Inflorescence architecture in Brazilian species of Aechmea subgenus Chevaliera (Bromeliaceae – Bromelioideae)†

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The inflorescences in Bromeliaceae are indeterminate, supported by a terminal scape of variable size, and with bracts of variable position, number, colour, shape and texture. Aechmea is the most diverse genus of Bromelioideae (c. 220 species) having large inflorescences of variable size and shape. Aechmea subgenus Chevaliera comprises 21 taxa distributed throughout Central and South America, with a centre of species richness in eastern Brazil. A study of the inflorescence morphology of 15 Brazilian species is presented here (A. alopecurus, A. castanea, A. conifera, A. depressa, A. digitata, A. hostilis, A. leucolepis, A. multiflora, A. muricata, A. ornata, A. perforata, A. rodriguesiana, A. saxicola, A. sphaerocephala and Aechmea sp. nov. unpublished). The study was based on living specimens and herbarium material with the inflorescence architecture observed at different developmental stages. The study describes the architectural form of the inflorescences in full flower or with at least half of the flowers open, as fruit development may produce architectural changes in the axis. The inflorescence in the subgenus ranges from simple to compound. Spicate inflorescences are the basic pattern, and a capituliform pattern is reported here for the first time in Bromeliaceae. Compound inflorescences are the rarest form in the subgenus, being represented by racemes of spikes. Descriptions, illustrations and schematic diagrams are presented. © 2008 The Linnean Society of London, Botanical Journal of the Linnean Society, 2008, 158, 584–592.

ADDITIONAL KEYWORDS: Brazil - Neotropics - monocotyledons - morphology - systematics.

INTRODUCTION

Since the start of the 19th century, many studies have been performed on Bromeliaceae, with various foci (Beer, 1857; Baker, 1879, 1889; Wittmack, 1888; Mez 1891–1894, 1896, 1935; Harms, 1930; Smith & Downs, 1974, 1977, 1979; Benzing, 2000), but few have detailed the organization of the inflorescences. Studies specifically addressing the subject of inflores-

cences in Bromeliaceae were developed by Sideris & Krauss (1938), Foster (1945) and Okimoto (1948). Of these, only the latter presents a detailed analysis of the inflorescence structure beyond the study of the fruit of *Ananas comosus* (L.) Merr.

Inflorescences in Bromeliaceae are indeterminate and are supported by a terminal scape the size of which varies from short, leaving the inflorescence included in the interior of the rosette, to long, projecting the inflorescence above the rosette. The scape is terminal, continuous with the rosette axis and has spirally arranged bracts which vary in number, shape, size, colour and texture. Lateral inflorescences

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are rare in the family, being reported in *Greigia* (Smith & Downs, 1979), *Hechtia* (Burt-Utley & Utley, 1987), *Dyckia* (Smith & Downs, 1974) and some species of *Quesnelia* and *Disteganthus* (Smith & Downs, 1979; Gouda, 1994).

In representatives of the three subfamilies, simple or compound inflorescences are found, as panicles, racemes or spikes. In Pitcairnioideae, the inflorescence, in general, is a simple raceme (Forzza, 2005). The greatest diversity of inflorescence types is present in Bromelioideae and Tillandsioideae, represented by panicles, racemes and spikes. In these two subfamilies, the inflorescences contain few to numerous flowers, sparsely disposed or congested, and borne distichously or polystichously. In Tillandsioideae, simple to many-branched inflorescences occur, with the maximum reduction of flower number in the genus *Tillandsia*, with *T. usneoides* (L.) L. and *T. albertiana* F.Vervoorst having only a single flower (Benzing, 2000; Tardivo, 2002).

Aechmea, the largest genus of Bromelioideae with about 220 species (Luther & Sieff, 1994, 1997; Luther, 2000, 2001) distributed in eight subgenera (Smith & Downs, 1979), has a highly variable pattern of inflorescence architecture.

Aechmea subgenus Chevaliera comprises 21 taxa distributed in Central and South America, with the highest species diversity in eastern Brazil. Presently, 17 species are recorded for Brazil and can be found in the Amazon Forest, Atlantic Forest and 'restingas' (Sousa, 2004).

