

Morphological analysis, phylogenies and classification in Velloziaceae

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A morphological (non-molecular) cladistic analysis of the Velloziaceae is presented. The terminal taxa are 47 species of Velloziaceae plus four taxa as outgroups: *Acanthochlamys bracteata* (Acanthochlamydaceae), *Encholirium scrutator* (Bromeliaceae), *Thoracocarpus bissectus* (Cyclanthaceae) and *Pandanus racemosus* (Pandanales). The species of Velloziaceae sampled represent a significant proportion of the morphological diversity of the family, including all recognized genera and sections. The analysis revealed two major groups within Velloziaceae, supported mainly by stomata, vascular bundles in the pedicel, aquiferous tissues, filaments, anthers, pollen, stigma, seeds, ploidy and chemical characters. Comparison between this and the previous phylogenetic hypotheses for Velloziaceae, together with the two conflicting current classifications, suggests that there is incompatibility concerning the support of current genera and sections. The only three groups supported in all phylogenies are Barbacenioidae *sensu* Menezes (= *Barbacenia sensu* Smith & Ayensu), *Xerophyta* sect. *Barbacenioides* and *Xerophyta* sect. *Xerophyta sensu* Smith & Ayensu. © 2005 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2005, 148, 157–173.

ADDITIONAL KEYWORDS: cladistic analysis – Pandanales – parsimony.

INTRODUCTION

Velloziaceae is a relatively small family of *c.* 250 tropical species, of mostly amphiatlantic distribution. Despite having been intensively studied in the past three decades, its phylogeny and classification remain debatable and in need of consensus. Its perplexing history (Kubitzki, 1988) is reflected in the oscillation between the two current systems of classification, Menezes (1971, 1980a) and Smith & Ayensu (1974, 1976). Both are gradistic and conflicting in the delimitation of supraspecific groups (Mello-Silva, 1991). Smith & Ayensu's system followed Vandelli (1788) and Jussieu (1789) and was directly based on Seubert (1847). They considered six genera in two subfamilies. *Vellozia*, with three sections, and *Nanuza* are placed in Vellozioidae; *Xerophyta*, with three sections, *Barbacenia*, *Barbaceniopsis* and *Talbotia* are placed in Barbacenioidae. Menezes' classification was based on

Sprengel (1827) and Baker (1875). There are also six genera and two subfamilies: *Vellozia* and *Xerophyta*, both divided in two sections, are placed in Vellozioidae; and *Pleurostima*, with two sections, *Aylthonia*, *Barbacenia*, and *Burlemarxia* are placed in Barbacenioidae (Fig. 1). The objective of this paper is to resume the work of Menezes, Mello-Silva & Mayo (1994) and Mello-Silva (2000), by analysing an expanded non-molecular matrix with 47 species of Velloziaceae as terminals, representing all accepted genera and sections of the family. The results are compared with four previous phylogenies, Menezes *et al.* (1994), Salatino (1999), Behnke *et al.* (2000) and Salatino *et al.* (2001), and a critical analysis of the two classification systems in the light of the phylogenies is presented.

MATERIAL AND METHODS

MORPHOLOGICAL STUDIES

Morphological studies were based on dried specimens and spirit collections. Herbaria consulted and material examined are listed in Table 1.

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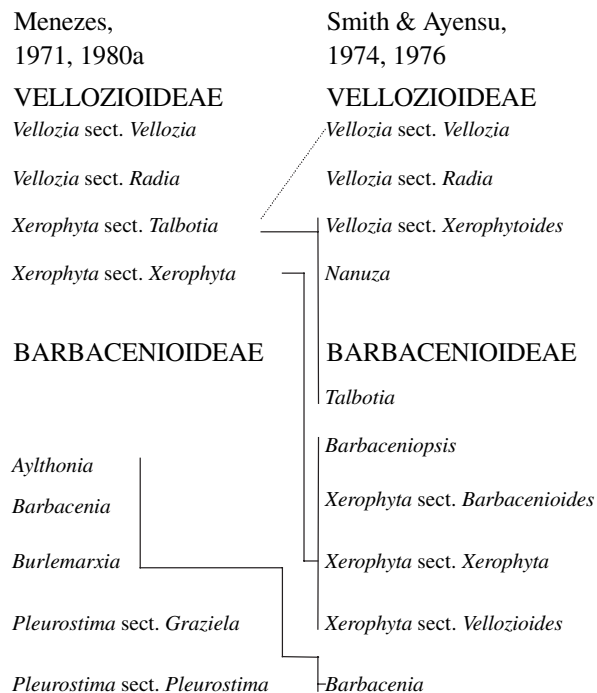


Figure 1. Comparison between the two current systems of classification, Menezes (1971, 1980a) and Smith & Ayensu (1974, 1976). Adapted from Mello-Silva (1991).

CLADISTIC ANALYSIS

The cladistic analysis was undertaken using four species representing four outgroup families and 47 species of Velloziaceae. Species of Velloziaceae were selected in order to represent all the recognized infra-familial groups, and informal groups presumed to be monophyletic, and to sample the morphological diversity of the family as a whole (Mello-Silva, 1991). The rationale for the selection of most species of *Vellozia* is presented in Mello-Silva (2000). *Vellozia burlemarxii*, *V. caudata*, *V. hemisphaerica* and *V. jolyi* belong to an informal group characterized by a broader than long ovary outline. *Aylthonia blackii* and *A. umbrosa* share the capitate stigma and the hairy lamina that characterize the genus (Menezes, 1971, 1980a). They share with *Barbacenia markgrafii* the long hypanthial tube and the type of fruit, and with *B. ignea* and *B. markgrafii* the indument of the lamina. In other respects, such as the clavate stigma, *B. markgrafii*, *B. ignea* and *B. reflexa* belong together in *Barbacenia* as defined by Menezes (1980a). Genera that are apparently well delimited in Menezes' system are *Burlemarxia* (Menezes & Semir, 1991) and *Pleurostima* (Menezes, 1980b). Two of the three recognized species of the former were selected. *Burlemarxia pungens* is similar to *Aylthonia* in its hairy lamina. *Pleurostima*

