio como la vascularización, la presencia de tricomas y el tipo de nectario fueron constantes en las especies analizadas, adquiriendo por lo tanto un importante valor taxonómico.

Palabras clave: Anatomía, Bignoniaceae, Flor, Nectario, Estomas

INTRODUCTION

Bignoniaceae Juss. is a family of woody vines, shrubs and trees, and occasional herbs. It comprises about 100 genera and 800 mostly Neotropical species (Cronquist, 1988). The family is commonly subdivided into eight tribes, five of which are restricted to the New World: Bignonieae, Crescentieae, Eccremocarpeae, Schlegelieae and Tourrettieae. The Tecomeae is found both in the Old and New World, while the Oroxylaeae and Coleeae are localized in Southeast Asia and Africa

respectively (Gentry, 1980). About 50 species grow in Argentina belonging to 22 genera, and are grouped into four tribes (Gentry, 1980; Gentry & Bernardello, 1984).

Flowers are usually large and showy, with a sympetalous, tubular-campanulate, commonly slightly bilabiate corolla. They are visited mainly for nectar by a diverse spectrum of pollinators, from bees, hummingbirds, and butterflies, to moths and bats (Gentry, 1980; 1990). Nectar is secreted by a nectary located at the base of the ovary, although the gland may be vestigial in some species. Nuptial nectaries in the family vary enormously with respect to anatomy, position, and secretion mechanisms (Elias & Gelband, 1976; Subramanian & Inamdar, 1989; Thomas & Dave, 1992; Belmonte et al., 1994; Galetto, 1995).

Nuptial nectary attributes were previously investigated in 24 taxa of Bignoniaceae (Rao, 1971; Elias & Gelband, 1976; Subramanian & Inamdar, 1986a, 1986b, 1989; Rudramuniyappa & Mahajan, 1991; Thomas & Dave, 1992; Belmonte et al., 1994; Galetto, 1995; Rivera, 1996). Except for one work (Galetto, 1995), they lack a comparative analysis among the studied species.

This paper examines nuptial nectary characteristics of 37 species, belonging to 18 genera, from 3 different tribes of Bignoniaceae, growing in Argentina. The aims of this investigation are 1: to observe and compare nectary characteristics, and 2: to determine if nectary anatomical and/or morphological features are relevant characters in the taxonomy of the family.

MATERIALS AND METHODS

The complete species names with authorities and the collections used in this study are listed in Appendix 1. Voucher material is kept at CORD (Museo Botánico de Córdoba). No species authorities are cited in the text to facilitate reading.

Material was fixed in FAA, and then transferred to 70% ethanol. For light microscopy, only flowers in the beginning of anthesis were used. Material was dehydrated through an ethyl alcohol/xylol series and the flowers were embedded in paraffin wax (Johansen, 1940). Sections, both cross and longitudinal, were cut at 8-12 µm, mounted serially, and stained with safranin-astral blue (Maácz & Vágás, 1961). Photographs were taken under a Zeiss Axiophot using Kodak T Max film, ISO 100.

Nectary volume was calculated with the non-circular-section toroids' formula: $V = 2.P.s.r$ (s = nectary sectional area; r = nectary radius measured from the sections' center of gravity). The nectary/ovary ratio was expressed in percentage of surface. This parameter was estimated with reference to the weight of the drawings of the nectary in longitudinal section and the ovary (style and receptacle were excluded). The nectary/ovary ratio was also calculated in order to estimate the relative nectary size, independently of nectary volume. The comparison was made with the ovary surface due to the difficulty of calculating the volume of the ovary.

For scanning electron microscopy, material was washed repeatedly in 70% ethanol and dehydrated through an ethyl alcohol/acetone series (Cohen, 1974). Flowers were critical-point dried using CO_2 (Crang, 1988) and coated with approximately 250Å of gold. Observations were carried out using a JEOL 35CF scanning electron microscope and photomicrographs were taking using AgfaPan APX 100.

RESULTS

A nuptial nectary in association with the floral axis is found in all species (Figs. 1; 2 A, C, 4). Two main different types can be distinguished according to their degree of development and functionality: vestigial, non-secretory, and well-developed, secretory nectaries.

Vestigial, non-secretory nectary

Clytostoma callistegioides and *C. binatum* have a reduced and poorly developed nectary around the base of the ovary (Fig. 1 D, E). In these species, the epidermis of the nectary has no stomata, and its parenchyma cells are very similar to those found in adjacent tissues. No secretion was found in the flowers of any individual among the different analyzed populations.

Well-developed, secretory nectary

These are the nectaries found in most of the studied species. Two different varieties can be found according to their position and shape:

Annular: an enlarged ring or disk usually surrounding the base of the ovary, commonly five-lobed. In longitudinal sections, a *groove* or *furrow* is observed dividing the nectariferous tissue from the base of the ovary, floral axis or gynophore (Figs.

