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Some aspects of comparative gynoecium morphology in three bromeliad species

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Summary: Comparative morphology of gynoecia was studied in *Aechmea fulgens* var. *discolor* Morr., *Pseudananas sagenarius* (Arruda) Camargo, and *Billbergia vittata* Mart. All are members of the subfamily Bromelioideae. The gynoecia of *Aechmea fulgens* var. *discolor* and *Pseudananas sagenarius* contain synascidiate, hemisynascidiate, hemisymplicate and asymplicate vertical zones. The gynoecium of *Billbergia vittata* shows an additional hypocarpous zone, but no synascidiate zone. Common septal nectaries in the hypocarpous structural zone are placed below locules. Twelve combinations of Leinfellner's structural zones of a hemisyncarpous gynoecium s.l. were established, most of them are not described in nature yet.

Keywords: *Aechmea fulgens* var. *discolor*, *Pseudananas sagenarius*, *Billbergia vittata*, Bromelioideae, Bromeliaceae, floral morphology, structural zones of the gynoecium, septal nectary

Basic principles of gynoecium differentiation on the vertical zones were introduced into the morphological analysis by Leinfellner (1950). He recognized three types of gynoecia: a) apocarpous – with non-fused carpels, represented by asymplicate zone; b) syncarpous – with fused carpels and synascidiate, symplicate, hemisymplicate and asymplicate zones; c) hemisyncarpous – with partly fused carpels and hemisynascidiate, hemisymplicate and asymplicate zones (Fig. 1). Leinfellner assumed that last type refers only to the gynoecium with septal nectary cavity. Böhme (1988) applied Leinfellner's classification to the gynoecium of bromeliads. She described the bromeliad's gynoecium as a hemisyncarpous one with hemisynascidiate (lower ovary part), hemisymplicate (upper ovary part and style) and asymplicate (stigma lobes) zones.

The gynoecium of bromeliads is complicated by the presence of nectary cavities in various positions in the ovary septa. Great interest was attached to the formalization and reconstruction of the development of nectary cavities. Septal nectaries are considered to be a product of the postgenital fusion of free edges of the neighboring carpels (Daumann 1970; Schmid 1985). Daumann (1970) distinguished 22 types of septal nectaries by the characters of their localization and shape and by the localization of a secretory tissue. He found that septal nectaries of bromeliads belong to three different types: l, m and o. Daumann considered that most septal nectaries have a body which is the largest part with secretory tissue on the wall surface, and terminal channels, which lead out the nectar.

On the base of space relations of the terminal channel and body, Böhme (1988) distinguishes three structural types of septal nectaries for bromeliads: apical-distance, apical and apical-proximal. Schmid (1985) suggests another view on the morphology of the septal nectaries. He differentiated five types of nectaries by the shape of nectary cavity on the cross-sections: primitive 'liliad', labyrinthine distinct, non-labyrinthine common, labyrinthine common and labyrinthine common with convoluted proliferations of the carpel's walls.

