

EVOLUTION OF THE ANTHOR IN THE FAMILY VELLOZIOACEAE (1)

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ABSTRACT - (Evolution of the anther in the family Velloziaceae). A detailed study of the anthers in the family Velloziaceae establishes that although all anthers display four sporangia, at dehiscence there may be either four or two locules. The formation of only two locules results from the reduction or total disappearance of a *residual tissue*, which is made up of connective plus endothecium. The sporangia may be lateral in position, internal due to formation of a *sustaining tissue* at the connective, or intermediate. The dehiscence of the anther may be latrorse or introrse. In the genus *Vellozia* there are four locules at maturity and the dehiscence is latrorse; all of the species shed their mature pollen grains as tetrads. In the genera of subfamily Barbacenioidae there are two locules at maturity, all of the species shed their mature pollen grains as monads and dehiscence is introrse. In the genus *Xerophyta*, which together with genus *Vellozia* constitutes subfamily Vellozioidae, are found a series of intermediate conditions in the position of the sporangia and in the type of dehiscence, and the mature pollen grains are shed as monads or tetrads.

RESUMO - (Evolução da antera na família Velloziaceae). Um estudo detalhado da estrutura da antera na família Velloziaceae demonstrou que embora a antera em todas as espécies apresente quatro esporângios, na deiscência pode haver tanto dois como quatro loculos. A formação de apenas dois loculos resulta da redução ou total desaparecimento do *tecido residual*, formado pelo conectivo mais endotécio. Os esporângios podem ter posição lateral, interna (devido à formação de um *tecido de sustentação* no conectivo), ou posição intermediária. A deiscência da antera pode ser latrorsa ou introrsa. No gênero *Vellozia* há quatro loculos, na maturidade da antera, a deiscência é latrorsa e todas as espécies apresentam grãos de pólen em tétrade. Nos gêneros da subfamília Barbacenioidae há dois loculos na maturidade, a deiscência é intorsa e todas as espécies apresentam grãos de pólen em mônade. No gênero *Xerophyta* que, juntamente com o gênero *Vellozia* constitui a subfamília Vellozioidae, verifica-se uma série de condições intermediárias, com relação à posição dos esporângios e à posição da deiscência, e os grãos de pólen podem ser em mônades ou tétrades.

1 - Financial support was provide by CNPq (Conselho Nacional do Desenvolvimento Científico e Tecnológico), Proc. 300939-80 (ZO) and by FAPESP (Fundação de Amparo à Pesquisa de São Paulo), Proc. 81/0088-2.

INTRODUCTION

In the Velloziaceae the androecium appears to be the best indicator of phylogenetic relationships. According to Menezes (1980, 1984), a large number of stamens may indicate a primitive condition in the group, while species with 6 stamens would have arisen through fusion of stamens or reduction of some of them to staminodes. The family apparently passed through a further degree of specialization with the appearance of the corona. Thus, according to Menezes (1980), the species of *Vellozia* Vand. belong to group I, the species of *Xerophyta* Juss. to group II, while species of the subfamily Barbacenioidae belong to group III (both genera mentioned by name belong to subfamily Velloziaceae). Group III is supposed by the author to be the most advanced and group I, the less advanced.

As shown by Menezes (1980), all species of *Vellozia* have stamens with a conspicuous filament, while all species in subfamily Barbacenioidae have sessile anthers, which are connected to a corona or to the upper part of the hypanthium (except *Barbacenia spiralis* which has stamens with filaments free from the corona lobes). On the other hand, according to the same author, the genus *Xerophyta* is composed of species with 6 stamens, which vary from having conspicuous filaments to almost sessile anthers (in fact with inconspicuous filaments). In the opinion of Menezes (l.c.) the genus *Xerophyta* thus presents characteristics which are all intermediate between the most primitive group, *Vellozia*, and the most advanced, *Aylthonia* Menezes and *Barbacenia* Vand. (the latter two being genera of the subfamily Barbacenioidae).