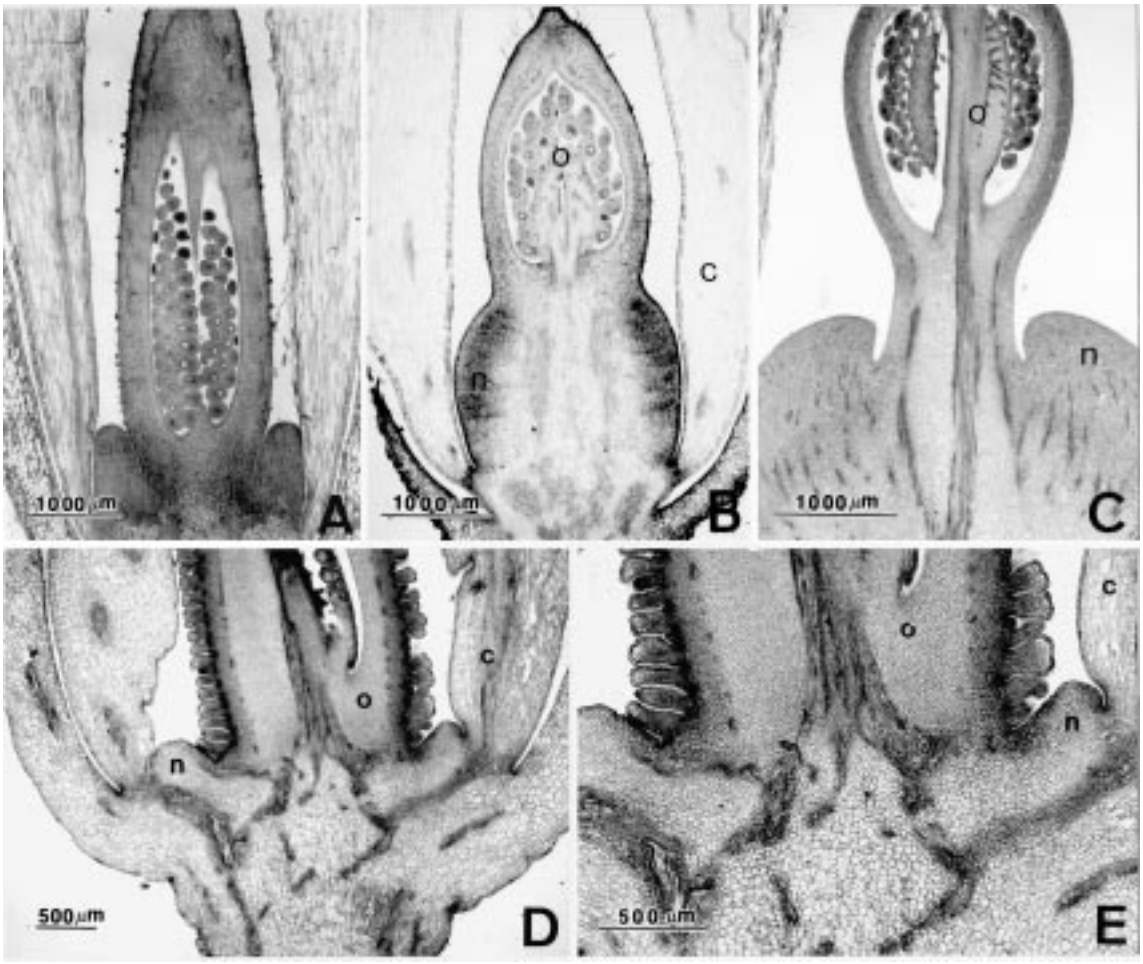

Fig. 1.- Floral nectary types in Bignoniaceae. Photomicrographs showing partial views of longisections. A: Annular nectary, *Tabebuia ochracea.* B: Cylindrical nectary, *Jacaranda mimosifolia.* C: Annular nectary, *Dolichandra cynanchoides.* D-E: Vestigial nectary. *Clytostoma callistegioides*. References: c, corolla; n, nectary; o, ovary.

1 A, C, 2 A). In some cases, the ovary is raised far from the secretory tissue by a long floral axis or gynophore (Fig. 1 C). It is found in *Adenocalymma marginatum, Amphilophium paniculatum, Anemopaegma flavum, Arrabidaea* sp., *Dolichandra cynanchoides, Eccremocarpus scaber, Macfadyena* sp., *Melloa quadrivalvis, Pithecoctenium* sp., *Tabebuia* sp., and *Tecoma* sp.

Cylindrical: an enlargement of the floral axis or gynophore and intimately related to it (Fig. 1 B). In longitudinal sections, *no groove* is observed between the nectary and the base of the ovary and the floral axis or gynophore. The secretory tissue displays different degrees of development. This type is found in *Argylia uspallatensis, Cuspidaria convoluta, Jacaranda* sp., *Mansoa difficilis, Parabignonia chodatii, Pyrostegia venusta,* and *Tynnanthus micranthus.*

The different types of nuptial nectaries described in this work (vestigial, annular, cylindrical and some subtle variations of these forms) were always consistent for all the species within a genus. Even in genera with different flower morphological types and visited by different pollinators for nectar (e.g. *Tecoma*), the type of nuptial nectary remained the same (Table 1).

Considering the anatomy of the nectaries, two tissues are distinguished: 1) a single layer of epidermis comprising cells covered by a cuticle and a variable number of stomata, and 2) a secretory tissue composed of compactly arranged