Table 1. Species composition of the supraspecific groups used in the discussion according to the classifications of Menezes (1971, 1980a) and of Smith & Ayensu (1974, 1976). Representative voucher material of the species used in the analysis are in square brackets. Herbarium codes according to Holmgren *et al.* (1990)

<i>Acanthochlamys bracteata</i> P.C.Kao [Kao s.n. – K] (China)
<i>Encholirium scruerum</i> (L.B.Sm.) Rauh [Forzza 1488 – BHCB, K, SP, SPF, US] (Brazil)
<i>Pandanus racemosus</i> Kurz [Pirani 4755 – SPF] (Madagascar?)
<i>Thoracocarpus bissectus</i> (Vell.) Harling [Fiaschi 603 – RB, SPF; Mello-Silva 986 – SPF] (Brazil)
<i>Aylthonia</i> N.L.Menezes (= <i>Barbacenia sensu</i> Smith & Ayensu). AYLTHON (Brazil)
<i>A. blackii</i> (L.B.Sm.) N.L.Menezes [Mello-Silva CFSC11309 – F, K, MBM, RB, SPF]
<i>A. umbrosa</i> (L.B.Sm. & Ayensu) [Mello-Silva CFCR8360 – F, RB, SPF, US]
<i>Barbacenia</i> Vand. BARBA (Brazil)
<i>B. flava</i> Mart. ex Schult. & Schult.f. [Mello-Silva CFSC10263, Menezes CFSC 9524 – K, MBM, SPF]
<i>B. ignea</i> Mart. [Mello-Silva CFCR8648 – F, K, MBM, NY, RB, SPF, UEC, US]
<i>B. markgrafii</i> Schulze-Menz [Mello-Silva 410 – K, MBM, MO, NY, RB, SPF, UB, US, 1504 – BHCB, K, NY, SPF, W]
<i>B. reflexa</i> L.B.Sm. & Ayensu [Harley CFCR6495 – F, K, RB, SPF; Mello-Silva CFCR8987 – K, MBM, SPF]
<i>Barbaceniopsis</i> L.B.Sm. (= <i>Xerophyta</i> sect. <i>Xerophyta sensu</i> Menezes). BARBOP (Argentina, Bolivia, Peru)
<i>B. castillonii</i> (Hauman) Ibisch [Mello-Silva 1882 – CESJ, CTES, K, LPB, MBM, MCNS, NY, SI, SP, SPF, US]
<i>B. humahuaguensis</i> Noher [Mello-Silva 1897 – B, BHCB, CESJ, CTES, F, K, LPB, MBM, MCNS, NY, SI, SP, SPF, US]
<i>Burlemarxia</i> N.L.Menezes & Semir (= <i>Barbacenia sensu</i> Smith & Ayensu). BURLEM (Brazil)
<i>B. pungens</i> N.L.Menezes & Semir [Menezes 1307, 1370 – SPF]
<i>B. spiralis</i> (L.B.Sm. & Ayensu) N.L.Menezes & Semir [Giulietti CFCR2240 – B, NY, MO, S, SP, SPF]
<i>Nanuza</i> L.B.Sm. & Ayensu (= <i>Xerophyta</i> sect. <i>Talbotia sensu</i> Menezes). NANUZA (Brazil)
<i>N. plicata</i> (Mart.) L.B.Sm. & Ayensu [Boudet Fernandes 1728, 2684, 2791 – MBML, SPF; Harley 27535 – CEPEC, K, SPF]
<i>Pleurostima</i> Raf. sect. <i>Graziela</i> N.L.Menezes (= <i>Barbacenia sensu</i> Smith & Ayensu). PLGRAZ (Brazil)
<i>P. longiscapa</i> (Goethart & Henrard) N.L.Menezes [Menezes 564 – F, K, RB, SP, SPF, 753 – F, K, MBM, RB, SPF, UB, US]
<i>P. plantaginea</i> (L.B.Sm.) [Menezes 558 – K, MBM, RB, SPF; Pirani CFSC12047 – BHCB, G, UB, SPF]
<i>Pleurostima</i> Raf. sect. <i>Pleurostima</i> (= <i>Barbacenia sensu</i> Smith & Ayensu). PLEURO (Brazil)
<i>P. purpurea</i> (Hook.) Raf. [Duarte 1947 – RB, SPF; Menezes 635 – SPF]