The scape is terminal, short or elongated, with imbricate bracts and variable coloration. The inflorescences are simple or compound with sessile flowers arranged polystichously. Each flower is subtended by a rigid floral bract. The fruit is a berry, typical of the subfamily Bromelioideae, and is dispersed by animals. With the objective of contributing to the understanding of the inflorescence patterns in Bromeliaceae, the present work details the inflorescence morphology of Brazilian species of *Aechmea* subgenus *Chevaliera*.

MATERIAL AND METHODS

For the present study, 15 of the 17 Brazilian species of *Aechmea* subgenus *Chevaliera* were collected from natural populations (*in situ*); in addition, herbarium material was consulted.

The analysis of specimens was performed at different developmental stages of the plants. However, an attempt was made to describe the inflorescences in full flower, or with open flowers along at least half of the inflorescence, as sometimes the infructescence undergoes modifications leading up to full fruit development.

The specific terminology adopted, for both the morphological descriptions and the inflorescence types, follows Weberling (1989), The term 'capituliform' is used in this paper instead of 'capitulum', because the flower organization in the inflorescence is distinct from the arrangement observed in species of Asteraceae. Elsewhere, morphological concepts of Radford *et al.* (1974), Smith & Downs (1979) and Stearn (2000) were used.

Table 1 presents, for each studied species, references to the consulted herbarium specimens.

RESULTS

The observed patterns of the inflorescences in the studied species are terminal and polytelic, with flowers variously borne in simple spikes (Figs 1–6, Table 2), capitula (Figs 7–10, Table 2) or compound inflorescences of racemes of spikes (Figs 11–14, Table 2). Inflorescences have a whitish or brown lepidote indument covering all surfaces except the petals. Sometimes, the inflorescence is completely covered in whitish lanate indument, leaving only the apical portion of the sepals and petals visible (Fig. 3).

The floral bracts are concave and accrescent with variable coloration (brown, pink, green or red) and different shapes (obpyramidal, oblong, ovate, lanceolate or spatulate). The apices are aristate, cuspidate or mucronate. The margins are entire or serrate.

The flowers are sessile and vary in size and coloration, especially the petals, which can be whitish, bluish, lilac or green (Figs 1, 3, 5, 7, 8, 13). Flower maturation in the spicate inflorescences is acropetalous (Figs 1, 3, 5), and, in the capitula, centripetal (Figs 7, 8). The flowers are at anthesis during the day and are visited by birds, especially hummingbirds. Each individual plant can have 3–12 flowers at anthesis simultaneously per day (Figs 5, 7, 8, 13).

Although it is true that the spike is the basic unit of the inflorescences in *Aechmea* subgenus *Chevaliera*, inflorescences vary from simple to compound, and with different dimensions of the axis and paraclades. The most complex pattern is found in *A. digitata* (Figs 11, 12) and *A. rodriguesiana* (Figs 13, 14), and the simplest patterns are found in the remaining taxa, as shown in Table 2 and Figures 1–10.

SIMPLE INFLORESCENCES

Simple, robust inflorescences with a strobiliform appearance constitute the most common pattern in *Aechmea* subgenus *Chevaliera* (Figs 1–6, Table 2).

The scape is covered by rigid, imbricate bracts, and may be short (13–20 cm) or long (22–120 cm), bearing the inflorescence above the rosette. The inflorescence axis (or rachis) may be delicate and elongated, as in

Table 1. Species and vouchers used in the analysis of the inflorescences of *Aechmea* subgenus *Chevaliera*. The herbarium acronyms follow Holmgren & Holmgren (2005)