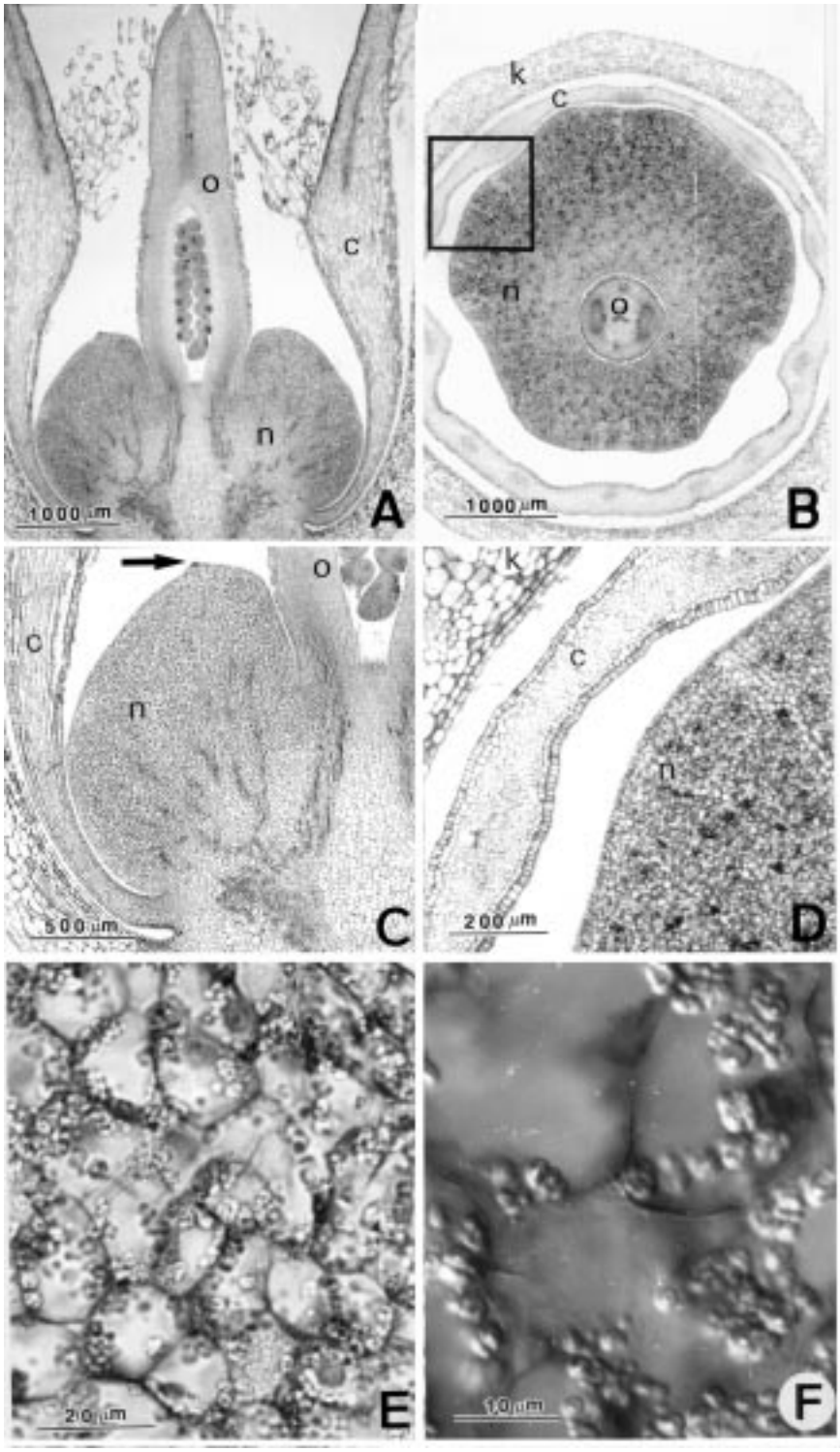

Fig. 2.- Photomicrographs showing floral nectary structure of *Arrabidaea corallina* (Bignonieae). A: Flower partial longisection. B: Flower cross-section. C: Detail of lower left portion of nectary in A. D: detail indicated in B. E-F: Starch grains of secretory tissue cells observed at different magnifications with phase contrast microscopy. c: corolla, k: calyx, n: nectary, o: ovary. Arrow indicates a stoma on the surface of the nectary.

Table 1.- Nuptial nectaries in Bignoniaceae. Types and morpho-anatomical features. Flower morphological types and frequent flower visitors from Gentry 1974, 1980; Rivera 1997). Volume measurements are means taken from 3 flowers at least, N/O = nectary ovary ratio. N.A.= not applicable.

Taxón	Habit	Type of nuptial nectary	Vascularization	Volume (mm^3)	N/O Ratio	Flower morphological type	Frequent flower visitor
Tribe Eccremocarpeae							
Eccremocarpus scaber	Shrub	Annular	Phloem	4.105	0.282	Campsidium	Hummingbird
Tribe Bignonieae							
Adenocalymma marginatum	Vine	Annular	Phloem	6.125	0.766	Anemopaegma	Bee
Amphilophium paniculatum	Vine	Annular	Phloem	11.261	0.328	Amphilophium	Bee
Anemopaegma flavum	Vine	Annular	Phloem	7.508	0.626	Anemopaegma	Bee
Arrabidaea chica	Vine	Annular	Phloem	1.088	0.436	Anemopaegma	Bee
A. corallina	Vine	Annular	Phloem	4.456	1.301	Anemopaegma	Bee
A. selloi	Vine	Annular	Phloem	3.581	0.774	Anemopaegma	Bee
Clytostoma binatum	Vine	Vestigial	N.A.	N.A.	N.A.	Cydista	Bee
C. callistegioides	Vine	Vestigial	N.A.	N.A.	N.A.	Cydista	Bee
Cuspidaria convoluta	Vine	Cylindrical	Phloem	0.371	0.154	Anemopaegma	Bee
Dolichandra cynanchoides	Vine	Annular	Phloem	15.895	0.979	Pyrostegia	Hummingbird
Macfadyena dentata	Vine	Annular	Phloem	12.118	0.393	Anemopaegma	Bee
M. uncata	Vine	Annular	Phloem	2.834	0.409	Anemopaegma	Bee
M. unguis-cati	Vine	Annular	Phloem	8.061	0.261	Anemopaegma	Bee
Mansoa difficilis	Vine	Cylindrical	Phloem	7.046	0.419	Anemopaegma	Bee
Melloa quadrivalvis	Vine	Annular	Phloem	1.561	0.153	Anemopaegma	Bee
Parabignonia chodatii	Vine	Cylindrical	Phloem	29.051	0.511	Anemopaegma	Bee
Pithecoctenium crucigerum	Vine	Annular	Phloem	16.522	0.789	Pithecoctenium	Bee/beetle
P. cynanchoides	Vine	Annular	Phloem	11.335	0.901	Pithecoctenium	Bee/beetle
Pyrostegia venusta	Vine	Cylindrical	Phloem	3.066	0.428	Pyrostegia	Hummingbird
Tynnanthus micranthus	Vine	Cylindrical	Phloem	0.05	0.121	Tynnanthus	Bee
Tribe Tecomeae							
Argylia uspallatensis	Shrub	Cylindrical	Phloem	0.352	0.121	Anemopaegma	Bee
Jacaranda micrantha	Tree	Cylindrical	Phloem	2.564	0.331	Anemopaegma	Bee
J. mimosifolia	Tree	Cylindrical	Phloem	3.993	0.367	Anemopaegma	Bee
Tabebuia alba	Tree	Annular	Phloem/xylem	2.464	0.211	Anemopaegma	Bee
T. aurea	Tree	Annular	Phloem/xylem	7.668	0.248	Anemopaegma	Bee
T. chrysotricha	Tree	Annular	Phloem/xylem	2.617	0.225	Anemopaegma	Bee
T. heptaphylla	Tree	Annular	Phloem/xylem	0.305	0.118	Anemopaegma	Bee
T. impetiginosa	Tree	Annular	Phloem/xylem	0.891	0.134	Anemopaegma	Bee
T. lapacho	Tree	Annular	Phloem/xylem	7.643	0.213	Anemopaegma	Bee
T. nodosa	Tree	Annular	Phloem/xylem	0.561	0.065	Anemopaegma	Bee
T. ochracea	Tree	Annular	Phloem/xylem	1.592	0.125	Anemopaegma	Bee
T. pulcherrima	Tree	Annular	Phloem/xylem	2.787	0.466	Anemopaegma	Bee
Tecoma capensis	Shrub	Annular	Phloem	0.881	0.166	Pyrostegia	Bee
T. garrocha	Shrub	Annular	Phloem	0.774	0.166	Pyrostegia	Hummingbird
T. stans	Tree	Annular	Phloem	0.442	0.156	Anemopaegma	Bee
T. tenuiflora	Tree	Annular	Phloem	0.686	0.142	Anemopaegma	Hummingbird