Table 1. Continued

P. riparia N.L.Menezes & Mello-Silva [Mello-Silva CFCR8400 – K, RB, SP, SPF, US]
Talbotia Balf. (= *Xerophyta* sect. *Talbotia sensu* Menezes). TALBOT (South Africa)
T. elegans Balf. [Coetzee 15 – PRU, SPF]
Vellozia Vand. sect. *Radia* (A.Rich.) L.B.Sm. VRADIA (Central and South America)
V. caput-ardeae L.B.Sm. & Ayensu [Menezes 1059 – F, G, NY, RB, SP, SPF, UB; Smith 15989 – MBM, SPF, US]
V. hirsuta Goethart & Henrard [Glaziou 15674, 19924 – K, L, P; Maguire 44742 – US; Mello-Silva 454, 462, 465, 508, 635, 739, CFCR8976 – K, MBM, SPF, 470, 520 – G, MO, SPF]
V. sessilis L.B.Sm. ex Mello-Silva [Mello-Silva 1020 – B, BHCB, CEN, IBGE, K, L, M, MBM, MO, NY, P, RB, S, SPF, UEC, US]
V. tubiflora (A.Rich.) Kunth [Dawson 14674 – B, US; Maguire 32307, 35131 – NY; Mello-Silva 548, 551, 553, 554, 556 – SPF]
Vellozia Vand. sect. *Vellozia*. VELLOZ (Bolivia, Brazil)
V. alata L.B.Sm. [Mello-Silva CFSC 10265 – K, SPF]
V. albiflora Pohl [Mello-Silva 341 – K, MBM, SPF, UB, US; Menezes 87 – F, K, MBM, SPF]
V. aloifolia Mart. [Furlan CFSC8362 – MBM, SPF, US; Mello-Silva 1050 – BHCB, SPF, W]
V. armata Mello-Silva [Mello-Silva 648 – CTES, K, MBM, SPF]
V. burlemarxii L.B.Smith & Ayensu [Harley 19287 – K, SPF; Mello-Silva 2148 – SPF]
V. candida J.C.Mikan [Giordano 876, 882 – RB; Menezes 723 – BHCB, K, MBM, MBML, NY, RB, SPF, VIES]
V. caudata Mello-Silva [Giulietti CFCR6857 HUEFS, K, MBM, MO, NY, PRU, R, SPF, U]
V. compacta Mart. ex Schult. & Schult.f. [Hatschbach 35356 – MBM, SPF, US; Menezes CFCR2869 – K, MBM, RB, SPF, US]
V. dasypus Seub. [Mello-Silva CFCR7124, CFCR7530 – K, SPF; Mori 14166, 14278, 14397 (NY, SPF)]
V. epidendroides Mart. ex Schult. & Schult.f. [Mello-Silva CFCR8655 – K, MBM, NY, SPF, US, 670 – F, K, MBM, NY, SPF, US]
V. geotegens L.B.Sm. & Ayensu [Hatschbach 50242 – MBM, SPF; Mello-Silva 1043 – SP, W, CFCR8700 – K, MBM, NY, SPF]
V. glauca Pohl [Arbo 5332 – CTES, K, MBM, SPF, UB; Mello-Silva CFCR11585 – BHCB, F, K, MBM, RB, SPF, UEC, US]
V. hatschbachii L.B.Sm. & Ayensu [Mello-Silva 1051 – G, K, MBM, SPF; Smith 16002 – MBM, SPF, US]
V. hemisphaerica Seub. [Conceição 184 – HUEFS, SPF; Stannard H52149 – CEPEC, HUEFS, K, MBM, SP, SPF]
V. jolyi L.B.Sm. [Harley 20580 – F, IPA, MBM, MO, NY, PRE, R, RB, SP, SPF, UEC, U, US]
V. luteola Mello-Silva & N.L.Menezes [Mello-Silva CFCR10051 – K, RB, SP, PF; Pirani 2275 – K, NY, SPF]
V. punctulata Seub. [Harley 18858 – CEPEC, K, SPF; Mori 13213 – CEPEC, NY, SPF]
V. tillandsioides Mello-Silva [Mello-Silva 283 – CTES, NY, RB, SP, SPF, US), 605 – CTES, K, MBM, SPF, UB]
Vellozia Vand. sect. *Xerophytoides* L.B.Sm. & Ayensu (= *Xerophyta* sect. *Talbotia sensu* Menezes). VXEROI (Brazil)
V. abietina Mart. [Mello-Silva 358 – K, MBM, RB, SPF, UB, UEC, US; Menezes 332 – K, MBM, NY, RB, SPF]
V. minima Pohl [Mello-Silva CFCR5508 – K, MBM, NY, PRE, RB, SPF, U, US; Menezes CFCR11891 – MO, SPF, UEC]
V. prolifera Mello-Silva [Mello-Silva CFCR9661 – F, NY, P, R, SP, SPF, UB, UEC; Menezes CFCR10180 – K, MBM, RB, SPF, US]
Xerophyta Juss. sect. *Barbacenioides* L.B.Sm. & Ayensu (= *Xerophyta* sect. *Xerophyta sensu* Menezes). XBAROID (Africa)
X. equisetoides Baker [Balsinhas 3411 – K, SPF]
X. retinervis Baker [Coetzee 11, Theron 1891, Pienaar 18 – PRU, SPF]
Xerophyta Juss. sect. *Vellozioides* L.B.Sm. & Ayensu (= *Xerophyta* sect. *Xerophyta sensu* Menezes). XVELOID (Africa, Yemen)
X. dasylirioides Baker [Leandri 4267 – P, SPF; Puy 176 – K, SPF]
X. humilis Baker [Coetzee 18, Theron 295 – PRU, SPF]
Xerophyta Juss. sect. *Xerophyta*. XEROPH (Madagascar)
X. eglandulosa H.Perrier [Puy 170, 175 – K, SPF]
X. pinifolia Lam. [Puy 167, 174 – K, SPF]

longiscapa and *P. plantaginea*, with different hypanthial length, represent *Pleurostima* sect. *Graziela*, and *P. purpurea* and *P. riparia* represent *Pleurostima* sect. *Pleurostima*. Other genera and sections were selected from Smith & Ayensu's (1974, 1976) system. In *Barbaceniopsis* two of the four recognized species (Ibisch *et al.*, 2001), and in *Xerophyta* two species for each of the three sections (Smith & Ayensu, 1974) were selected. Outgroups are *Encholirium scrutator*, Bromeliaceae (Dahlgren & Rasmussen, 1983; Dahlgren, Clifford & Yeo, 1985; Gilmartin & Brown, 1987), *Thoracocarpus bissectus*, Cyclanthaceae, *Pandanus racemosus*, Pandanaceae (Chase *et al.*, 1993,

1995b; Clark *et al.*, 1993; Duvall *et al.*, 1993), and *Acanthochlamys bracteata*, Acanthochlamydaceae (Chase *et al.*, 1995a). Table 1 lists the species and corresponding groups used in the discussion according to the different classifications.