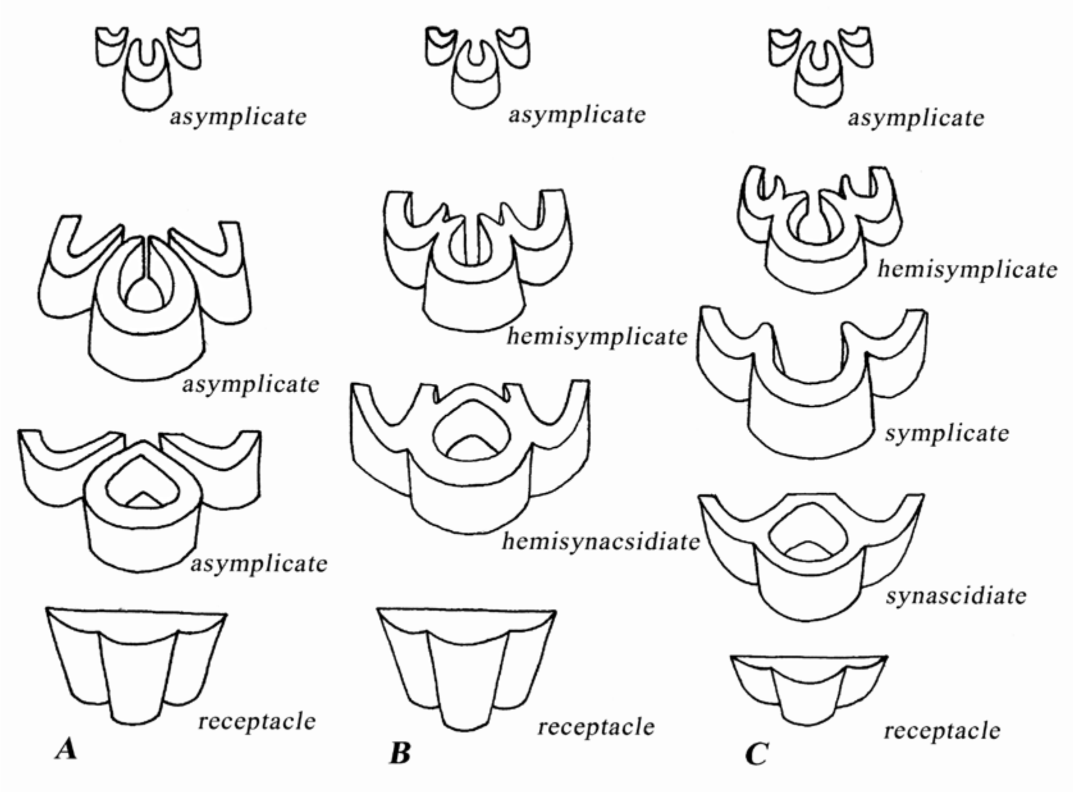

Figure 1: Structural types of gynoecia and their structural zones, after Leinfellner (1950). A – apocarpous, B – hemisyncarpous, C – syncarpous type.

Interesting research data were presented by van Heel (1988). He investigated the development of nectary cavity on example of several monocot species and supposed that carpels of the ovaries with septal nectary cavity originate freely or partly freely. Septal nectary cavities get shaped by dermal fusion of the sides of the carpel surrounding them (1), by upward growth of the apex (2), and mostly also by meristematic continuity of part of the ovary wall on the outside (3). This consideration extends the view, that septal nectaries are a product of the postgenital fusion of the carpels and must be examined as essential determinants of structural zonality of the gynoecium.

There is no concept about variability of the vertical structure of the ovaries with nectary cavities inside. In particular, zonality of the ovaries with so called ‘infralocular septal nectaries’, cavity of which is situated partial or fully below the locules, is not known. Division into interlocular, supralocular and infralocular nectaries, introduced by Simpson (1998), is concerned with the ovary conditions (Smets et al. 2000; Sajo et al. 2004), but the difference of proportion between epigynous and hypogynous flower does not reveal the difference between structural zones of hemisyncarpous gynoecium.

We studied the gynoecium structure in three representatives of the subfamily Bromelioideae: *Aechmea fulgens* var. *discolor* Morr., *Pseudananas sagenarius* (Arruda) Camargo and *Billbergia vittata* Mart. We intend to examine the structural zonality of the gynoecium with septal nectaries and interpret the information about structure of septal nectaries in this family.

Material and methods

Flowers were collected in the Botanical Garden of Ivan Franko National University of Lviv, Ukraine in 2004–2006. They were fixed in 70% alcohol. For morphological investigations we used total and permanent specimens. For permanent specimens the material was dehydrated with absolute ethanol and embedded in a mixture of paraffin and 5% beeswax according to the standard method with chloroform (Gerlach 1984). After that, the material was cut into 13 µm cross-sections with a rotary microtome 'MC-2' (USSR). Sections were stained with Mayer haematoxylin and 1% safranin. Then they were mounted in Canadian Balm. Figures were drawn by means of the microscopes 'MBS-9' (USSR) and 'Lomo Mikmed-1' (USSR) and a camera lucida 'Lomo RA-1' (USSR).

The total ovary height was calculated on the series of transverse sections from the base of the ovary to the style base.

Results

All studied species have epigynous actinomorphic flowers, slightly curved from the side of inflorescence's axis. The flowers have three sepals and petals and six stamens. The gynoecium is trimerous, with antesepalous fused carpels. On the cross-sections the style is rounded-triangular at the base with small furrows between the carpels. The stigma consists of three vertically directed lobes; it belongs to the simple-erected structural type (Brown & Gilmartin 1984).

Aechmea fulgens var. *discolor*

The flowers are about 1.5 cm in height (Fig. 2 A). Sepals are massive half-spherical, whereas petals are smaller and thin, fused together at their bases. Petals appendages are absent. Stamens with short thick filaments are fused with petals at the base. The ovary is spherical without clear borders between the carpels. The total ovary height is about 1.5 mm. The transition from pedicel to ovary is gradual.