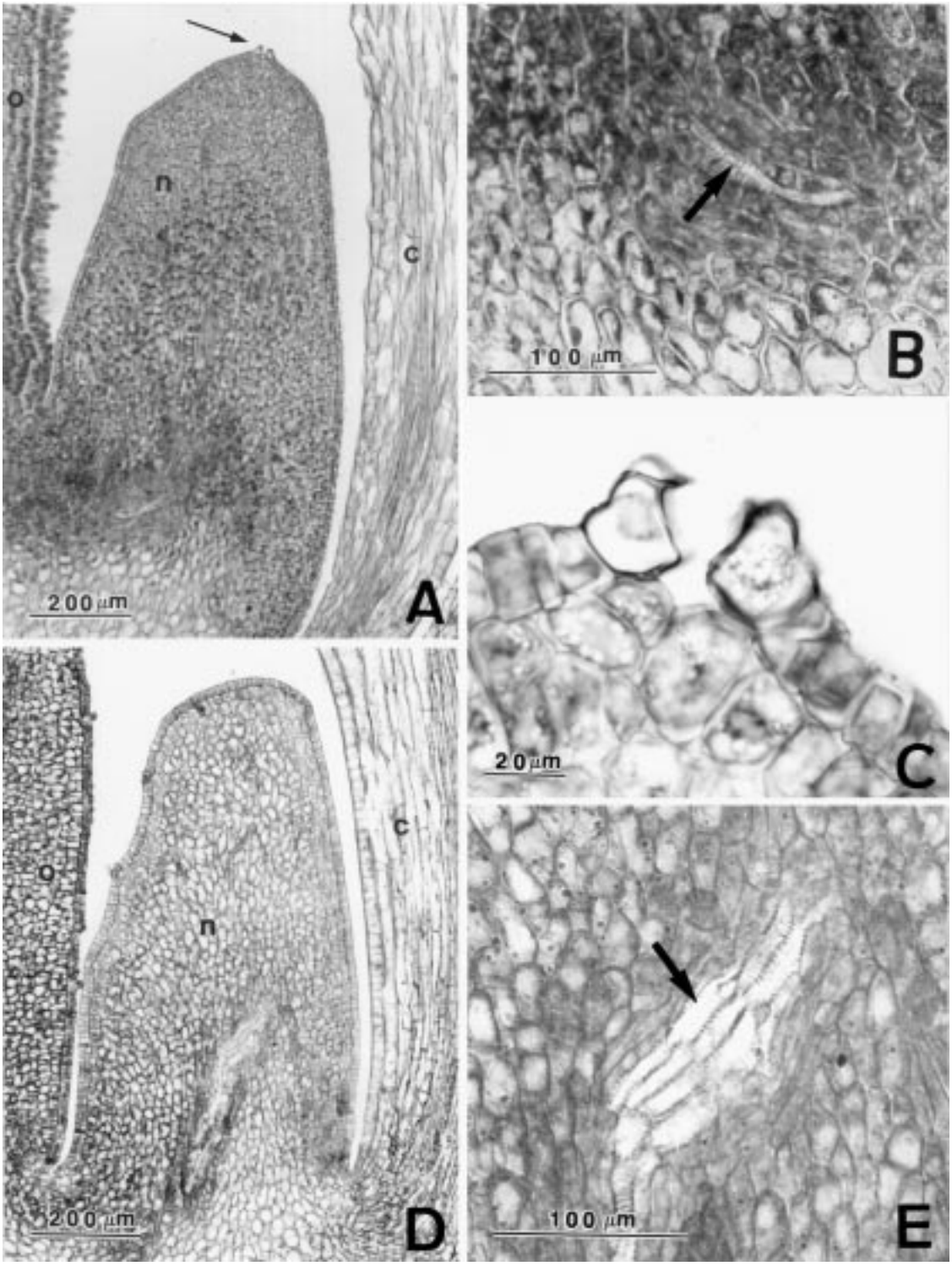

Fig. 3.- Photomicrographs showing floral nectary structure of *Tabebuia* sp. (Tecomeae) in longisection. A-C. *Tabebuia chrysotricha.* A. Detail of nectary. B: detail of secretory tissue showing xylem. C: Detail of stoma indicated in A. D-E: *Tabebuia ochracea*. D: Detail of nectary. E: Detail of secretory tissue showing xylem. c: corolla, n: nectary, o: ovary. Arrows show xylem.