In the analysis, 75 characters were used, of which 40 were used by Mello-Silva (2000). Autapomorphies were not considered in the matrix. Characters used and the occurrence of their different states in the terminal taxa are listed in Tables 2 and 3. Those characters not present in Mello-Silva (2000) are discussed below. Simultaneous analysis was accomplished with all terminals in order to obtain global

Table 2. Character analysis and coding

1. Ptyxis (D & C, S & L) supervolute (0) conduplicate (1) plicate (2)	15. Abaxial strands absent (0) present (1)
2. Phyllotaxis tristichous (0) spirotristichous (1) spirally (2)	16. Marginal bundle rounded (0) triangular (1) absent (2)
3. Abscission of leaf persistent (0) sheath persistent, blade deciduous (1) deciduous (2)	17. Conducting tissues in marginal bundle present (0) absent (1)
4. Distal portion of leaf blade attenuate (0) truncate (1)	18. Aquiferous hypodermis extending to bundle sheaths only (0) extending to bundle sheaths and furrows (1) absent (2)
5. Transverse posture of leaf blade arcuate (0) plane (1)	19. Aquiferous parenchyma between bundles absent (0) present (1)
6. Longitudinal posture of the dry leaf blade involute (0) flat (1) revolute (2)	20. Sclerenchyma pattern <i>Xerophyta</i> type (0) <i>Vellozia</i> type (1) <i>Barbacenia</i> type (2) other types (3)
7. Furrows in leaf blade absent (0) on abaxial surface only (1) on both surfaces (2)	21. Phloem strands two (0) one (1)
8. Papillae in furrows absent or inconspicuous (0) coronulate (1) finger-like (2)	22. Minor fibro-vascular bundles absent (0) present (1)
9. Leaf trichomes or emergences absent (0) multicellular base, on the lamina (1) multicellular base, on margins and midrib (2) uni or multicellular with unicellular base (3)	23. Sheath of leaf vascular bundles (M & <i>al.</i>) simple (0) double (1)
10. Stomata paracytic (0) tetracytic (1)	24. Vessel in leaves (M & <i>al.</i>) absent (0) present (1)
11. Stomatal distribution in leaves hypostomatic (0) hypoamphistomatic (1) amphistomatic (2)	25. Transfusion tracheids (M & <i>al.</i>) absent (0) present (1)
12. Subsidiary cells smooth (0) ridged (1)	26. Inflorescence (M & <i>al.</i>) with the major axis (0) suppression of the major axis (1)
13. Specialized cells absent (0) present on adaxial surface only (1) present on both surfaces (2)	27. Flower number solitary or grouped (0) always solitary (1)
14. Adaxial strands absent (0) present (1)	28. Pedicel position evident (0) hidden by the leaves (1)
	29. Transverse section of the pedicel triangular (0) circular (1)

Table 2. *Continued*

30. Vascular bundles in the pedicel six (0) nine (1) 12 (2) 15 (3) 18 (4) 24 (5)	42. Corona absent (0) present (1)
31. Belt of sclerified cells in the pedicel absent (0) present (1)	43. Floral expression monoclinous (0) diclinous (1)
32. Emergence type capitate or capitate-truncated (0) subulate (1)	44. Stamen number six (0) nine (1) 12 (2) 15 (3) 18 (4) 24 (5) 30 (6) 36 (7) more (8)
33. Pedicellar emergences absent (0) laxly disposed (1) densely disposed (2)	45. Staminal appendages absent (0) present (1)
34. Hypanthial emergences absent (0) laxly disposed (1) densely disposed (2)	46. Filaments cylindrical (0) flat (1) coronoid (2)
35. Ovary outline longer than broad (0) ± as long as broad (1) broader than long (2)	47. Anther attachment on the filament (0) on the corona (1) on the hypanthium (2)
36. Transverse section of the ovary trigonous (0) circular-trilobate (1)	48. Anther insertion basifixed (0) dorsifixed (1)
37. Septal nectaries (S & L) absent (0) internal (1)	49. Apical appendage in anther absent (0) present (1)
38. Placentation (S & L) axile (0) parietal (1)	50. Auricles in anther absent (0) present (1)
39. Hypanthial tube absent or much shorter than ovary (0) shorter than ovary (1) equal to ovary (2) longer than ovary (3)	51. Anther position in antisepalous stamens extrorse (0) latrorse (1) latero-introrse (2) introrse (3)
40. Perianth (S & L) differentiated (0) undifferentiated (1) absent (2)	52. Anther position in antipetalous stamens extrorse (0) latrorse (1) latero-introrse (2) introrse (3)
41. Tepal colour violet (0) white (1) yellow (2) red (3) green (4) orange (5) pink (6)	53. Anther dehiscence each pair of microsporangia dehiscing by a single common slit (0) each pair of microsporangia dehiscing by a separated slit (1) bisporangiate (2)

Table 2. *Continued*

54. Anther colour	34 (2)
yellow (0)	48 (3)
violet (1)	
white (2)	66. Cyanogenic compounds (S & L)
cream (3)	absent (0)
	present (1)
55. Pollen colour	67. Main alkanes of epicuticular waxes
yellow (0)	19 (0)
white (1)	21 (1)
56. Pollen units	25 (2)
monads (0)	27 (3)
tetrads (1)	29 (4)
57. Relative position of stigma and stamens	31 (5)
stigma above stamens (0)	33 (6)
stigma at same level or below stamens (1)	35 (7)
58. Style X stigma	68. Flavone C-glycosides (Williams <i>et al.</i> , 1991)
much longer (0)	– (0)
more or less of the same length (1)	+ (1)
much shorter (2)	69. Quercetin (Williams <i>et al.</i> , 1991)
59. Stigma lobes	– (0)
horizontal, fused at centre (0)	(+) (1)
vertical, fused at apex (1)	+ (2)
free (2)	70. Kaempferol (Williams <i>et al.</i> , 1991)
60. Stigmatic surface (S & L)	– (0)
dry (0)	(+) (1)
wet (1)	+ (2)
61. Fruit	71. Isohamnetin (Williams <i>et al.</i> , 1991)
loculicidal capsule (0)	– (0)
poricidal capsule (1)	(+) (1)
intercostal capsule (2)	+ (2)
basal loculicidal capsule (3)	72. Simple flavones (Williams <i>et al.</i> , 1994)
septicidal capsule (4)	– (0)
other types (5)	+ (1)
62. Hypanthium in fruit	73. 'Free' flavones (Williams <i>et al.</i> , 1994)
persistent (0)	– (0)
deciduous (1)	(+) (1)
63. Outer integument of empty cells in seed	+ (2)
persistent (0)	74. Surface simple flavonol methyl ethers (Williams <i>et al.</i> , 1994)
vanishing (1)	– (0)
64. Nucellus (S & L)	(+) (1)
crassinucellate (0)	+ (2)
tenuinucellate (1)	75. 6-8-hydroxyflavones (S & L)
65. Chromosome number ($2n$)	absent (0)
14 (0)	trace (1)
16 (1)	