Here it should be made clear that for a very long time the genus *Xerophyta* Jussieu (1789) remained in synonymy. Although Baker (1875) gave perfectly adequate reasons for considering Jussieu's genus as valid - including citation of Brazilian species with 6 stamens - the same author, in a later work (Baker 1898), accepted the findings of Bentham and Hooker (1880), who considered *Vellozia* and *Barbacenia* as being the only two genera of the family Velloziaceae. Almost all other later taxonomists who have followed in the study of the Velloziaceae, (most recently, Smith 1962) kept the genus *Xerophyta* in synonymy, some with *Vellozia*, some with *Barbacenia* (see Menezes 1980). Only Perrier (1946, 1950) upheld *Xerophyta* as a valid genus, including in it Brazilian species with 6 stamens. After initial studies in the family, Menezes (1970, 1971) supported Baker (1875) and Perrier (l.c.) in opting for the re-establishment of the genus *Xerophyta*, involving 16 new combinations for species of the Old and the New World. Smith and Ayensu (1974) finally accepted the genus *Xerophyta*, but exclusively for Old World species. Thus, while Menezes (1970, 1971, 1980) regards all species with 6 stamens but no corona as belonging to the genus *Xerophyta*, Smith and Ayensu (1976) distribute these same species among 5 different genera: *Xerophyta*, *Vellozia*, *Barbaceniopsis* L.B. Smith, *Nanuza* L.B. Smith & Ayensu and *Talbotia* Balf.

Attention is also to be called to the anther. According to the 19th century morphologists (Eames 1961), and also to Dahlgren and Clifford (1982), the basic anther type in the monocotyledons is basifixed. The dorsifixed type results from modification of the

basifixed type. According to Menezes (1980, 1984), in the genus *Vellozia* all anthers are basifixed; in *Xerophyta*, they are basifixed or basifixed with auricles; and in the subfamily Barbacenioidae the anthers may be basifixed with auricles (genus *Pleurostima*) or dorsifixed (genera *Barbacenia* and *Aylthonia*). Among the African species of *Xerophyta* there are two [*Xerophyta eylesii* (Greves) Menezes and *X. squarrosa* Baker] that have basifixed petalar anthers and dorsifixed sepalar anthers in the same flower (Menezes 1980, 1984).

The present work is directed towards a detailed examination of the anthers in the Velloziaceae, with the intention of obtaining further information for an understanding of the taxonomy of the group, and of the evolutionary tendencies in the family as a whole.

MATERIAL AND METHODS

A - Material

The material used in this work may be listed as follows: *Aylthonia gentianoides* * (Goeth. & Henr.) Menezes (Menezes 29-SPF). *Barbacenia flava* * Mart ex Schult. f. var. *flava* (Menezes 26-SPF); *B. involucrata* * L.B. Smith (Menezes 32-SPF); *B. selovii* * Goeth. & Henr. (Menezes 5-SPF); *Barbacenia spiralis* * Smith & Ayensu (Menezes 1043-SPF); *Pleurostima spectabilis* * (Smith & Ayensu) Menezes (Menezes 51-SPF); *Vellozia burle-marxii* * Smith & Ayensu (Menezes 1162-SPF); *V. jolyi* Smith & Ayensu (Joly & Menezes 316-SPF); *Xerophyta arabica* (Baker) Menezes - África - (Lunt 205-K); *X. boliviensis* (Baker) Menezes - Bolivia (Castellanos, s.n. BA 46678); *X. dasylirioides* Baker - África - (Humbert 3920 - P); *X. minima* * (Pohl) Baker (Menezes 36 - SPF); *X. pinifolia* Lam. - Madagascar - (Thomas Croat. 32124 - K) and *X. plicata* * Spreng (Menezes 55 - SPF).

B - Methods

Anatomical studies were based on sections made in series on a rotating microtome from material fixed in FAA 50 (Johansen 1940) and embedded in paraffin using the usual methods. Staining was out with safranin and fast green (Sass 1951).

RESULTS

Figures 1-6 show anthers of different species and prove that all four sporangia may remain distinct at the time of dehiscence, with the tissue between them, here called *residual tissue* (Rt), well developed. This characteristic is displayed by the anthers of *Vellozia jolyi* (Fig. 1), *V. burle-marxii* (Fig. 2), *Xerophyta minima* (Fig. 3) and *X. plicata* (Fig. 4). In these species even after latrorse dehiscence (Fig. 3 and 4), the anther is divided into four locules. In the anther of *X. boliviensis* (Fig. 5) the residual tissue (Rt) is much reduced, so that the anther has two locules. At the time of its (lateral) dehiscence.

* All Brazilian species

The same is true of *X. pinifolia* (Fig. 6). In the species of *Vellozia* examined (Fig. 1, 2) and in *Xerophyta minima* (Fig. 3) the mature pollen shed as tetrads whereas in *X. plicata* (Fig. 4) and *X. pinifolia* (Fig. 6), it is shed as monads. The mature pollen of *X. boliviensis* (Fig. 5) appears to be shed as a mixture of tetrads, dyads and monads.

