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# 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.

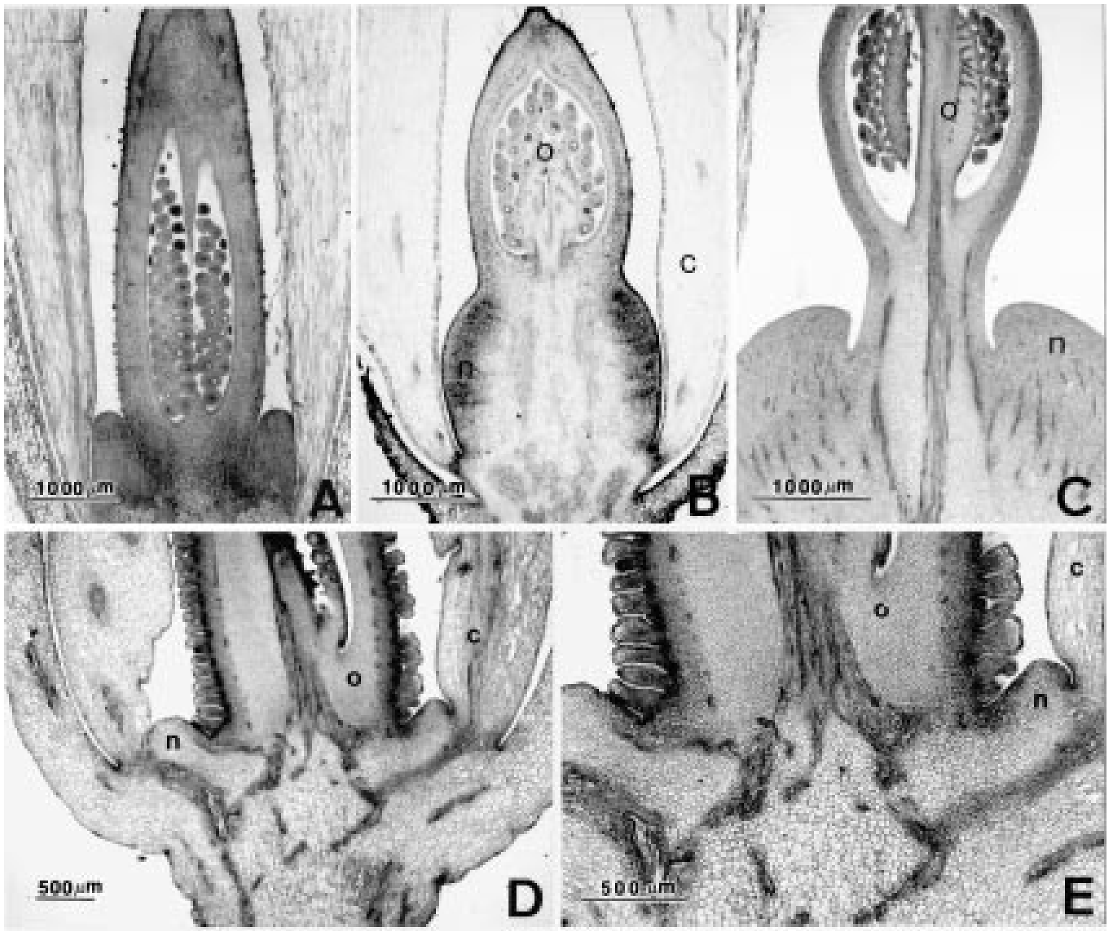


Fig. 1.- Floral nectary types in Bignoniaceae. Photomicrographs showing partial views of longisections. A: Annular nectary, *Tabebuia ochracea.* B: Cylindrical nectary, *Jacaranda mimosifolia.* C: Annular nectary, *Dolichandra cynanchoides.* D-E: Vestigial nectary. *Clytostoma callistegioides*. References: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