Taxon	Voucher information		
Aechmea alopecurus Mez	Brazil. Bahia: Macarani, <i>Carvalho et al. 7023</i> (CEPEC). Minas Gerais: Salto da Divisa. <i>Lombardi et al. 5281</i> (BHCB)		
Aechmea castanea L.B.Sm.	Brazil. Espírito Santo: Cariacica, Sousa et al. 473 (SP). Santa Teresa, Estação Biológica de Santa Lúcia, Sousa et al. 317 (SP); Sousa et al. 481 (SP)		
Aechmea conifera L.B.Sm.	Brazil. Bahia: Una, Sousa et al. 490 (CEPEC, SP)		
Aechmea depressa L.B.Sm.	BRAZIL. Bahia: Una, Sousa et al. 308 (CEPEC, SP, TEPB); Santa Cruz da Vitória, Fazenda Uruguaiana, Amorim et al. 3582 (CEPEC, SP); Sousa et al. 491(SP)		
Aechmea digitata L.B.Sm & R.W.Read.	Brazil. Bahia: Almadina, <i>Sousa et al.</i> 311 (CEPEC, SP, TEPB). Santa Cruz da Vitória, Fazenda Uruguaiana, <i>Amorim et al.</i> 3581 (CEPEC, SP)		
Aechmea hostilis E.Pereira	Brazil. Espírito Santo: Santa Teresa, Sousa et al. 318 (MBML, SP); Santo Antônio, Sousa et al. 321 (SP, TEPB)		
Aechmea leucolepis L.B.Sm.	Brazil. Espírito Santo: Santa Teresa, <i>Demuner et al. 1109</i> (MBML); Cachoeira do Medalhão, <i>Kollmann et al. 4449</i> (MBML); <i>Sousa et al. 499</i> (SP)		
Aechmea multiflora L.B.Sm.	BRAZIL. Bahia: Ilhéus, <i>Sousa et al. 300</i> (SP, CEPEC); Mata de São João, Sousa <i>et al. 354</i> (SP, TEPB). Sergipe: Santa Luzia do Itanhim, <i>Sousa et al. 357</i> (SP); Santo Amaro das Brotas, <i>Sousa et al. 358</i> (SP)		
Aechmea muricata (Arruda) L.B.Sm.	BRAZIL. Alagoas: Marechal Deodoro, Esteves & Lyra-Lemos, 2168 (MAC). Pernambuco: Igarassu, Ramage s.n. (BM 596982). Recife, Baker & Collins s.n. (NY 376503, S, SP, SPF, US); Foster 2429 (R, US). São Lourenço da Mata, Andrade-Lima 63–4197 (IPA); Sousa et al. 169 (UFP)		
Aechmea ornata Baker	Brazil. São Paulo: Peruíbe, <i>Sousa et al. 387</i> (SP). Eldorado, Parque Estadual de Jacupiranga, <i>Araujo & Ficher 33486</i> (UEC). São Miguel Arcanjo, <i>Martinelli et al. 15769</i> (RB)		
Aechmea perforata L.B.Sm.	BRAZIL. Bahia: Jussarí, <i>Sousa et al. 312</i> (CEPEC, SP). Espírito Santo: Santa Teresa, <i>Sousa et al. 313</i> (MBML, SP, TEPB); Estação Biológica de Santa Lúcia, <i>Sousa et al. 315</i> (SP)		
Aechmea rodriguesiana (L.B.Sm.) L.B.Sm.	Brazil. Amazonas: Manaus, Sousa et al. 390 (INPA, SP); Sousa et al. 495 (INPA)		
Aechmea saxicola L.B.Sm.	Brazil. Espírito Santo: Santa Teresa, <i>Kollmann et al. 4018</i> (MBML, SP). Soretama, <i>Sousa et al. 319</i> (SP). Rio de Janeiro: Rio das Ostras, <i>Pablo s.n.</i> (SP 363887)		
Aechmea sphaerocephala Baker	Brazil. Rio de Janeiro: Restinga de Grumari, Sousa et al. 510 (SP); Sousa et al. 511 (SP, TEPB)		
Aechmea sp. nov. unpublished	BRAZIL. Espírito Santo: Cariacica, Sousa et al. 331 (SP)		