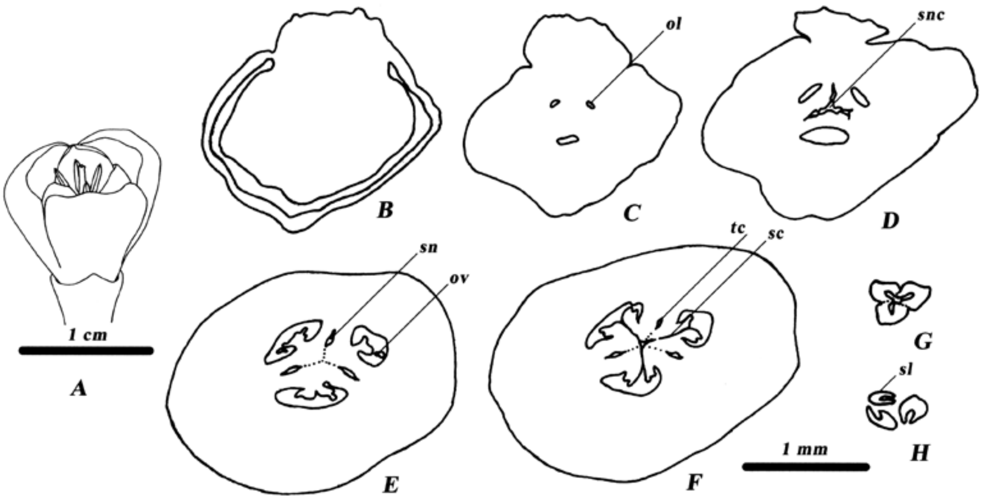

Figure 2: *Aechmea fulgens* var. *discolor*; flower (A) and series of cross-sections of the gynoecium from base to top (B–H). ol – ovary locule, ov – ovule, sc – style channels, sl – stigma lobe, sn – septal nectary cavity, tc – terminal channel; postgenital carpel fusions signed by dots.

Table 1: Structural zones of the hemisyncarpous gynoecium in studied species and their percentage in the ovary.

Structural zones		*Aechmea fulgens* var. *discolor*	*Pseudananas sagenarius*	*Billbergia vittata*
Hypocarpous		——	——	3.2%
Synascidiate		3.6%	3.7%	——
Hemisynascidiate		65.5%	72.6%	68.9%
Symplicate		——	——	——
Hemisymplicate		30.9%	23.7%	27.9%
Asymplicate		Style and stigma lobes. Percents are not accounted.		

The gynoecium of *Aechmea fulgens* var. *discolor* (Fig. 2 B, C) has a short sterile part with isolated locules at the base. The height of this first (synascidiate) zone is about 4% of the total ovary height. Above this part a tri-ray split of septal nectary appears (Fig. 2 D), with rays on the radii of septa. The height of this second sterile part is about 42% of the total ovary height. Above the tri-ray split the septal nectary closes postgenitally at its center and forms three separated splits

(Fig. 2 E). On cross-sections of this level ovules are present in the ovary locules. This fertile part is about 24% of the total ovary height. The second as well as the third part has a nectary cavity and isolated locules, they belong to the hemisynascidiate structural zone. Together they make up about 66% of the total ovary height. From the base of the style channels up to the style base there is a fourth, fertile part (Fig. 2 F). It has postgenital isolated locules with 1–2 ovules at its base. It belongs to the hemisymplicate structural zone. Its height is about 30% of the total ovary height (Tab. 1).

There are about 6 ovules per locule. Ovules are anatropous, sessile, without halasial appendages. They are fastened to placentas which look mushroom-like on cross-sections. The placentation is axile at the base and parietal at the level of postgenital fusion of carpel margins (Fig. 2 E, F).

The cavity of the septal nectary is present on all levels of the ovary except the lowest. On longitudinal sections it has an elongated shape. The septal nectary has a body, which is situated first in the ovary center and then in the septa, and the three terminal channels. The body of the septal nectary has a secretory tissue on its entire surface. Terminal channels are formed near the bases of the style channels. They open at the base of style on the radial septa.

Pseudananas sagenarius

The flowers are elongated up to 5 cm in height (Fig. 3 A) with a short pedicel. The sepals are tough with sharp edges at the apex. Petals are fleshy with twin appendages at the base. Bud-like petal appendages are formed by an epidermal tissue. Stamens have long cylindrical filaments. The petal appendages clasp the bases of filaments. The ovary of *Pseudananas sagenarius* is obconical without clear borders between carpels. The total ovary height is about 3.5 mm.