In *Xerophyta arabica* (Fig. 7, 8) and *X. dasylirioides* (Fig. 9, 10), which like all the species mentioned earlier, belongs to the subfamily Velloziaceae, as well as in *Barbacenia spiralis* (subfamily Barbaceniaceae, fig. 11, 12) there is a tendency in the anthers towards introrse dehiscence (in the former only in the sepal anthers).

At the same time, its flowers exhibited the growth of two lateral areas of the connective, here called *sustaining tissue* (St), which is more developed in those anthers with introrse dehiscence (Fig. 7, 9, 11). These three species shed their mature pollen as monads.

Figures 13-18 show additional species of the subfamily Barbaceniaceae. In all, the mature pollen grains are shed as monads. All anthers display introrse dehiscence; the residual tissue (Rt) is relatively well developed in *Pleurostima spectabilis* (Fig. 13, 14), reduced in *Barbacenia involucreta* (Fig. 15), *B. flava* (Fig. 16) and *B. sellovii* (Fig. 17), and almost absent in *Aylthonia gentianoides* (Fig. 18). In the same way the sustaining tissue (St), which is well developed in *P. spectabilis* (Fig. 14), is reduced in the species of *Barbacenia* (Fig. 15-17) and almost absent in *Aylthonia* (Fig. 18).

DISCUSSION

One of the most amply debated ideas about the evolution of the androecium in Angiosperms concerns the position of the sporangia in the anther. According to Eames (1961), the tendency among 19th century phylogenists was to consider sporangia (like ovules) as being adaxially positioned in their most primitive form, and later to have migrated to an abaxial position. Comparative studies of primitive groups, however, shows that both conditions - adaxial and abaxial sporangia - seem to have occurred in primitive Angiosperms. Families with laminar stamens may display adaxial sporangia (Magnoliaceae and Nymphaeaceae, for example) or abaxial sporangia (Annonaceae and Degeneriaceae, for example).

The marginal position of the sporangia (as seen in fig. 1), in which one member of each pair is apparently adaxial and the other abaxial, suggests (Eames l.c.) that two of the sporangia may belong on the abaxial side, and two on the adaxial side, of the sporophyll.

Although the pollen sacs of most angiosperms are fused in pairs before dehiscence (Eames, 1961), such fusion is uncommon in anthers with latrorse dehiscence. In Velloziaceae, the union of the locules into pairs occurs as a result of a phylogenetic reduction of the connective and endothecium tissues, which are here called *residual tissue* (Rt).

In the species of *Vellozia* and species of section *Talbotia* of genus *Xerophyta* [that is, all Brazilian species plus the African *Xerophyta elegans* (Ralf.) Baker] the anther has four

locules at dehiscence. In species of *Xerophyta* section *Xerophyta*, [that is, all remaining Old World species plus *Xerophyta boliviensis*, *X. vargasiana* (L.B. Smith) Menezes and *X. humahuaguensis* (Noher) Menezes from Bolivia, Argentina, and Peru] and in all species of subfamily Barbacenioidae, there are two locules at dehiscence of the anther. According to Eames (1961, p. 129) "in the primitive stamen, the sporangia lie close together in lateral pairs; in advanced stamens, they remain so or have been brought even closer together by reduction of intermediate laminar tissues", Velloziaceae have probably evolved from a gradual reduction of the amount of residual tissue, from the condition in the genus *Vellozia*, where it is well developed, to that in *Barbacenia* (except in *B. spiralis*), where it is vestigial, to the condition in *Aylthonia*, in which it is absent. Within the genus *Xerophyta*, the residual tissue is well developed in some species and much reduced in others, as it is in *Barbacenia spiralis* and in *Pleurostima* (Fig. 11-14, Rt).

With regard to position, the sporangia in Velloziaceae may be lateral, may show a tendency to be internal, or may be fully internal. This modification of the position of the sporangia occurs, in the Velloziaceae, on account of the development of the two arms of the connective which here are called *sustaining tissue* (St) as they appear to support the sporangia. This tissue appears to allow to a phylogenetic migration of the sporangia from a lateral to an internal position. The greater the tendency towards an internal position or-indeed, in the case of *Pleurostima* occupation of a wholly internal position - the greater the development of the sustaining tissue. In genus *Barbacenia* the sustaining tissue is substantially reduced (except in the species *B. spiralis*); in *Aylthonia* it is practically absent.