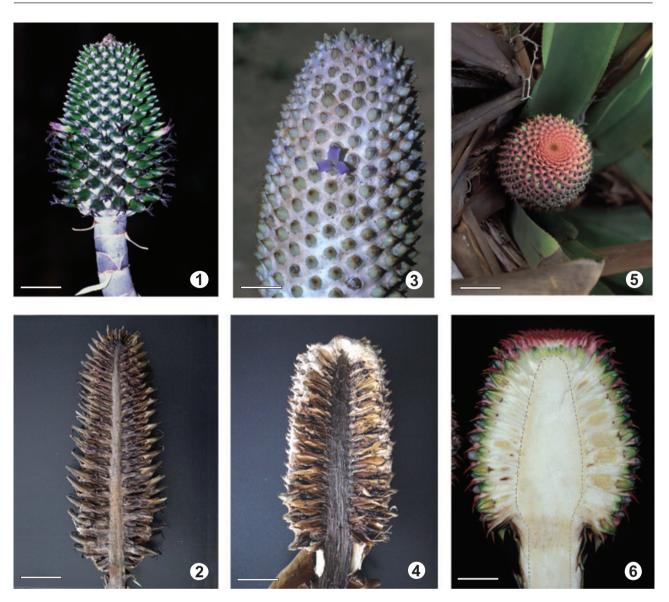
most spicate inflorescences (Fig. 2), or short and robust (long in *A. depressa*), as in the capitulate inflorescences (Fig. 10).

Spikes

Simple spikes occur in ten of the 15 studied species, and differ in the type of indument, floral morphology and dimensions of the axis. All studied species have a long scape (30–73 cm). The bracts of the scape are of various colours. They are red in A. alopecurus and A. ornata, and dark grey in A. castanea, A. leucolepis and A. muricata, with entire margins and a sharply pointed apex in all taxa. In A. alopecurus, A. castanea (Figs 1, 2), A. leucolepis, A. muricata and A. ornata, the inflorescence axis is elongated and thin. In this group, only A. alopecurus has inflorescences com-

pletely covered by a whitish lanate indument. The remaining species have a whitish lepidote indument restricted to the floral bracts and sepals. The floral bract is broadly ovate and pinkish in *A. alopecurus* and obpyramidal and green in the remaining taxa. The apex of the floral bract is aristate in *A. alopecurus*, *A. muricata* and *A. ornata* and mucronate in *A. leucolepis* and *A. castanea*. The margins of the floral bract are entire in all species. The flowers have greenish-white petals with the central portion bluish in *A. leucolepis*, pinkish to burgundy in *A. alopecurus* and blue to purple in the remaining taxa.

Another group of species has spikes with the inflorescence axis slightly expanded and elongated. In these species, the scape is long (22–80 cm), supporting the inflorescence above the rosette. The bracts of



Figures 1–6. Spikes of *Aechmea* subgenus *Chevaliera*. Figs 1, 2. *Aechmea castanea*. Fig. 1. General view. Fig. 2. Longitudinal section. Figs 3, 4. *Aechmea perforata*. Fig. 3. General view. Fig. 4. Longitudinal section. Figs 5, 6. *Aechmea multiflora*. Fig. 5. General view. Fig. 6. Longitudinal section (broken line, enlarged inflorescence axis. Scale bars: Fig. 1, 4.0 cm; Fig. 2, 3.0 cm; Fig. 3, 2.5 cm; Fig. 4, 3.2 cm; Fig. 5, 7.4 cm; Fig. 6, 3.6 cm. Figs 1–5, Sousa G.; Fig. 6, Amorim EA.

the scape are green with serrate margins in *A. conifera*, dark grey with entire to slightly serrate margins in *A. perforata*, and red with entire margins in *A. sphaerocephala*. A whitish lanate indument is found only in *A. perforata* (Figs 3, 4), whose floral bracts and sepals are totally covered, leaving visible only the apical portion of the sepals and petals. In the remaining species, a whitish lepidote indument covers only the apical portions of the floral bracts and sepals. The floral bract is ovate in *A. conifera* and obpyramidal in *A. perforata* and *A. sphaerocephala*. The coloration of the floral bracts varies from green in

A. sphaerocephala and A. perforata to green with brown margins in A. conifera. All taxa have floral bracts with entire margins and a mucronate apex. The flowers vary from lilac to bluish (flowers were not seen in A. conifera).