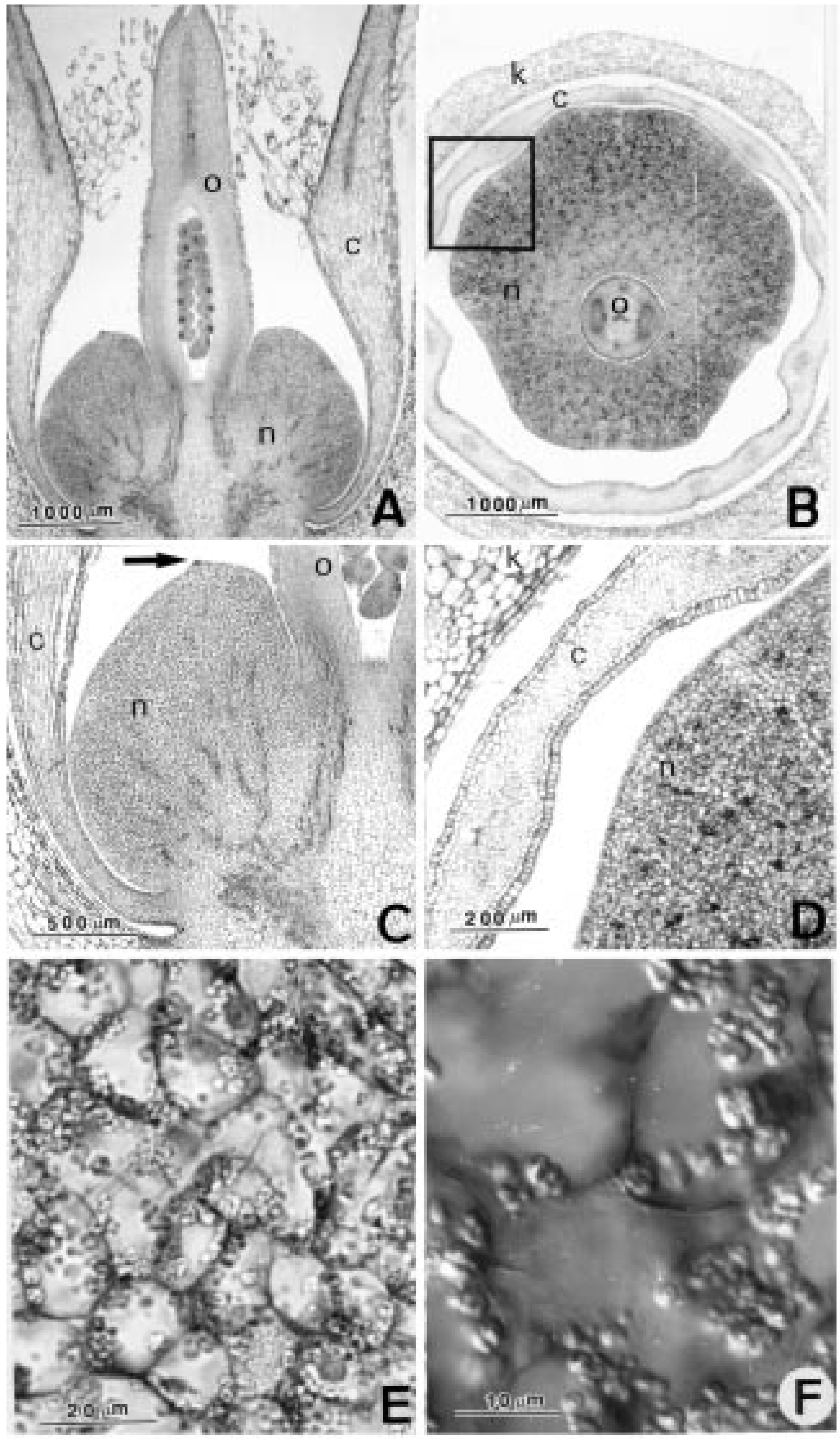


Fig. 2.- Photomicrographs showing floral nectary structure of *Arrabidaea corallina* (Bignonieae). A: Flower partial longisection. B: Flower cross-section. C: Detail of lower left portion of nectary in A. D: detail indicated in B. E-F: Starch grains of secretory tissue cells observed at different magnifications 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 |