M & *al.* = Menezes *et al.* (1994), D & C = Dahlgren & Clifford (1982), and S & L = Stevenson & Loconte (1995).

Table 3. Data matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	
<i>Acanthochlamys bracteata</i>	?	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
<i>Encholirium scrutator</i>	0	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	
<i>Pandanus racemosus</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	
<i>Thoracocarpus bissectus</i>	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100		
<i>Aylthonia blackii</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	
<i>Aylthonia umbrosa</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	
<i>Barbacenia flava</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	
<i>Barbacenia ignea</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	
<i>Barbacenia markgrafii</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	
<i>Barbacenia reflexa</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	
<i>Barbaceniopsis castillonii</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	
<i>Barbaceniopsis humahuaguensis</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	
<i>Burlemarxia pungens</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	
<i>Burlemarxia spiralis</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	
<i>Nanuza plicata</i>	1																																																																																																				

Warming (1893) and Diogo (1926), and have been used to characterize and differentiate species (e.g. Ayensu, 1974; Mello-Silva, 1995). The leaf anatomical differentiation of *Vellozia hirsuta* is due mainly to variation in these characters (Mello-Silva, 1990: figs 1, 2). Because adaxial and abaxial strands can occur independently, they are here treated as different characters.

Characters 16 and 17. Marginal bundles and conduction tissues in marginal bundle: The presence of a marginal bundle on each side of the leaf blade, different in size and shape from the fibro-vascular bundles, is an autapomorphy of Velloziaceae. They can be rounded (e.g. Ayensu, 1974: fig. 24E) or triangular, and sometimes include vascular tissue (Mello-Silva, 1990: fig. 2A,C).

Character 19. Aquiferous parenchyma between bundles: The two different types of organization of aquiferous parenchyma stated by Mello-Silva (2000), i.e. radially extend either exclusively to the fibro-vascular bundles or both to the bundles and to the furrows, is apparently not homologous with the aquiferous parenchyma present in most Barbacenoioideae (*sensu* Menezes, 1973, 1980a), which is located in the median area of the mesophyll among the vascular bundles (Mello-Silva, 1995: figs 3–5, 7, 8). These organizations of aquiferous parenchyma were already noted by Warming (1893).

Character 20. Sclerenchyma pattern: Three major types of sclerenchyma pattern associated with the vascular bundles occur in both the African and the American species of Velloziaceae (Ayensu, 1969, 1974). In the *Xerophyta* type, the vascular bundles are accompanied on the adaxial side by an inverted crescentiform or V-shaped cap; the abaxial sclerenchyma can be described as a W-shaped cap. In the *Vellozia* type, the adaxial sclerenchyma is generally inverted crescentiform or cap-shaped; the abaxial sclerenchyma is either U- or Y-shaped. The adaxial sclerenchyma does not extend to the epidermis, as it does in the *Barbacenia* type (Ayensu, 1969).

Character 22. Minor fibro-vascular bundles: Warming (1893) first noted the presence of minor fibro-vascular bundles in Velloziaceae when analysing transverse sections of leaves of *Nanuza plicata* and of *Vellozia hemisphaerica*. These minor bundles are present in few other species, all related to *V. hemisphaerica*. In those species, the minor bundles are orientated radially above the furrows (Mello-Silva, 1993: fig. 2B, E, F).

Character 42. Corona: The corona in Velloziaceae is of perianthal origin (Menezes, 1973), although Noher &

Cocucci (1971) hypothesized its staminal origin. Menezes *et al.* (1994) used this character with different states. I here consider anther attachment to the corona to be a state of another character (46), as the filament can be independent of the corona lobes (Menezes & Semir, 1990: fig. 2).

Character 46. Filaments: The filaments in Velloziaceae are mostly cylindrical, but some are triangular and others are expanded and resemble small corona lobes (Smith & Ayensu, 1974: fig. 4). Studies concerning the ontogeny of these small corona lobes are lacking, but they do not seem to be of petal origin, as they have no vascularization (N. L. Menezes, pers. comm.).

Character 47. Anther attachment: Independently of basifixed or dorsifixed insertion, anthers can attach to the filament, as in most *Vellozia* species, to the corona, as in most *Barbacenia* species, or sometimes directly to the hypanthium, as in some *Pleurostima* species (Menezes, 1980b: figs 23–26).

Characters 49 and 50. Apical appendage and auricles in anther: Menezes (1980b) considered these two characters important in the delimitation of the genus *Pleurostima*. Nevertheless, they are also present in other genera of Velloziaceae, except in *Vellozia*.

Characters 54 and 55. Anther and pollen colour: Pollen grains exhibit only two different colours, and the anthers can exhibit at least four different colours (see Ayensu, 1973, for colourful photographs).

Character 58. Style X stigma: Menezes *et al.* (1994) used this as a binary character. I here consider a third state to reflect better the variation occurring within Velloziaceae.