In addition, in this group, A. multiflora (Figs 5, 6) and A. saxicola have a greatly enlarged inflorescence axis. In spite of the inflorescences being included in the rosettes of some individuals of A. multiflora and A. saxicola, the scape is long (60–120 and 50–65 cm, respectively), surpassing the leaf sheaths and leaving the inflorescence visible. The bracts of the scape are

Table 2. Synthesis of types of inflorescence pattern in *Aechmea* subgenus *Chevaliera* (FB, floral bract; FL, flower; PB, primary bract; SB, bract of the scape)

Inflorescence type	Inflorescence pattern	Studied taxa	Schematic inflorescence patterns
SIMPLE	SPIKE	A. alopecurus	1147
		A. castanea	
		A. conifera	
		A. leucolepis	
		A. muricata	FB
		A. ornata	
		A. perforata	
		$A.\ sphaerocephala$	SB
		A. multiflora	
		A. saxicola	1/
	CAPITULIFORM	A. depressa	
		A. hostilis	
		Aechmea sp. nov.	
COMPOUND	RACEMES OF SPIKES	A. digitata	PB SB
		A. rodriguesiana	

red in A. multiflora and green to greenish-burgundy in A. saxicola, both species having floral bracts with serrate margins.

In *A. multiflora* (Figs 5, 6), the floral bracts are spatulate, red, with serrate or creno-serrate margins and a cuspidate apex; the flowers have green petals. By contrast, *A. saxicola* has floral bracts that are lanceolate, red, with serrate margins and a cuspidate

apex; the flowers have greenish petals. Both taxa have floral bracts and sepals covered in a whitish lepidote indument.

Capituli form

In A. depressa, the scape is long (50–73 cm), with the inflorescence surpassing the spread of the well-developed leaf sheaths (Fig. 7). The bracts of the scape

are green to burgundy with serrate margins. The floral bracts are oblong, red, whitish-lepidote, with serrate margins and a cuspidate apex. The proximal bracts of the inflorescence are triangular (Fig. 7), red, with serrate margins and a cuspidate apex, forming a protective involucre that is also attractive to pollinators. The petals in this species are greenish.

In A. hostilis (Fig. 8) and Aechmea sp. nov. (Figs 9, 10), the scape is short (13–20 and 18–20 cm, respectively), bearing the inflorescence only slightly above the centre of the rosette and not surpassing the leaf sheaths. The scape is covered in foliaceous bracts, with the distal ones red in A. hostilis (Fig. 8) and green in Aechmea sp. nov. (Fig. 9). In both species, the proximal bracts surpass the height of the inflorescence. The floral bracts have serrate margins and a cuspidate apex, being red in A. hostilis (Fig. 8) and green in Aechmea sp. nov. (Fig. 9). In Aechmea sp. nov., the floral bracts are succulent. The flowers in the two taxa are greenish.

COMPOUND INFLORESCENCES

This pattern is rarer in the subgenus, represented only by *A. digitata* and *A rodriguesiana* (Figs 11–14, Table 2), having the spike as the basic unit.

Racemes of spikes

This complex inflorescence pattern of indeterminate racemes (Figs 11–14) is often difficult to interpret, principally because of the slight dislocation of the main inflorescence which gives it an apparently lateral position (Fig. 14).

Careful analysis of the branches of *A. digitata* and *A. rodriguesiana* confirms their treatment as heterothetic racemes, in other words, as a terminal inflorescence with lateral branches. Only one first-order branching is seen in *A. digitata* (Figs 11, 12) and, in *A. rodriguesiana* (Fig. 14), second-order branching occurs only at the base of the inflorescence, the rest being first-order branches. In both species, spikes are the basic unit of the inflorescence.

In A. digitata (Figs 11, 12), the two spikes are close branches (paraclades) and the inflorescence develops a digitiform aspect. The inflorescence is borne on a long scape (50–68 cm) that projects the inflorescence, in most cases, outside the rosette. The bracts of the scape are brown to blackish throughout, imbricate, with serrate margins distal to the middle, and a sharply pointed apex. In this species, the inflorescence usually has two, rarely three, or with reduction to only one spike, with an elongated and slightly expanded axis. The paraclades are short (2.5–3.5 cm), bearing primary bracts similar to those of the scape, making one sometimes difficult to distinguish from the other. The flowers are protected by a green to

brown floral bract that is lepidote and ovate, with entire margins and a sharply pointed apex. The petals are whitish.