The zonality of the gynoecium of *Pseudananas sagenarius* is similar to that of *Aechmea fulgens* var. *discolor*. The gynoecium of *Pseudananas sagenarius* has a short sterile part with isolated locules

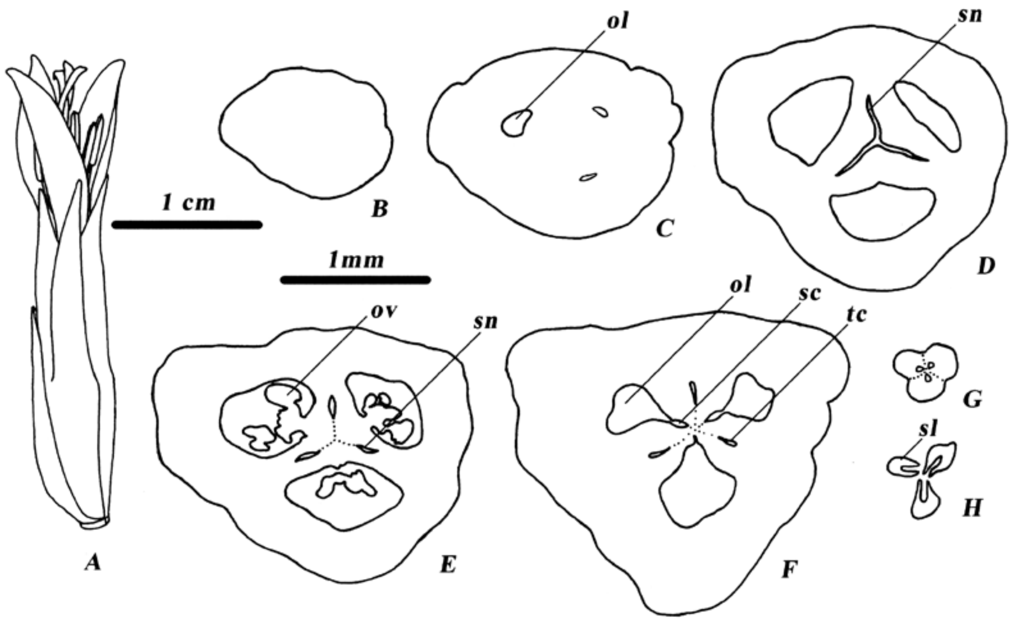

Figure 3: *Pseudananas sagenarius*; flower (A) and series of cross-sections of the gynoecium from base to top (B–H).

(Fig. 3 B, C) at the base. The height of this first (synascidiate) zone is about 4% of the total ovary height. Above this part a tri-ray split of septal nectary is present (Fig. 3 D). This sterile second part is about 42% of the total ovary height. Above the tri-ray split the septal nectary closes postgenitally at the center and makes up three separated splits in the septa (Fig. 3 E). This third part contains the ovules – it is fertile. The height of this part up to the base of the style channels is about 31% of the total ovary height. The second and third parts have a nectary cavity and congenital isolated locules. Together they belong to the hemisynascidiate structural zone and make up about 73% of the total ovary height. From the base of the style channels up to the style base a fourth part can be found (Fig. 3 F). It doesn't contain ovules. Its three locules become postgenitally isolated. The height of this hemisymplicate structural zone is about 23% of the total ovary height (Tab. 1).

There are about 12 elongated ovules per locule. The ovules are anatropous, oval-like, without halasial appendages. They are fastened to placentas with complex shape. The funiculi are strong, placentation belongs to the 'axile' type (Fig. 3 E).

Similar to *Aechmea fulgens* var. *discolor*, the cavity of the septal nectary is present inside the ovary in the three upper levels. On longitudinal sections the septal nectary also has an elongated shape. It has a body, which is situated first in the ovary center and then in the septa, and it has three terminal channels above. The body of the septal nectary has a secretion tissue on the whole surface. Terminal channels are hardly formed below the bases of the style channels. They open at the base of the style on the radial septa.

Billbergia vittata

The flowers are mostly elongated, up to 8 cm in height (Fig. 4 A). The pedicel is short and wide. Sepals are long, boat-like and tough, petals are thin and twice longer than the sepals. The petals have convolute apexes and twin scale-like appendages at the base. Petal appendages are formed by the epidermal tissue. They clasp the bases of the filaments. Stamens have long cylindrical filaments. Calyx, corolla and filaments are fused at the base and form a short hypanthium.

The ovary of *Billbergia vittata* is rectangular in the longitudinal plane and triangular in the transverse plane with furrows between the carpels. It has a more or less smooth external wall in the lower part which hangs over the pedicel. On the higher levels the inner wall of the gynoecium shows strong ribs: in groups of three on the lateral-distal verges and groups of four on the proximal verge. The total ovary height is about 13 mm. The style is long, the stigma lobes are widening upwards.