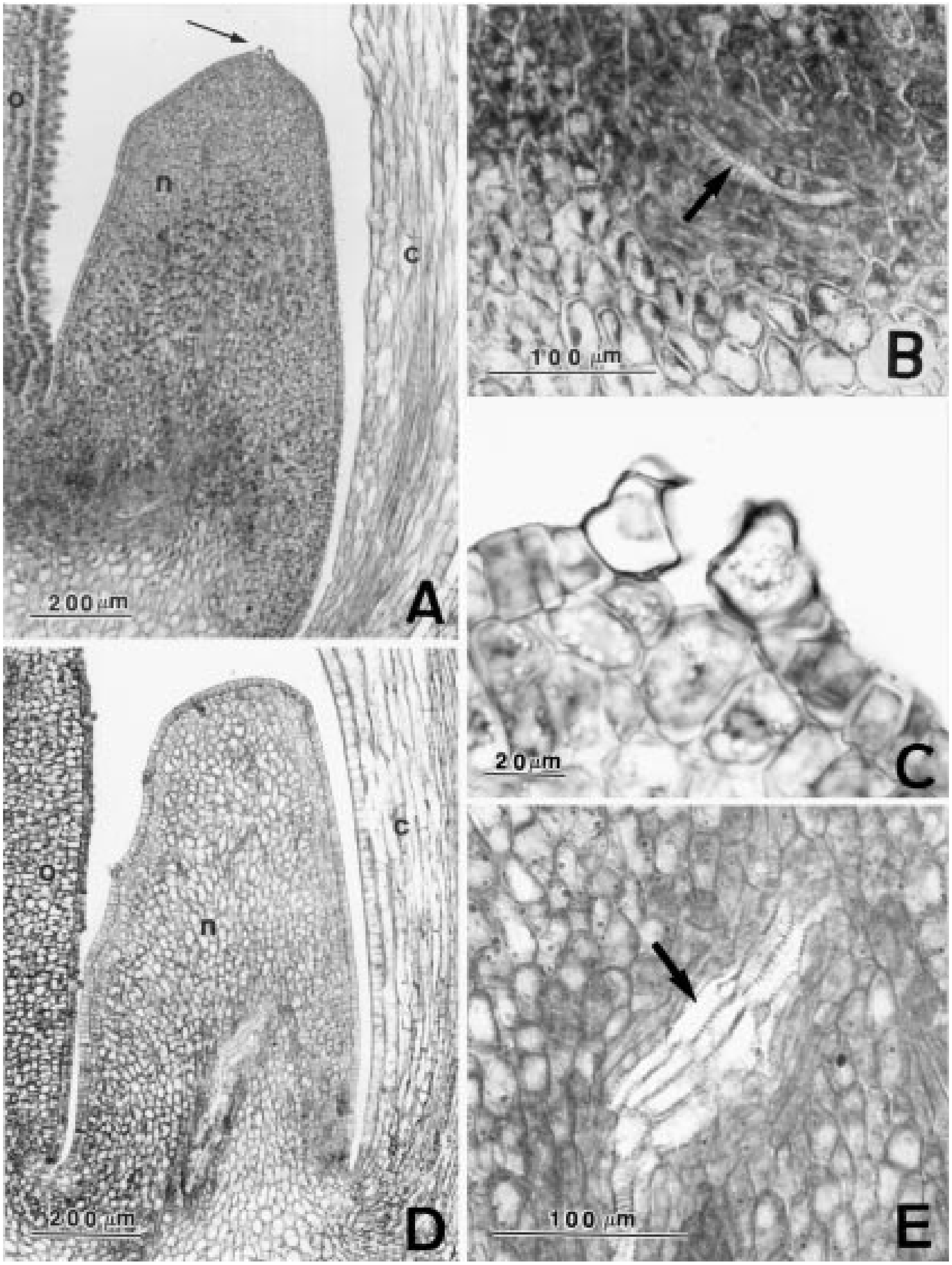


Fig. 3.- Photomicrographs showing floral nectary structure of *Tabebuia* sp. (Tecomeae) in longisection. A-C. *Tabebuia chrysotricha.* A. Detail of nectary. B: detail of secretory tissue showing xylem. C: Detail of stoma indicated in A. D-E: *Tabebuia ochracea.* D: Detail of nectary. E: Detail of secretory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