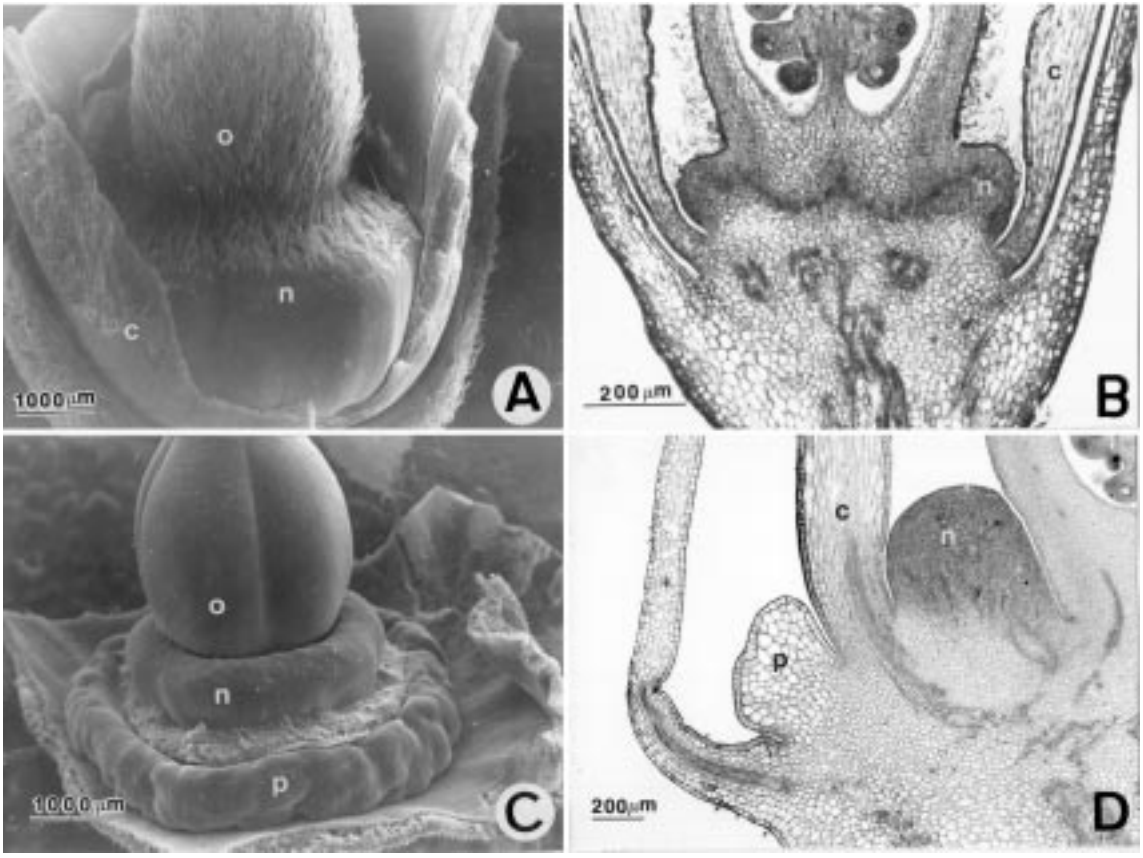

Fig. 4.- Floral nectary of *Pithecoctenium crucigerum, Tynnanthus micranthus, and Melloa quadrivalvis* (Bignonieae). A: *Pithecoctenium crucigerum*. SEM photomicrograph of lower portion of flower with sepals and petals partially removed, showing ovary and nectary covered by hairs. B:. *Tynnanthus micranthus.* OM photomicrograph of lower flower cross-section showing nectary covered by hairs. C-D: *Melloa quadrivalvis.* C: SEM photomicrograph of lower portion of flower with sepals and petals removed, showing ovary, nectary and protuberance. D: OM photomicrograph of flower partial cross-section showing protuberance. c: corolla, n: nectary, o: ovary, p: protuberance.

parenchyma cells (Fig. 2 A-D). Intensely stained parenchyma cells have large nuclei and numerous vacuoles as well as starch grains (Fig. 2 E-F). The secretory tissue lacks intercellular spaces. Generally it is supplied only by phloem traces, which are distinguished by their distinct affinity to stain (e.g. Fig. 2 C). However, the vascularization is both by xylem and phloem in all species of *Tabebuia* (Fig. 3 A, B arrow, D, E arrow).

The surface of the nectary is glabrous in most species (Figs. 1; 2 A, C; 3 A, D, 4 C) except for that of *Pithecoctenium* sp. (Fig. 4 A) and *Tynnanthus micranthus* (Fig. 4 B). In these species, non-secretory multicellular simple hairs similar to those found on the surface of the ovary, cover the nectary surface.

Nectary stomata were always anomocytic (Fig. 5) and usually located at the apical portion of the nectaries (Figs. 2 C arrow; 3 A arrow, C). Usually they were found open (Fig. 5 A, C). Nevertheless some stomata were barely open (Fig. 5 D) while others were completely closed (Fig. 5 B, E, F). They were always flush with the surface of the epidermis except those found in *Tabebuia aurea, T. chrysotricha, T. nodosa,* and *T. ochracea* whose stomata were raised above the epidermal layer (Fig. 3 C).

An annular protuberance was found between the perianth whorls in *Parabignonia chodatii, Macfadyena dentata,* and *Melloa quadrivalvis* (Fig. 4 C, D). The anatomy of this tissue showed differences from a typical secretory tissue found in

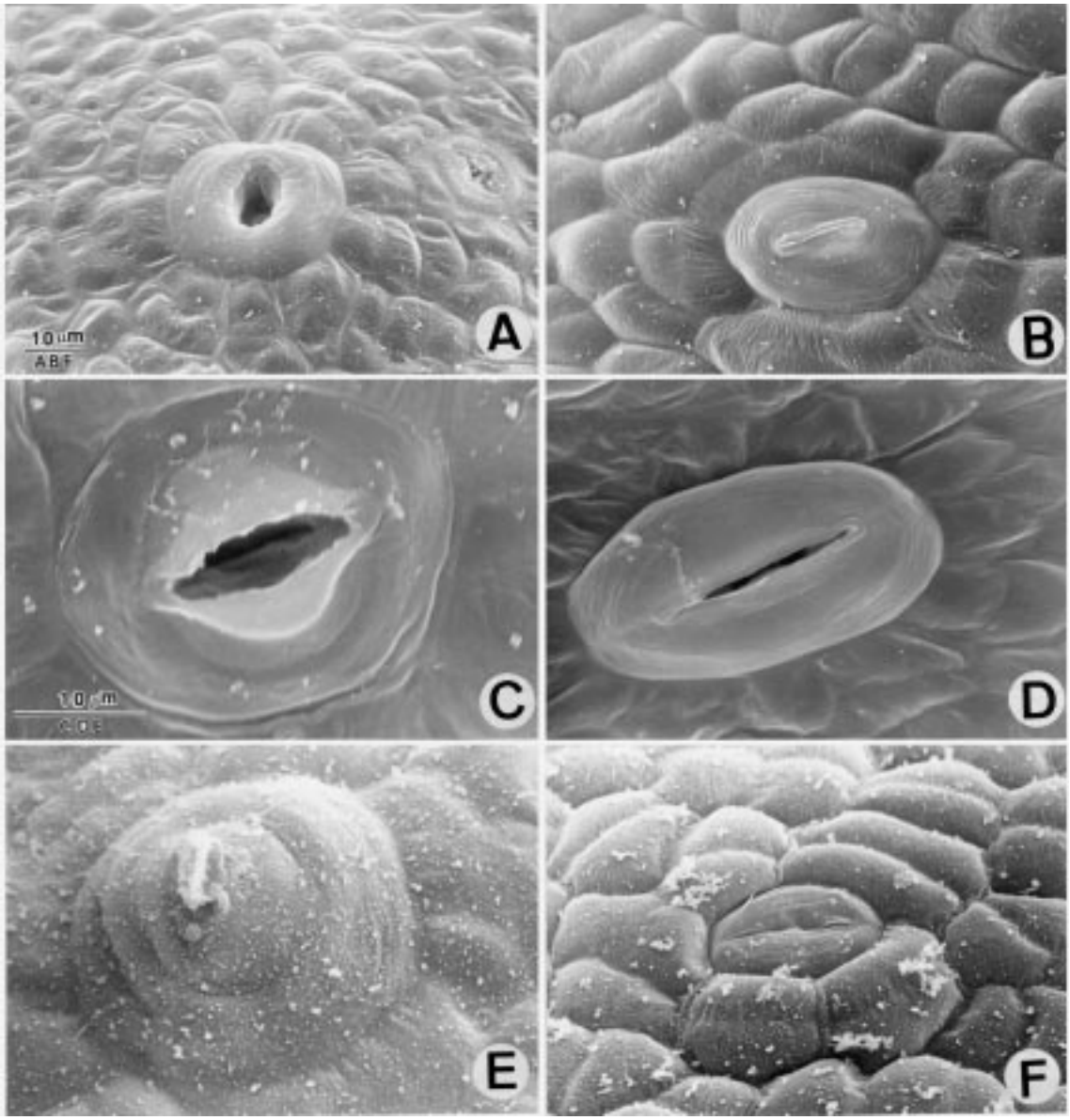

Fig. 5.- SEM photomicrographs of nectary stomata in Bignoniaceae. A. *Arrabidaea corallina.* B. *Macfadyena unguis-cati.* C. *Parabignonia chodatii.* D. *Tecoma stans.* E. *Dolichandra cynanchoides.* F. *Tabebuia heptaphylla.*