Character 65. Chromosome number: Goldblatt & Poston (1988) and Melo *et al.* (1997) carried out the most significant investigations of chromosome number in Velloziaceae. The results show three groups that comprise diploid, tetraploid and hexaploid species. Those groups correspond, in Menezes' (1971) system, to the American Vellozioidae, Barbacenoioideae and African Vellozioidae, respectively. In *Vellozia*, the number can be $n = 7$ or $n = 8$, the former being interpreted as a derivative number from the basic number $x = 8$ (Melo *et al.*, 1997).

Character 67. Main alkanes of epicuticular waxes: Salatino *et al.* (1991) found alkanes to be taxonomically useful in Velloziaceae. The states of this character are the main alkanes found in foliar epicuticular waxes by Salatino *et al.* (1989), in which the authors analysed 110 species of Velloziaceae.

Characters 68–74. Leaf flavonoids: The results of a leaf flavonoid survey of 99 species of Velloziaceae (Williams, Harborne & Menezes, 1991; Williams *et al.*, 1994) provide the chemical characters used here.

Characters used by Mello-Silva (2000) but with a different coding.

Character 9. Leaf trichomes or emergences: This character encompasses characters 8 and 9 of Mello-Silva (2000) as there is some doubt about the nature of the spines in serrate leaves, and these two characters are mutually exclusive.

Characters 30 and 44. Vascular bundles in pedicel and stamen number: These characters, corresponding, respectively, to character 19 and 28 in Mello-Silva (2000), are newly coded to discriminate the variation observed among and within species. Although they can vary within a species, the intervals are perfectly discrete.

Character 35. Ovary outline: (Character 24 in Mello-Silva, 2000). A new state, broader than longer, has been added to represent the *Vellozia hemisphaerica* group. This character state was used by Smith & Ayensu (1976) in their identification key, and was also cited by Menezes (e.g. Menezes, 1980a) in her discussion of evolution in Velloziaceae.

Character 41. Tepal colour: (Character 27 in Mello-Silva, 2000). Four colour states have been added to encompass the diversity of genera other than *Vellozia*. I assume that, as for characters 54 and 55 above, the pigments for a given colour are homologous and that the variation observed in some violet and white coloured *Vellozia* are due to genetic differences rather than ecological conditions (Ayensu, 1973; Gottsberger & Gottlieb, 1980). Investigations on this subject in Velloziaceae are lacking.

Character 59. Stigma lobes: (Character 46 in Mello-Silva, 2000). A new state has been added because of a possible interpretation of the evolution of stigmas in Velloziaceae, proposed by S. J. Mayo (pers. comm.), from horizontal, apex fused stigmas to vertical, free lateral stigmas.

Characters 51 and 52. Anther position in antisepalous and in antipetalous stamens: These characters correspond to the divided character 40 of Mello-Silva (2000). This new situation is a better interpretation of the occurrence of different anther positions in Velloziaceae, as described by Menezes (1980a) for African species. In some species, e.g. *Xerophyta arabica* (Menezes, 1988: fig. 7), anther dehiscence strongly differs between the two rows of stamens.

Character 61. Fruit: (Character 30 in Mello-Silva, 2000). This character has been refined to include all fruit types of Velloziaceae.

RESULTS

This study involves about 20% of the species of Velloziaceae and is therefore partial in scope. Furthermore, although the strict consensus cladogram presented is well resolved (Figs 2A, 3), its branches are not well supported with bootstrap values (Fig. 2B).

The 2452 most parsimonious trees have 429 steps, a consistency index (CI) of 0.29, and a retention index (RI) of 0.66. The strict consensus tree with the characters states is shown in Figure 3.

CHARACTERS

The analysis shows the following probable plesiomorphic character states in Velloziaceae: tristichous phyllotaxis (2); leaf blade persistent (2), attenuate (4), arcuate (5), involute (6), without furrows, papillae or trichomes (7, 8, 9); paracytic stomata (10); leaves hypostomatic (11); subsidiary cells smooth (12); specialized cells on adaxial surface of leaf blade absent (13); abaxial strands absent (15); marginal bundles rounded (16); aquiferous hypodermis absent (18); aquiferous parenchyma between bundles absent (19); *Barbacenia* type of sclerenchyma pattern (20); two phloem strands (21); minor fibro-vascular bundles absent (22); sheath of vascular bundles simple (23); vessels present in leaves (24); flowers solitary or grouped (27) with evident pedicel (28), triangular in transverse section (29), with nine vascular bundles (30) and with a belt of sclerified cells (31); emergences absent from pedicel (33) and hypanthium (34), or, if present, capitate (32); ovary longer than broad in outline (35); hypanthial tube absent or much shorter than ovary (39); tepals violet (41), without corona (42); flowers monoclinal (43); six stamens (44), without staminal appendages (45); yellow, latero-introrse anthers without apical appendage or auricles (49, 50, 51, 52, 54), basifixed and attached to cylindrical filaments (46, 47, 48), with each pair of microsporangia dehiscing by a separated slit (53); pollen yellow (55), shed in monads (56); stigma above stamens (57), much shorter than style (58) and horizontal, fused at apex (59); fruit with persistent hypanthium (62); outer integument of seed with empty cells (63); absence of flavone C-glycosides, kaempferol, isohamnetin, simple flavones, 'free' flavones and surface simple flavonol methyl ethers (68, 70, 71, 72, 73, 74) and presence of quercetin (69).