The gynoecium of *Billbergia vittata* (Fig. 4 C) has a multi-ray complicated split of the septal nectary at the base. There are no ovary locules. This first (hypocarpous) zone has about 3% of the total ovary height. Ovary locules are present above the first zone (Fig. 4 D). The split of the septal nectary increases, but ovules are absent. This second part with congenital isolated locules has about 11% of the total ovary height. In the zone above, the complicated split of the septal nectary fuses at the center and forms three separated splits in the ovary septa (Fig. 4 E). This third part contains the ovules – it is fertile. Its height up to the base of the style channels is about 58% of the total ovary height. The second and third part together make up about 69% of the total ovary height and belong to the hemisynascidiate zone. Above these parts up to the style base the fourth part is situated (Fig. 4 F). It doesn't contain ovules and has three postgenital isolated locules. Its height is about 28% of the total ovary height (Tab. 1). The structure is hemisymplicate.

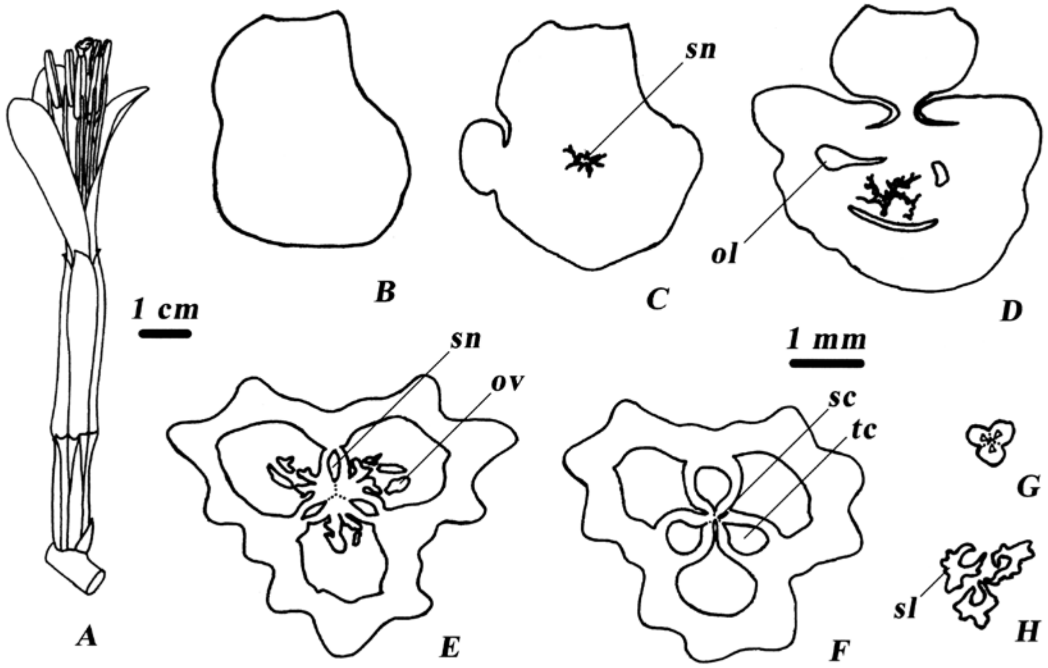

Figure 4: *Billbergia vittata*; flower (A) and series of cross sections of the gynoecium from base to top (B–H).

There are about 12 anatropous, lemon-like ovules per locule. Funiculi are strong; halasial appendages of different length are present. Placentas have a complicated shape and many vertical furrows. The placentation is axile (Fig. 4 E).

Unlike *Aechmea fulgens* var. *discolor* and *Pseudananas sagenarius*, the cavity of the septal nectary of *Billbergia vittata* is present below the ovary locules. On longitudinal sections the septal nectary also has an elongated and most complicated shape. It has a body, which is first situated in the ovary center and then in the septa. The body of the septal nectary has a secretory tissue on its entire surface. The secretory tissue is more developed than in the previous species and it has many small fissures. It is supplied by numerous small vascular bundles. The septal nectary has three terminal channels. They open at the base of the style on the radial septa.

Discussion

The septal nectaries of all studied species have terminal channels in apical position and therefore they belong to the 'apical' type after Böhme (1988). Besides, they have septal nectaries with a body, entirely covered by a secretory epidermis, and an inferior ovary. Classified after Daumann (1970), these nectaries belong to the same structural type 'o'.

Böhme's (1988) zonality of the bromeliad gynoecium doesn't consider all possible structural modifications of gynoecia with a septal nectary cavity. After Böhme, nectary can exit only at the base of the stigma lobes. We couldn't observe exit of nectary at this place, but we observed it on the level of the ovary roof or even lower. We consider that the bromeliad gynoecium must be determined as hemisyncarpous in a wide sense with septal nectary cavity inside, but the zonality of such a gynoecium needs a more precisely specification.