nectaries, and it appeared to be regular parenchyma tissue similar to that found in the flower receptacle (Fig. 4 D). Observations under SEM (Fig. 4 C) also revealed lack of stomata on its surface, as is customary in mesenchymatic secretory tissues. In short, it was a structure not related to the nectary, located between the petals and sepals, and made up of non-secretory parenchyma cells and of unknown function.

The nectaries of Bignonieae were usually larger than those of Tecomeae, reaching almost 30 mm^3 in *Parabignonia chodatii* and over 15 mm^3 in both *Dolichandra cynanchoides* and *Pithecoctenium crucigerum* (Table 1). The volume was variable among species of the same genus. For example in *Tabebuia*, some species attained a volume of over 7 mm^3 (*T. aurea* and *T. lapacho*), others ranged between 1.5 a 2.7 mm^3 (*T. alba, T. chrysotricha, T. ochracea* and *T. pulcherrima*), while some had a

very small nectary (0.3-0.9 mm^3 in *T. heptaphylla, T. impetiginosa* and *T. nodos*a). This variability was also observed among the species of *Macfadyena*. In *Tecoma* sp., however, the volume was almost constant (Table 1). The nectary/ovary ratio (N/O) was also commonly larger in Bignonieae, with extreme cases in *Arrabidaea* sp. where the nectary area in a longisection exceeded that of the ovary. In most genera where more than one species was observed (e.g. *Tabebuia* and *Macfadyena*) N/O ratios gave more uniform results than did volume measurements (Table 1).

DISCUSSION

According to a topographical classification depicted by Fahn (1979a), annular secretory nectaries found in Bignoniaceae would correspond to type 4 ("nectary as a disk surrounding the base of the ovary"), while cylindrical secretory ones, would belong to type 3 ("nectaries on receptacles"). However this classification (Fahn, 1979a), only refers to the nectaries' position and the fact that the nectaries of Bignoniaceae fall into two distinct categories, is simply due to a difference in their degree of development and position.

Clytostoma sp., on the other hand, shows a vestigial nectary. This type of gland is characteristic of other genera of the family such as *Cydista* and *Phryganocydia* (Gentry, 1980), but it was also found in one species of *Catalpa* (Rivera, 1996). The lack of a functional nectary was associated with pollination by deception and multiple-bang-flowering phenology (Gentry, 1980), which also holds true for the studied populations of *Clytostoma* (Rivera, 1997).

Nectary anatomical characteristics found in the studied species agree with those reported by several authors in other species of Bignoniaceae (Elias & Gelband, 1976; Subramanian & Inamdar, 1986a, 1989; Thomas & Dave, 1992; Belmonte et al., 1994; Galetto, 1995; Rivera, 1996). No intercellular spaces were found in the secretory parenchyma as it is distinctive in mesenchymatic nectaries (Fahn, 1979a, 1979b; Subramanian & Inamdar, 1989; Thomas & Dave, 1992). This could be explained by the fact that these spaces appear at the end of the secretion period, when the secretory tissue becomes less dense (Subramanian & Inamdar, 1989), while the material used in this study was all young flowers or buds near anthesis.

The vascularization of nectaries is always by phloem, except for the species of *Tabebuia* whose nectaries are supplied by both phloem and xylem. Galetto (1995) had already reported this distinction in *T. heptaphylla* while Thomas & Dave (1992) did not comment on the nectary vascularization in their study of *T. serratifolia*. According to Frey-Wyssling (1955), a correlation exists between type of vascularization of secretory structures and the concentration of their secreted nectar. This relationship however was not detected in a study of nectar chemistry (Rivera, 1997).

Raised stomata, as those found in four species of *Tabebuia*, are rare in the family, but have been reported for *Podranea ricasoliana* (Rivera, 1996) and *Tecoma capensis* (Subramanian & Inamdar, 1989). Stomata were always found on the apical portion of the nectary, which corresponds to the region of secretory activity in the nectary. The apical location of stomata has already been noted in Bignoniaceae and other families (Davis & Gunning, 1992; Galetto, 1995). According to some authors (Davis & Gunning, 1992), nectary stomata are modified in that their guard cells have lost their ability to close completely. This theory has always been suggested as a reason for the fact that nectary stomata were always detected open. On the contrary, other studies have confirmed the guard cells capacity to alter the aperture regulating nectar secretion (Zandonella, 1967; Davis & Gunning, 1993). Stomata in the nectaries of *T. heptaphylla, T. pulcherrima* and *Macfadyena unguis-cati* revealed an open ostiole in flowers just opened, while they had a closed ostiole in 1-2 day-old flowers. The stomata regulatory effect on secretion or resorption was not corroborated.

Gentry (1980) reports that the trichomes on the surface of the nectary of *Tynnanthus micranthus* are responsible for the secretion of nectar in this species but field observations and tests revealed no secretion. On the other hand, it was also observed that the nectary, although small, has a typical secretory parenchyma and stomata on the epidermis, as is typical for functional secretory nectaries.

Gentry (1980) proposed the term «double» disk to describe the secretory structure along with the protuberance located between the perianthic whorls in *Melloa*, also present in *Macfadyena dentata* and *Parabignonia chodatii*. The expression "double" probably arose from a macroscopic

analysis of flowers without their corolla, in which the nectary, resting on this protuberance would appear as two stacked disks. Since this structure does not perform any secretory function, nor is it directly associated with the gland, it is recommended that the term "double" disk be abandoned.