Aechmea rodriguesiana (Figs 13, 14) differs from A. digitata in the number of spikes that branch closely together, creating an unusual umbelliform appearance different from the other species in the subgenus Chevaliera. The inflorescence in this species has first-and second-order branching only at the base of the inflorescence, the rest being all first order. The paraclades are short (0.5–1.8 cm), with basal bracts similar to the floral bracts. The flowers are subtended by a pinkish, ovate bract with a whitish lepidote indument, entire margins and a sharply pointed apex. The petals are whitish.

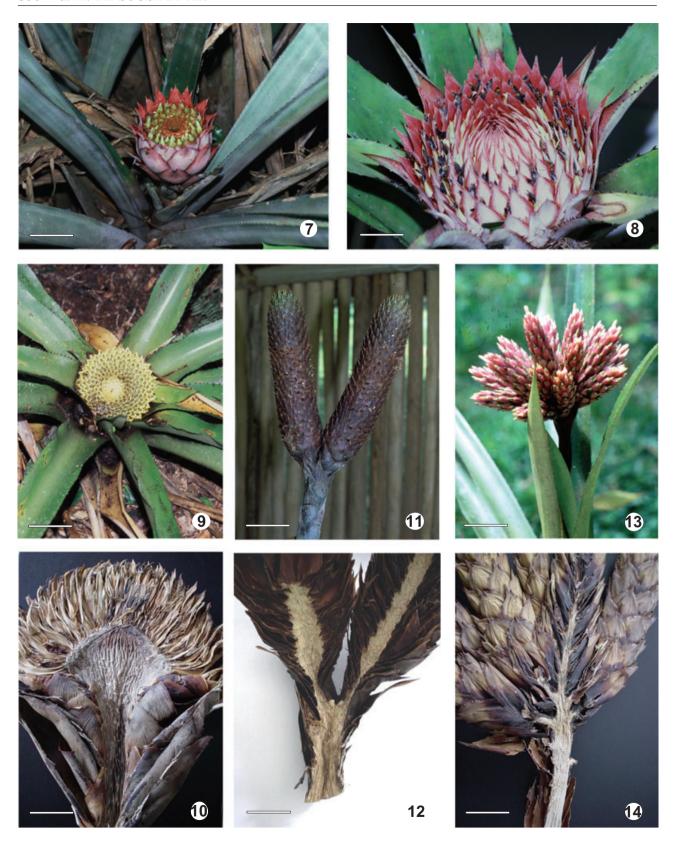
DISCUSSION

The typology of inflorescences in Bromeliaceae is diverse and poorly known. The inflorescence descriptions in published floras are, in general, based on shape, without detail or interpretation of the structures. The analysis of the architectural patterns of inflorescences in the three subfamilies of Bromeliaceae clearly shows the homoplastic nature of their organization (Benzing, 2000).

Spicate inflorescences are distributed in the three subfamilies, with the greatest occurrence in the Tillandsioideae and Bromelioideae. In Bromelioideae, where the greatest generic diversity and great variability in inflorescence patterns occur, simple or compound spikes are found in different genera (Smith & Downs, 1979). In *Acanthostachys*, the inflorescence is a simple spike with congested flowers arranged helically along a thin axis, similar to a strobilus (Smith & Downs, 1979).

In the genus *Quesnelia*, which has many morphological affinities with *Aechmea*, the species *Q. testudo* Lind. and *Q. arvensis* (Vell.) Mez have flowers arranged polystichously in congested spikes, but differ from species of *Aechmea* subgenus *Chevaliera* in that the floral bracts are not coriaceous.