Septal nectaries of the species investigated have characteristic transverse shapes on the different levels. In particular, the lower part of the septal nectaries of *Pseudananas sagenarius* and *Aechmea fulgens* var. *discolor* can be interpreted as 'liliad' type after Schmid (1985), but the upper part as a non-labyrinthine common type. The basal part of the septal nectary of *Billbergia vittata* has the shape of a labyrinthine common type with convoluted proliferations, the upper part shows the shape of labyrinthine common and non-labyrinthine common types. Thus, a classification of the septal nectaries after Schmid is difficult to use for a morphological analysis of the gynoecium.

In the gynoecium of *Billbergia vittata* the septal nectary is present below the locules (Fig. 4C). Such inner nectaries, which have a body partly or completely situated below the ovary locules, can be determinated by a great development of the flower apex, as van Heel (1988) supposed. These nectaries look like typical septal nectaries, but they cannot to be called 'septal' because they are not situated in ovary septa. They are better described as 'gynopleural' (Smets et al. 2000) than as 'septal in a broad sense'.

For the first time we distinguish a 'hypocarpous' structural zone, which has a septal nectary cavity below the locules. This zone is interpreted as a lower part of the gynoecium, but it can be formed by an invaginated floral apex. The hemisyncarpous gynoecium with a 'hypocarpous' structural zone never has a synascidiate zone, but a hemisynascidiate zone above the 'hypocarpous' one.

By the data of our study, the gynoecium of the investigated species is hemisyncarpous s.l. The gynoecia of *Pseudananas sagenarius* and *Aechmea fulgens* var. *discolor* consist of synascidiate (first level, about 4% of the total ovary height for both), hemisynascidiate (second and third levels together, about 73% and 66% of the total ovary height), hemisymplicate (fourth level, about 23% and 30% of the total ovary height) and asymplicate (the style, percents are not accounted) structural zones (Tab. 1). The gynoecium of *Billbergia vittata* consists of hypocarpous (first level, about 3% of the total ovary height), hemisynascidiate (second and third levels together, about 69% of the total ovary height), hemisymplicate (fourth level, together they compose about 28% of the total ovary height) and asymplicate (the style, percents are not accounted) structural zones (Tab. 1). A symplicate zone could not be found in the hemisyncarpous gynoecium of the studied species.

The recent work of Sajo et al. (2004) concerns the same subject as well as floral vasculature, petal appendages, and the evolution of epigyny in ten species of Bromeliaceae. The authors found out, that the hypogynous flowers of Tillandsioideae and Pitcairnioideae possess mostly labyrinthine infralocular nectaries, fully or partly embedded in the receptacular region. All studied Bromeliaceae have common septal nectaries, which open to the exterior at the base of the ovary (or up to ⅓ of the ovary height). This evidence indicates, that the gynoecium of Tillandsioideae and Pitcairnioideae is mostly apocarpous; it contains hypocarpous, hemisynascidiate, hemisymplicate and asymplicate zones.

Another problem may arise, when we interpolate vertical gynoecium zonality after Leinfellner (1950) on real objects: the definition of the border of consecutive zones. In superior ovaries this problem doesn't come up, but when we analyze epigynous flowers, we often can't define the border between hemisymplicate and asymplicate structural zones. Fig. 5 shows that in the superior ovary the visual lower border of the asymplicate zone coincides with the real (actual) one. However, in the inferior ovary this visual and real (actual) borders can be different. This