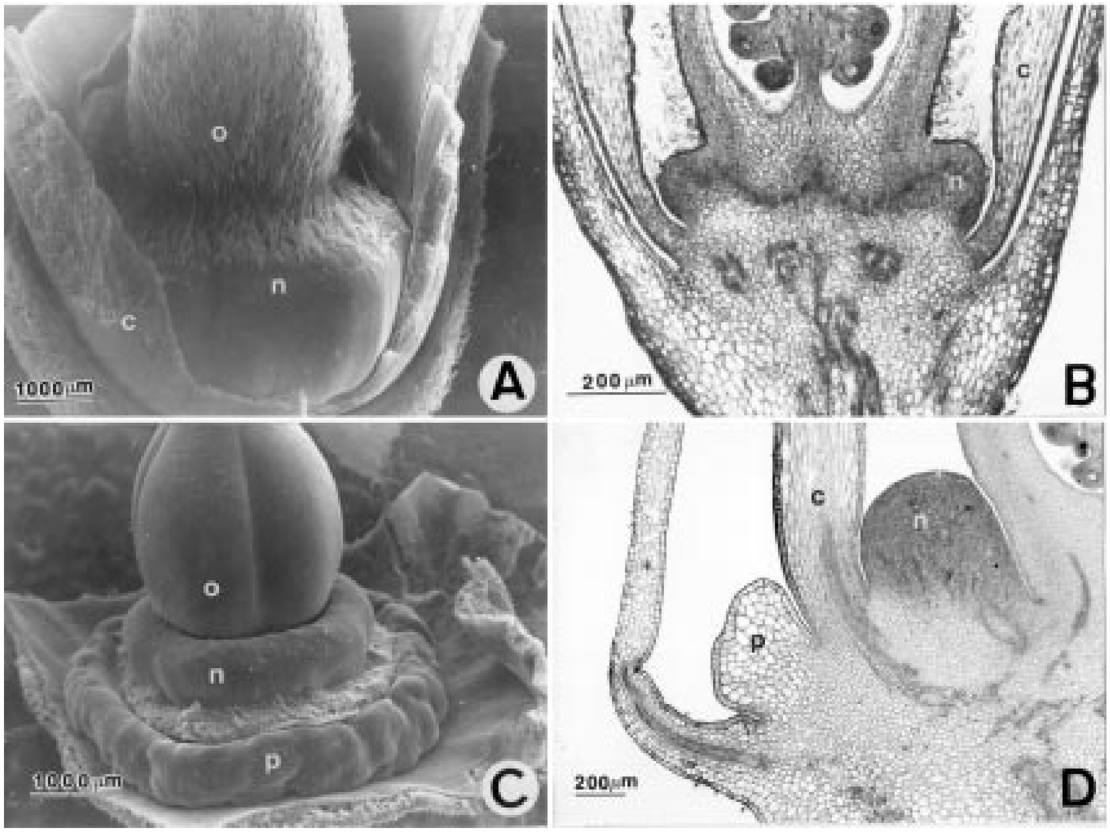


Fig. 4.- Floral nectary of *Pithecoctenium crucigerum*, *Tynnanthus micranthus*, and *Melloa quadrivalvis* (Bignonieae). A: *Pithecoctenium crucigerum*. SEM photomicrograph of lower portion of flower with sepals and petals partially removed, showing ovary and nectary covered by hairs. B:. *Tynnanthus 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