GROUPS

Velloziaceae s.s., not including *Acanthochlamys*, is supported by the non-homoplastic apomorphic states

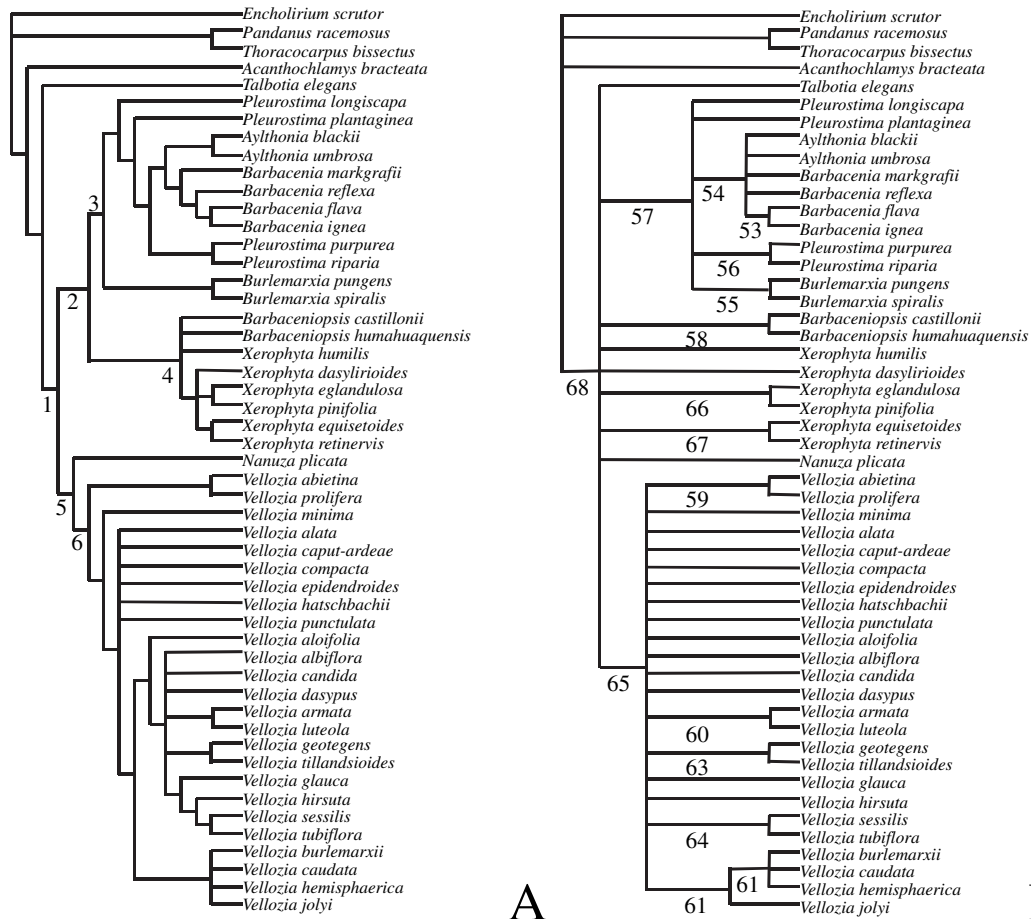


Figure 2. A, strict consensus tree generated from data in Table 3. Numbers in branches correspond to the six large clades identified within Velloziaceae. B, bootstrap tree from data in Table 3; bootstrap values of 100 replicates are given below shared branches.

of the characters 16 (marginal bundle present and rounded), 20 (sclerenchyma pattern of *Barbacenia* type), 25 (transfusion tracheids) and 26 (suppression of the major axis of the inflorescence), and by the homoplastic characters 2 (tristichous phyllotaxis), 3 (persistent leaf blades), 59 (stigma lobes horizontal, fused at apex) and 63 (outer integument of seed with empty cells). Within Velloziaceae, six large clades can be identified (Fig. 2A):

1. All Velloziaceae except *Talbotia*. This clade is supported by character states 9 (leaf trichomes or emergences with multicellular base, on margins and midrib) and 30 (six vascular bundles in pedicel), both homoplastic. This clade is collapsed in the bootstrap tree.
2. *Aylthonia* + *Barbacenia* + *Barbaceniopsis* + *Burlemarxia* + *Pleurostima* + *Xerophyta*. This clade is supported by character states 11 (amphistomatic stomatal distribution in leaves), 33 (lax disposition of pedicellar emergences), 36 (transverse section of ovary circular-trilobate), 50 (auricles in anther present), 53 (each pair of microsporangia dehiscing by a single common slit) and 59 (stigma lobes vertical, fused at apex). This clade also collapses in the bootstrap tree.
3. *Aylthonia* + *Barbacenia* + *Burlemarxia* + *Pleurostima*. This clade is supported by character states 23 (double sheath in leaf vascular bundles), 24 (vessel in leaves absent), 30 (12 vascular bundles in pedicel), 34 (hypanthial emergences laxly disposed), 39 (hypanthial tube shorter than ovary), 41 (pink tepals), 42 (corona present), 54 (violet anther), 65 (tetraploidy) and 70 (presence of kaempferol). This clade is maintained in the bootstrap tree.
4. *Barbaceniopsis* + *Xerophyta*. This group is supported by character states 7 (furrows in leaf blade on both surfaces), 29 (transverse section of pedicel circular), 34 (hypanthial emergences densely disposed), 49 (apical appendage in anther present), 51 and 52 (anther position in antisepalous and in anti-

petalous stamens latrorse), and 57 (stigma at same level or below stamens). This clade collapsed in the bootstrap tree.

5. *Nanuza* + *Vellozia*. This clade is supported by character states 3 (sheath persistent, blade deciduous), 5 (plane leaf blade), 10 (tetracytic stomata), 14 (adaxial strands present), 18 (aquiferous hypodermis extending to bundle sheaths only), 20 (*Vellozia* type of sclerenchyma pattern), 31 (six vascular bundles in pedicel), 65 (diploidy), 68 (presence of flavone C-glycosides) and 69 (absence of quercetin). This clade collapses in the bootstrap tree.
6. *Vellozia* is supported by character states 2 (spiro-tristichous phyllotaxis), 4 (truncate distal portion of leaf blade), 24 (vessel in leaves absent), 27 (always solitary flower), 46 (filaments cylindrical), 56 (pollen shed in tetrads), 63 (outer integument of empty cells in seed absent), 72 (presence of simple flavones), 73 (presence of 'free' flavones) and 74 (presence of surface simple flavonol methyl ethers). This clade is maintained in the bootstrap tree.