The nectary volume was very variable as Galetto (1995) reported. Nevertheless, there is a tendency in the Bignonieae to form larger nectaries than those present in Tecomeae. This propensity, as expected, was also true for nectary/ovary ratios. The larger nectary volume is probably related to the fact that the flowers of lianas secrete more nectar than trees, as was found in secretion studies (Rivera, 1997). Nevertheless, the relationship between nectary features and flower visitors is not apparent. Opler (1983) reported a connection between flower size and maximum secretion and different flower visitors when analyzing several species of different families in a tropical community. This relationship is not apparent among the studied species when comparing either nectary size or ovary/nectary ratio, even when looking at different species of a genus, visited by both hummingbirds and bees.

Although information of the taxonomic distribution of nuptial nectaries in the family is far from complete, it is apparent that structures similar to those found in these species occur in members of all Bignoniaceae. The nuptial nectary terms proposed in this study provide a useful generic character for future studies in other species, as the types (secretory and vestigial) and the varieties of the former (annular and cylindrical) remain constant within a genus.

ACKNOWLEDGEMENTS

The author thanks E. Di Fulvio, A. E. Cocucci, A. A. Cocucci, and two anonymous reviewers for constructive comments to the manuscript, and R. Munch for photographic assistance. CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas) and CONICOR (Consejo de Investigaciones Científicas y Técnicas de la Provincia de Córdoba) provided support for this study.

LITERATURE CITED

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

Cohen, A. L. 1974. Critical point drying, pp. 44-112, en M. A. Hayat (ed.), *Principle and techniques of scanning electron microscopy*. Van Nostrand Reinhold Company, New York.

Crang, R. F. E. 1988. Artifacts in specimen preparation for scanning electron microscopy, pp. 107-129, en R. F. E. Crang & K. L. Komplareus (eds.), *Artifacts in biological electron microscopy*. Kluwer Academic Publishers. New York.

Cronquist, A. 1988. *The evolution and classification of flowering plants*. New York Botanical Garden, New York.

Davis, A. R. & Gunning, B. E. S. 1992. The modified stomata of the floral nectary of *Vicia faba* L. 1. Development, anatomy and ultrastructure. *Protoplasma* 166: 134-152.

—— & ——. 1993. The modified stomata of the floral nectary of *Vicia faba* L. 3. Physiological aspects, including comparison with foliar stomata. *Bot. Acta* 106: 241-253.

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

Fahn, A. 1979a. Nectaries, pp. 51-111, en A. Fahn (ed.), *Secretory tissues in plants*. Academic Press, London.

——. 1979b. Ultrastructure of nectaries in relation to nectar secretion. *Amer. J. Bot.* 66: 977-985.

Frey-Wyssling, A. 1955. The phloem supply to the nectaries. *Acta Bot. Neerl.* 4: 358-369.

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

Gentry, A. H. 1974. Coevolutionary patterns in Central America Bignoniaceae. *Ann. Missouri Bot. Gard.* 61: 728-759.

——. 1980. Bignoniaceae, Part I (Crescentieae and Tourrettieae). *Fl. Neotrop. Monogr.* 25: 1-150.

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

—— & Bernardello, L. M. 1984. Bignoniaceae, pp. 68-71, en A.T Hunziker (ed.), *Los géneros de Fanerogámas de Argentina*. Bol. Soc. Argent. Bot., 23: 68-71.

Johansen, D. 1940. *Plant Microtechnique*. McGraw Hill, New York.

Maácz, C. J. & Vágás, E. 1961. A new method for staining cellulose and lignified walls. *Mikroscopie (*Wien*)* 16: 40-43.

Opler, P. 1983. Nectar production in a tropical ecosytem, pp. 30-79, en B. Bentley, & T. S. Elias (eds.), *The biology of nectaries*. Columbia University Press, New York.

Rao, V. S. 1971. The disk and its vasculature in the flowers of some dicotyledons. *Bot. Not.* 124: 442-450.

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

——. 1997. Biología reproductiva en Bignoniaceae de Argentina. Tesis Doctoral. Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba. 234 pp.

Rudramuniyappa, C. K. & Mahajan, P. B. 1991. Morphogenesis and histochemistry of ovarial nectaries in *Spathodea campanulata* Beauv. *J. Indian Bot. Soc.* 70: 169-174.

Subramanian, R. B. & Inamdar, J. A. 1986a. Nectaries in *Bignonia illicium* L. Ontogeny, structure and function. *Proc. Indian Acad. Sci.* 96: 135-140.

—— & ——. 1986b. Occurrence, structure, ontogeny and biology of nectaries in *Kigelia pinnata* DC. *Bot. Mag.* 98: 67-73.

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

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

Zandonella, P. 1967. Stomates des nectaires floraux chez les Centrospermales. *Bull. Soc. Bot. France* 114: 11-20.

Original recibido el 10 de noviembre de 1999; aceptado el 3 de agosto de 2000.

Appendix 1.- The species of Bignoniaceae included in the investigation are listed below. Department name and the site of collection follow province name. N = number of specimens studied. The collectors were AAC= A.A. Cocucci, C= A. Cabrera; GLR= G.L. Rivera; K= A. Krapovicas; L= R. Legname; PP= Pedro Prieto; wn= without collection number.