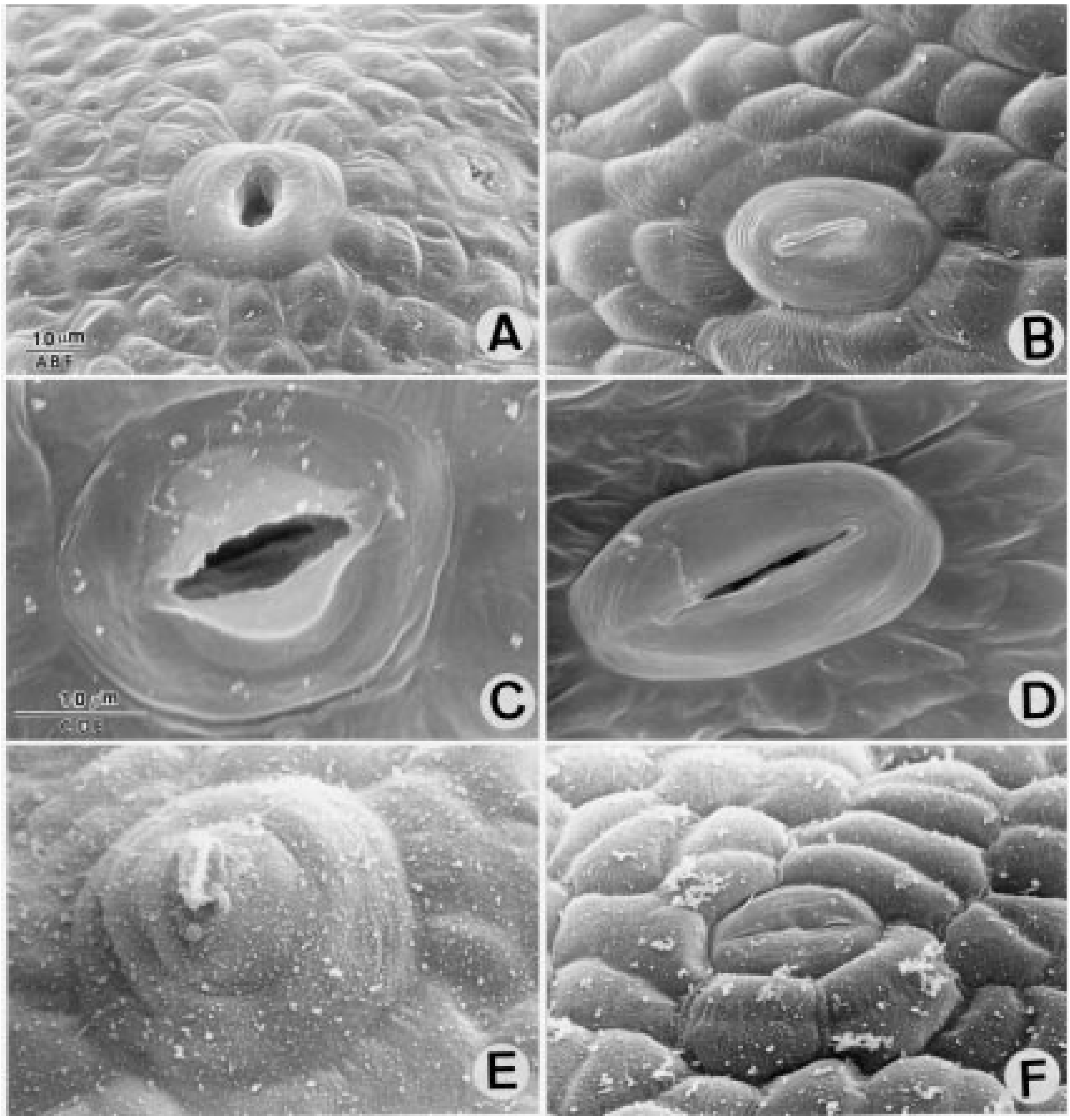


Fig. 5.- SEM photomicrographs of nectary stomata in Bignoniaceae. A. *Arrabidaea corallina.* B. *Macfadyena unguis-cati.* C. *Parabignonia chodatii.* D. *Tecoma stans.* E. *Dolichandra cynanchoides.* F. *Tabebuia heptaphylla.*

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. nodosa*). 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.

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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.