Dehiscence of the anther in the Velloziaceae follow the position of the sporangia. It may be latrorse, or introrse or, as in some African species of *Xerophyta*, latrorse and introrse anthers may occur in the same flower (Fig. 7, 9). Anthers with latrorse dehiscence are the only form found in genus *Vellozia* which has well developed residual tissue. In subfamily Barbacenioidae, all species have introrse dehiscence, with a few (or none) residual tissue.

It is also important to observe on the pollen grains in the Velloziaceae. In the genus *Vellozia* all species have pollen grains in tetrads. All genera in subfamily Barbacenioidae have pollen grains in monads. In the genus *Xerophyta*, however, the following may be observed: Brazilian species all have pollen grains in tetrads, with the exception of one species, *Xerophyta plicata*, which has pollen grains in monads; *Xerophyta boliviensis* has pollen grains in tetrads, diads or monads. All *Xerophyta* species of the Old World have pollen grains in monads.

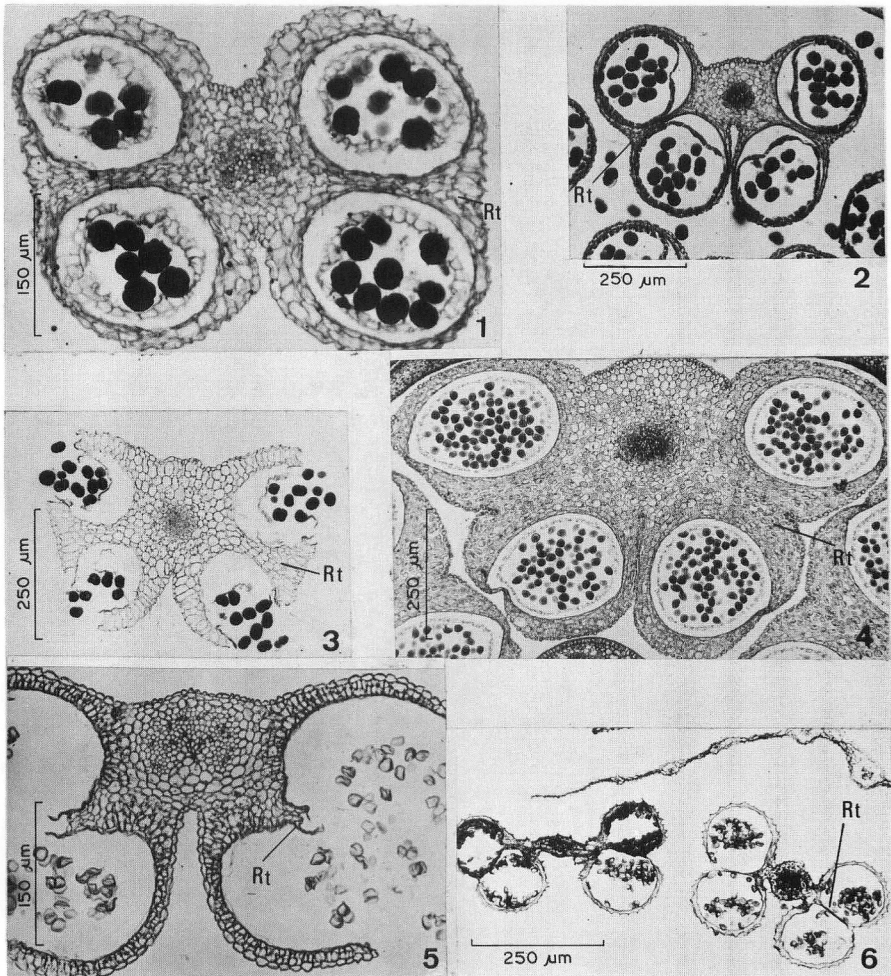
All the above-mentioned facts including the anther insertion would seem to reinforce the idea put forward by the author in previous works (Menezes 1980, 1984), namely: the genus *Vellozia* is the most primitive in the family, with more than 6 stamens with distinct filaments, basifixed anthers, with four locules at maturity, a well developed residual tissue, pollen grain shed as tetrads and latrorse dehiscence; the genera *Barbacenia* (except *B. spiralis*) and *Aylthonia* are the most advanced, with

six sessile and dorsifixed anthers adnate to the corona, with two locules at maturity, without (or with a little) residual tissue, pollen grains as monads and introrse dehiscence.