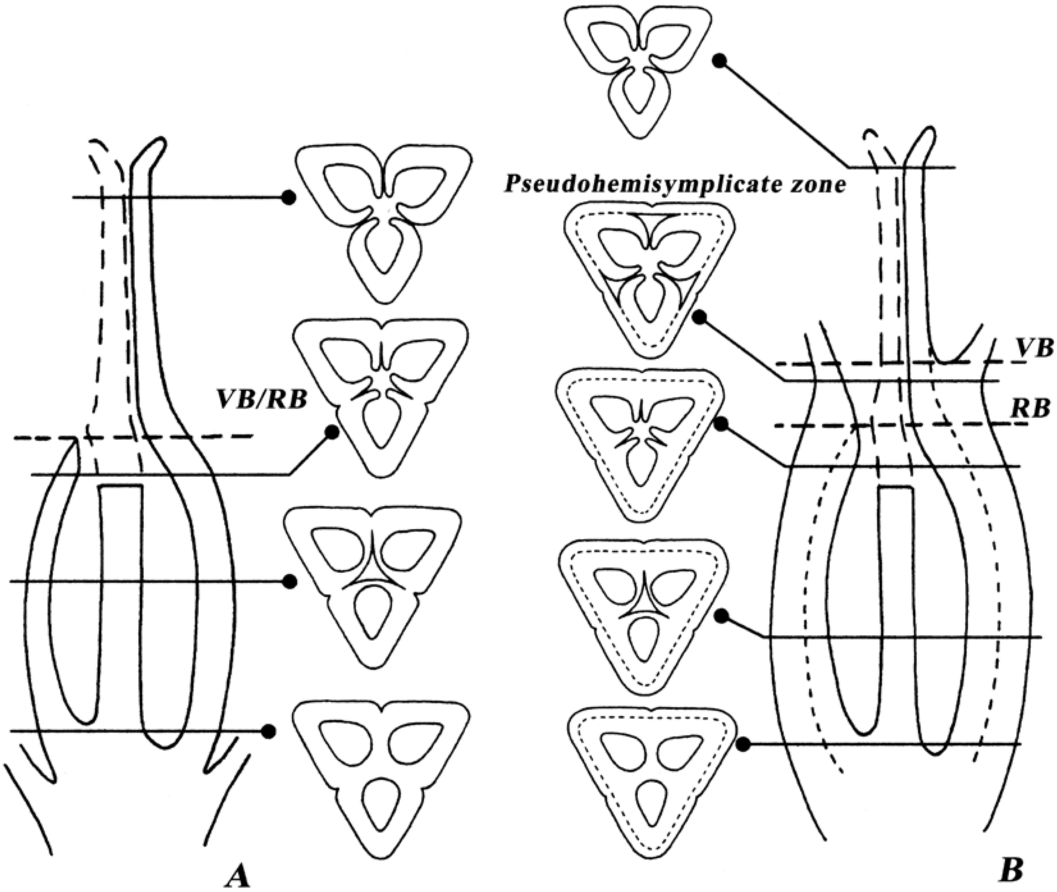

Figure 5: Vertical zonality of the hemisyncarpous gynoecium with superior (A) and inferior (B) ovary. VB – visual border of asymplicate zone, RB – real border of asymplicate zone.

happens, when the floral tube of appendicular or receptacular origin is fused with carpels in the asymplicate zone. Here, the asymplicate zone looks like a hemisymplicate one. We call this part 'pseudohemisymplicate' zone. In this case we can't define at all the upper border of the hemisymplicate structural zone in the gynoecium. In the studied species a border between hemisymplicate and asymplicate structural zones is not clearly detectable.

Now we suppose the existence of at least 12 different structural types of gynoecia with septal nectary cavity (hemisyncarpous gynoecia s.l.) (Tab. 2). These structural types we distinguish on the base of the analysis of vertical zonality of the studied hemisyncarpous gynoecium after Leinfellner (1950), and space reconstruction of possible combinations of structural zones (Fig. 6). The gynoecia of *Pseudananas sagenarius* and *Aechmea fulgens* var. *discolor* belong to the structural type 'A'. The gynoecium of *Billbergia vittata* belongs to the structural type 'K'. The other cells of the table are not filled with real objects yet. Therefore, further investigations of the structural zonality of hemisyncarpous gynoecia s.l. in a wider scope of representatives and search for gynoecia of certain types have to be carried out. Some of the structural types proposed here may remain unrealized in nature.

Table 2: Structural zones of supposed types of the gynoecium with septal nectaries.

Structural type of the hemisyncarpous gynoecium s.l.	Consecutive structural zones
A	synascidiate, hemisynascidiate, hemisymplicate, asymplicate
B	synascidiate, hemisynascidiate, asymplicate
C	synascidiate, hemisymplicate, asymplicate
D	synascidiate, symplicate, hemisymplicate, asymplicate
E	symplicate, hemisymplicate, asymplicate
F	hemisynascidiate, hemisymplicate, asymplicate
G	hemisynascidiate, asymplicate
H	hemisymplicate, asymplicate
I	hypocarpous, hemisynascidiate, asymplicate
J	hypocarpous, asymplicate
K	hypocarpous, hemisynascidiate, hemisymplicate, asymplicate
L	hypocarpous, hemisymplicate, asymplicate

Conclusions

Existing approaches to the classification of septal nectaries are not applicable to the characterization of structural types of the hemisyncarpous gynoecium s.l. of Bromeliaceae. Only the concept of vertical zonality of the hemisyncarpous gynoecium sensu Leinfellner (1950) can provide adequate analysis of such gynoecia and their typification.

For the first time, we describe the 'hypocarpous' structural zone, where common septal nectary cavity is placed below the locules.