In Aechmea, a great variation in inflorescence types is found, and this pattern is important for the delimitation of some subgenera. Simple, spicate, strobiliform inflorescences are common in three subgenera of Aechmea: Pothuava, Macrochordion and Chevaliera. These subgenera share morphological similarities (vegetative and reproductive), sometimes making it difficult to identify material in situ. In the subgenus Pothuava, Aechmea nudicaulis (L.) Griseb. is the only Brazilian species that has spicate inflorescences with more or less lax flowers, distinct from the pattern of congested spikes found in the rest of the species of the subgenus. According to Wendt (1997), this species has an inflorescence pattern similar to



Figures 7–14. Figs 7–10. Capituliform inflorescences. Fig. 7. Aechmea depressa, general view. Fig. 8. Aechmea hostilis, general view. Figs 9, 10. Aechmea sp. nov. Fig. 9. General view. Fig. 10. Longitudinal section. Figs 11–14. Racemes of spikes. Figs 11, 12. Aechmea digitata. Fig. 11. General view. Fig. 12. Longitudinal section. Figs 13, 14. Aechmea rodriguesiana. Fig. 13. General view. Fig. 14. Longitudinal section. Scale bars: Fig. 7, 4.0 cm; Fig. 8, 0.5 cm; Fig. 9, 6.5 cm; Fig. 10, 2.4 cm; Fig. 11, 12.5 cm; Fig. 12, 14.6 cm; Fig. 13, 4.6 cm; Fig. 14, 3.18 cm. Figs 7–14 Sousa G.

that of *Aechmea* subgenus *Ortigiesia*. Other species in the subgenus *Pothuava* have congested spikes, similar to those of subgenus *Chevaliera*. However, the organization and characteristics of the floral structures are clearly distinct.

Aechmea bromeliifolia (Rudge) Baker, of the subgenus Macrochordium, is easily recognized by the strobiliform spicate inflorescence, covered almost completely in a whitish lanate indument, similar to that found in A. alopecurus and A. perforata, which are analysed in this work. However, the floral bracts and flower colour are very distinct: the bracts are aristate in A. alopecurus and mucronate in A. perforata, both with lilac flowers. In A. bromeliifolia, the flowers are yellow to greenish and the floral bracts are truncate.

Capituliform inflorescences are encountered in different angiosperm families (Weberling, 1989); however, there is no record of this pattern in the Bromeliaceae. This pattern is registered here for the first time in A. depressa, A. hostilis and Aechmea sp. nov.

According to Weberling (1989), heterothetic compound racemes are composed of a terminal raceme and lateral racemes. In this inflorescence type, the main (distal) florescence and the co-florescences are close to each other as a result of the compression of the hypopodia and the internodes. Racemose inflorescences have been recorded previously for Bromeliaceae (Benzing, 2000). However, a more detailed study of inflorescence patterns in Bromeliaceae is needed because the indeterminate pattern is the only type recorded for the family. Many-branched inflorescences occur in many representatives of the family, often varying within the same species, as in species of Vriesea that have simple to many-branched inflorescences. The arrangement of flowers can be lax to dense, an easily observed fact within the subgenus Aechmea, whereas strobiliform inflorescences with congested flowers can be found in the subgenus Chevaliera.

The present study has established three basic inflorescence patterns for the subgenus *Chevaliera*. Amongst the representatives with simple inflorescences, the spicate type is the most common, occurring in ten species. The capituliform type is cited here for the first time in some of the studied species. Amongst the compound inflorescences (racemes of spikes), the variation lies in the number of spikes and

also in the degree of shortening of the axes and paraclades. *Aechmea rodriguesiana* possibly represents the most complex pattern, with numerous spikes concentrically disposed, whereas, in *A. digitata*, the pattern is reduced to two (or one) spikes. The greatest simplification in this subgenus results in simple inflorescences, as found in the majority of species.

The interpretation of inflorescence types in angiosperms is often superficial, especially in monocots, where descriptions are generally incomplete with regard to structural organization. A more profound interpretation of inflorescence patterns constitutes an important foundation for understanding the taxonomic relationships between different groups. In Bromeliaceae, a more complete analysis will require the investigation of natural populations and cultivated plants, together with studies of herbarium material, in order to grasp the morphological variation of the inflorescence architecture.

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