Taxon	N	Provenance, collectors, date
Tribe Eccremocarpeae Hogg.		
Eccremocarpus scaber Ruiz & Pav.	1	**Río Negro**. *Dpto. El Bolsón*: Piltriquitrón, 9-I-1994. AAC 531
Tribe Bignonieae Dumort		
Adenocalymma marginatum (Cham.) DC.	1	**Misiones**. *Dpto. Iguazú*: Cataratas, 2-II-1994. GLR 34
Amphilophium paniculatum DC.	1	**Tucumán**. *Dpto. Burruyacu*: El Cajón, 22-IX-1994. GLR 68
Anemopaegma flavum Morong	1	**Santa Fe**. *Dpto. Obligado*: Ocampo, 12-XI-1958. C 10487
Arrabidaea chica (Humb. & Bonpl.) Verl.	1	**Misiones**. *Dpto. Iguazú*: Cataratas, 1-II-1994. GLR 32
	2	**Misiones**. *Dpto. Iguazú*: Yacuy, 2-II-1994. GLR 33
Arrabidaea corallina (Jacq.) Sandwith	1	**Jujuy**. *Dpto. Ledesma*: Calilegua, 5-XI-1993. GLR 16
	2	**Jujuy**. *Dpto. Ledesma*: Urundel, 20-09-1994. GLR 62
	3	**Salta**. *Dpto. Orán*: Pichanal, 20-IX-1994. GLR 3
Arrabidaea selloi (Spreng.) Sandwith	1	**Misiones**. *Dpto. Iguazú*: Cataratas, 1-II-1994. GLR 30
	2	**Misiones**. *Dpto. Iguazú*: Iguazú, 20-XII-1994. GLR 87
Clytostoma callistegioides (Cham.) Bureau ex Griseb.	1	**Córdoba**. *Dpto. Capital*: cultivada, 15-XI-1993. GLR 10
	2	**Jujuy**. *Dpto. Ledesma*: Calilegua, 5-XI-1993. GLR 14
Clytostoma binatum (Thumb.) Sandwith	1	**Misiones**. *Dpto. Iguazú*: Cataratas, 1-II-1994. GLR 28
	2	**Misiones**. *Dpto. Iguazú*: Iguazú, 20-XII-1994. GLR 86
Cuspidaria convoluta (Vell.) A. H. Gentry	1	**Córdoba**. *Dpto. Colón*: cultivada, 11-XI-1994. GLR 79
Dolichandra cynanchoides Cham.	1	**Córdoba**. *Dpto. Colón*: El Diquecito, 12-I-1994. GLR 40
	2	**Córdoba**. *Dpto. Capital*: Villa Warcalde, 30-IV-1994. GLR 41
Macfadyena dentata K. Schum.	1	**Córdoba**. *Dpto. Capital*: cultivada, 15-X-1993. GLR 23
	2	**Misiones**. *Dpto. Iguazú*: Cataratas, 23-XII-1994. GLR 90
Macfadyena uncata (Andr.) Sprague & Sandwith	1	**Misiones**. *Dpto. Iguazú*: Ruta 101, 23-XII-1994. GLR 89
Macfadyena unguis-catis (L.) A. H. Gentry	1	**Jujuy**. *Dpto. Ledesma* : Calilegua, 5-XI-1993. GLR 17
	2	**Córdoba**. *Dpto. Capital*: Villa Allende, 20-X-1993. GLR 22
	3	**Salta**. *Dpto. Sta. Victoria*: Los Toldos, 21-IX-1994. GLR 65
Mansoa difficilis (Cham.) Bureau & K. Schum.	1	**Misiones**. *Dpto. Iguazú*: Ruta 101, 28-X-1994. GLR 75
Melloa quadrivalvis (Jacq.) A. H. Gentry	1	**Jujuy**. *Dpto. Ledesma*: Calilegua, 5-XI-1993. GLR 15
Parabignonia chodatii (Hassler) A. H. Gentry	1	**Jujuy**. *Dpto. Ledesma*: Calilegua, 5-IV-1995. GLR 100
Pithecoctenium crucigerum (L.) A. H. Gentry	1	**Misiones**. *Dpto. Iguazú*: Garganta Diablo, 26-X-1994. GLR 71
	2	**Misiones**. *Dpto. Iguazú*: Ruta 101, 27-X-1994. GLR 72
Pithecoctenium cynanchoides DC.	1	**Córdoba**. *Dpto. Colón*: Villa Warcalde, 15-I-1994. GLR 26
	2	**Córdoba**. *Dpto. Colón*: La Calera, 20-II-1994. GLR 56
Pyrostegia venusta (Ker-Gawl.) Miers	1	**Córdoba**. *Dpto. Capital*: cultivada, 18-V-1994. GLR 42
Tynnanthus micranthus Corr. Méllo ex K. Schum.	1	**Misiones**. *Dpto. Iguazú*: Ruta 101, 22-XI-1994. GLR PP 80
Tribe Tecomeae Endlicher		
Argylia uspallatensis DC.	1	**Mendoza**. *Dpto. Uspallata*: Uspallata, 14-XII-1994. AAC wn.
Jacaranda micrantha Cham.	1	**Misiones**. *Dpto. Iguazú*: Garganta Diablo, 22-XII-1994. GLR 91
Jacaranda mimosifolia D. Don	1	**Córdoba**. *Dpto. Colón*: El Diquecito, 12-I-1994. GLR 39
Tabebuia alba Sandwith	1	**Misiones**. *Dpto. Cainguás*: Aristóbulo del Valle, 14-IX-1972. K 18612
Tabebuia aurea (Silva Manso) Benth. & Hook.	1	**Maui**. *Kahului*: Hawaii, U.S.A. cultivada. 20-III-1994. GLR 36
Tabebuia chrysotricha (Martius & DC.) Standl.	1	**Tucumán**. *Dpto. Burruyacú:* 22-IX-1994. GLR 67
	2	**Misiones**. *Dpto. Capital*: cultivada, 28-X-1994. GLR 76

Taxon	N	Provenance, collectors, date
Tabebuia heptaphylla (Velloso) Toledo	1	**Córdoba**. *Dpto. Capital*: cultivada, 4-X-1993. GLR 5
Tabebuia impetiginosa (Martius ex DC.) Standl.	1	**Salta**. *Dpto. Capital*: Cerro San Bernardo, 19-XI-1994. GLR wn
Tabebuia lapacho (K. Schum.) Sandwith	1	**Salta**. *Dpto. Santa Victoria*: Los Toldos, 21-IX-1994. GLR 64
Tabebuia nodosa (Griseb.) Griseb.	1	**Córdoba**. *Dpto. Ischilin*: Cruz del Eje, 24-I-1995. GLR 92
Tabebuia ochracea (Cham.) Standl.	1	**Córdoba**. *Dpto. Capital*: cultivada, 14-IX-1993. GLR 2
	2	**Jujuy**. *Dpto. Ledesma*: Calilegua, 5-XI-1993. GLR 5
Tabebuia pulcherrima Sandwith	1	**Córdoba**. *Dpto. Capital*: cultivada, 10-XII-1995. GLR 101
Tecoma capensis (Thunb.) Lindl. [a]	1	**Córdoba**. *Dpto. Capital*: cultivada, 18-V-1994. GLR 44
Tecoma garrocha Hieron.	1	**La Rioja**. *Dpto. Capital*: Los Sauces, 16-IX-1994. GLR 50
Tecoma stans (L.) Kunth	1	**Tucumán**. *Dpto. Tafí*: San Javier, 2-XI-1993. GLR 12
	2	**Salta**. *Dpto. La Caldera*: La Caldera, 6-XI-1993. GLR 19
	3	**Jujuy**. *Dpto. Ledesma*: Calilegua, 5-IV-1995. GLR 96
Tecoma tenuiflora (DC.) Fabris	1	**Salta**. *Dpto. Santa Bárbara*: without locality, 15-10-1948. L 546

[a] Native to South Africa, but commonly cultivated in the subtropics and in the Neotropics.