For the hemisyncarpous gynoecium with an inferior ovary the 'pseudohemisymplicate' zone is distinguished by an asymplicate zone, which looks like a hemisymplicate one because of the fusion of free carpels to the floral tube.

The existence of at least 12 different structural types of gynoecia with septal nectary cavity (hemisyncarpous gynoecia s.l.) is assumed, but most of them are not revealed in real objects until now.

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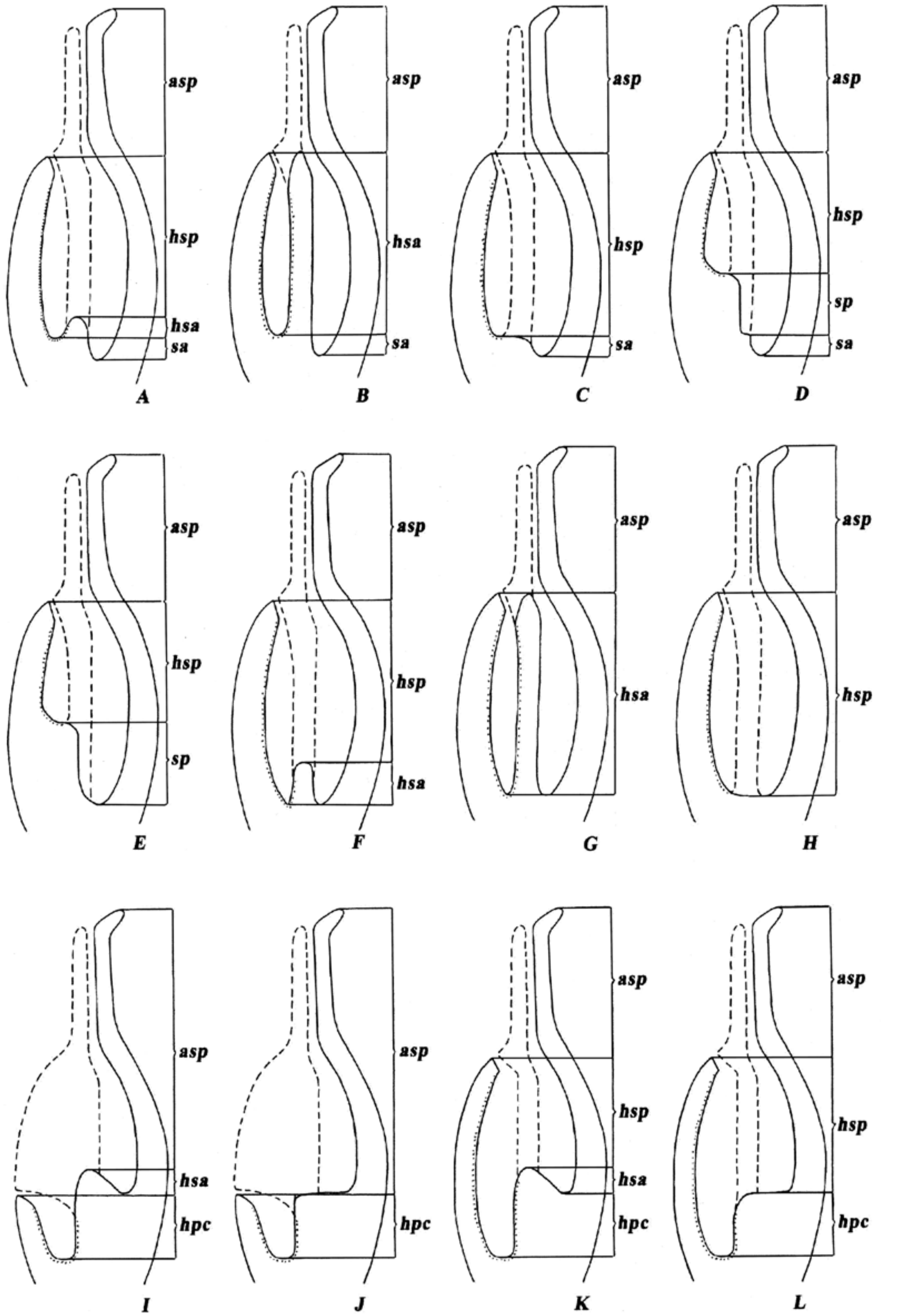

Figure 6: Visual reconstruction of the supposed types of gynoecia with septal nectary, A–L. The structural zones: asp – asymplicate, hpc – hypocarpous, hsa – hemisynascidiate, hsp – hemisymplicate, sa – synascidiate, sp – symplicate; secretory tissues are signed by dots, postgenital fusions are signed by broken lines.

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