Acknowledgements - To Dr. Peter Raven, of the Missouri Botanical Garden, for critical suggestions.

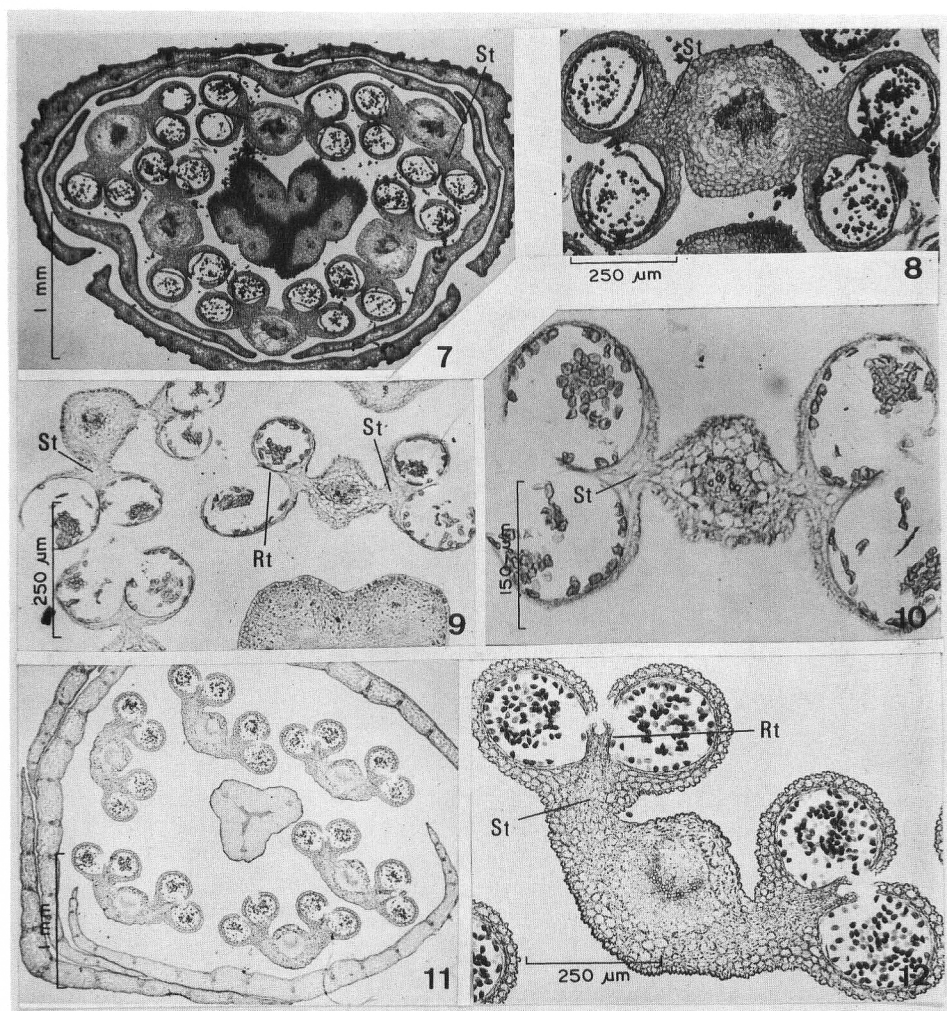
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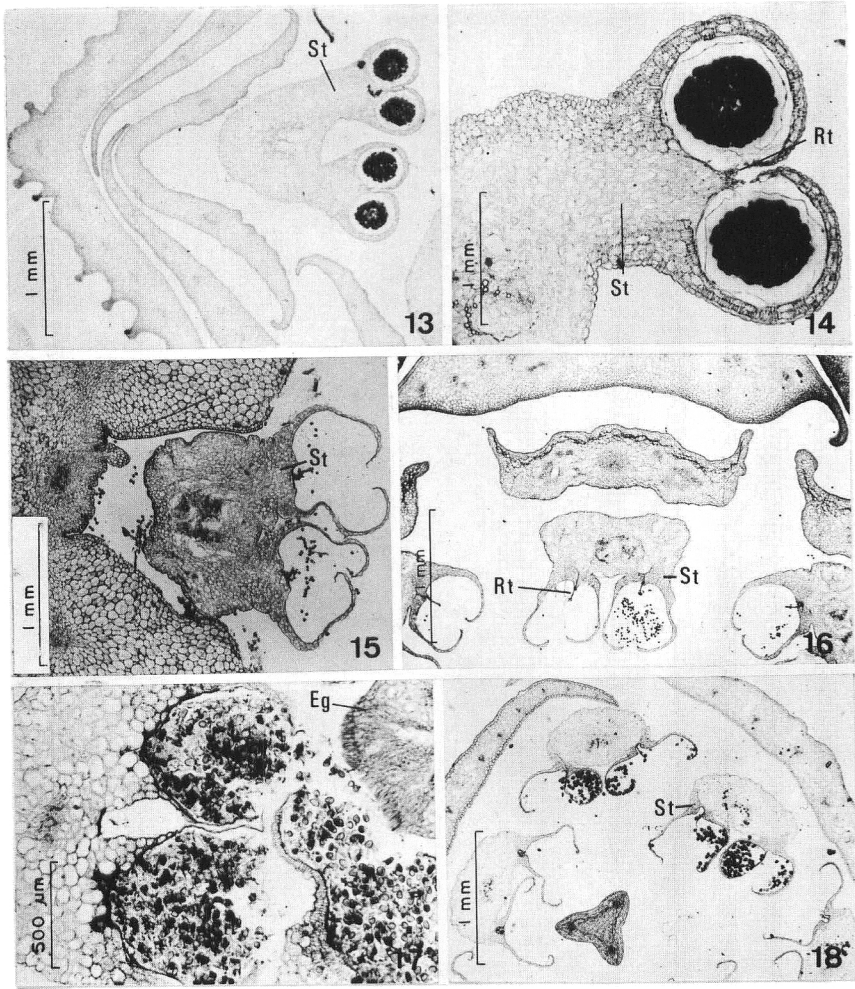
Figs. 1-6 - Cross section of anthers, respectively of *Vellozia jolyi*, *V. burle-marxii*, *Xerophyta minima* (with pollen grains in tetrads), *X. plicata* (with pollen grains in monads), *X. boliviensis* (with pollen grains in tetrads, dyads and monads) and *X. pinifolia* (with pollen grains in monads). Rt. - residual tissue.

Figs. 1-6 - Cortes transversais às anteras, respectivamente de Vellozia jolyi, V. burle-marxii, Xerophyta minima (com grãos de pólen em tétrades) X. plicata (com grãos de pólen em mônades), X. boliviensis (com grãos de pólen em tetrades, diades e mônades) e X. pinifolia (com grãos de pólen em monades) . Rt - tecido residual.



Figs. 7-8 - Cross section of *Xerophyta arabica* bud flower and a petalar anther, respectively. The petalar anthers have lateral sporangia and the sepalar anthers show a tendency toward internal sporangia; fig. 9-10 - Bud of *X. dasyliroioides*, with two kinds of anthers in the same flower, also; figs. 11-12 - Bud flower and anther of *Barbacenia spiralis*. All of them with pollen grains in monads. Rt. - residual tissue; St - sustaining tissue.

Figs. 7-8 - Corte transversal ao botão de *Xerophyta arabica* e a um estame petalar (respectivamente). As anteras petalares apresentam esporângios, laterais e as anteras sepalares apresentam-nos deslocados pra o interior; figs. 9-10 - Botão de *X. dasyliroioides* também com dois tipos de anteras na mesma flor; figs. 11-12 - Botão de *Barbacenia spiralis*, mostrando todas as anteras com grãos de pólen em mônades. Rt - tecido residual; St - tecido de sustentação.



Figs. 13-14 - Cross section of *Pleurostima spectabilis*, flower bud and anther respectively. Figs. 15-17 - Respectively *Barbacenia involucrata*, *B. flava* and *B. sellowii* and figure 18, *Aylthonia gentianoides*. All of the anthers have internal sporangia, introrse dehiscence and pollen grains in monads. Rt - residual tissue; St - sustaining tissue.

Figs. 13-14 - Corte transversal ao botão e à antera (respectivamente) de *Pleurostoma spectabilis*. Figs. 15-17 - Respectivamente, *Barbacenia involucreta*, *B. flava* e *B. sellowii* e figura 18, *Aylthonia gentianoides*, onde se verifica que todas as anteras têm esporângios situados internamente, com deiscências introrsas e os grãos de pólen apresentam-se em mônades. Rt - tecido residual; St - tecido de sustentação.