DISCUSSION

CLASSIFICATION AS COMPARED WITH THE PHYLOGENIES

The first cladistic analysis of the Velloziaceae (Menezes *et al.*, 1994) was performed with a morphological matrix of 22 characters using genera and sections as terminals. From this analysis, with multistate characters unordered and successive weighting, the hypothesized relationships were ((VELLOZ VRADIA VXEROI) NANUZA (TALBOT ((XBAROID (BARBOP XVELOID XEROPH)) (AYLTHON BARBA (BURLEM (PLEURO (PLEURO PLGRAZ PLGRAZ)))))). When those results are compared with Menezes' system, it implies a paraphyletic Velloziaceae and *Pleurostima* sect. *Pleurostima*, a potentially paraphyletic *Vellozia* and *Pleurostima* sect. *Graziela*, and a polyphyletic *Xerophyta* and *Xerophyta* sect. *Talbotia* (Fig. 4A). When compared with Smith & Ayensu's classification, it implies a paraphyletic Velloziaceae and *Xerophyta* (Fig. 4B).

The maximum parsimony analysis of *trnL-F* sequence data of 20 species of Velloziaceae, presented by Salatino (1999) and Salatino *et al.* (2001) shows (((((VELLOZ VXEROI VXEROI) VELLOZ (VELLOZ VRADIA)) NANUZA) TALBOT (PLEURO (AYLTHON (AYLTHON BARBA (AYLTHON AYLTHON AYLTHON BARBA BURLEM BURLEM)))))). In Menezes' system, this makes Velloziaceae potentially paraphyletic, *Vellozia* paraphyletic or polyphyletic, *Burlemarxia* potentially paraphyletic or polyphyletic, and *Aylthonia*, *Barbacenia* and *Xerophyta* sect. *Talbotia* polyphyletic (Fig. 4C). In Smith & Ayensu's system it makes Barbaceniaceae and *Vello-*

zia sect. *Xerophytoides* potentially paraphyletic, and *Vellozia* sect. *Vellozia* polyphyletic (Fig. 4D).

Part of the maximum parsimony analysis of *rbcL* nucleotide sequences by Behnke *et al.* (2000) showed the 24 terminals of Velloziaceae as follows: (((PLEURO (PLGRAZ (BARBA PLEURO))) (NANUZA VRADIA VELLOZ VELLOZ VELLOZ (VRADIA VELLOZ))) BARBOP (XVELOID ((XVELOID XEROPH) (TALBOT XBAROID))). This result implies, in Menezes' classification (Fig. 5A), a paraphyletic Velloziaceae and *Pleurostima*, a polyphyletic *Xerophyta*, *Xerophyta* sect. *Talbotia*, *Pleurostima* sect. *Pleurostima*, and *Vellozia* sect. *Vellozia*, a paraphyletic or polyphyletic *Xerophyta* sect. *Vellozioides*, and *Vellozia* sect. *Radia*. In Smith & Ayensu's classification (Fig. 5B), it implies a paraphyletic Barbaceniaceae, a paraphyletic or polyphyletic *Vellozia* sect. *Radia*, and a polyphyletic *Xerophyta* sect. *Vellozioides* and *Vellozia* sect. *Vellozia*.

The analysis presented here (Figs 2, 3) shows (TALBOT ((((((AYLTHON BARBA) PLEURO) PLGRAZ) PLGRAZ) BURLEM) (BARBOP BARBOP XVELOID (XBAROID XEROPH XVELOID)) (NANUZA (VXEROI (VXEROI (VRADIA VELLOZ VELLOZ VELLOZ VELLOZ (VELLOZ (VELLOZ (VELLOZ VELLOZ VELLOZ VELLOZ (VELLOZ VRADIA)))))))))). These results imply, in Menezes' system, a paraphyletic Velloziaceae, *Pleurostima* and *Pleurostima* sect. *Graziela*, and a polyphyletic *Xerophyta*, *Vellozia* sect. *Radia*, *Vellozia* sect. *Vellozia* and *Xerophyta* sect. *Talbotia* (Fig. 5C). In Smith & Ayensu's system it implies a paraphyletic Barbaceniaceae, and *Vellozia* sect. *Xerophytoides*, a potentially paraphyletic or polyphyletic *Barbaceniopsis* and *Xerophyta*, a paraphyletic or polyphyletic *Xerophyta* sect. *Vellozioides*, and a polyphyletic *Vellozia* sect. *Radia* and *Vellozia* sect. *Vellozia* (Fig. 5D). This analysis could lead to the recognition of six genera (excluding *Acanthochlamys*) in a splitter treatment (Fig. 6A) or of four genera (Fig. 6B) in a lumpers treatment. A more radical position would be to merge *Xerophyta* into *Barbacenia*, leading to the recognition of only three genera (Fig. 6C). Given that many of the now recognized *Xerophyta* have been classified as *Barbacenia* at some point, there is no problem concerning the stability of the classification. Therefore, the question of whether to recognize *Xerophyta* should be debated on the basis of the characters that support each taxon within that clade, maximizing support for monophyly and ease of identification (Backlund & Bremer, 1998). On the one hand, the presence of the corona (character 42), the double sheath of leaf vascular bundles (character 23) and the chromosome number $2n = 34$ (character 65) are exclusive of *Barbacenia* (Fig. 2A, clade 3), favouring the maintenance of *Barbacenia* and *Xerophyta* (Fig. 6B). On the other hand, the characteristic anther dehiscence (character 53) and vertical stigmas (character 59) occur both in *Barbacenia* and in *Xerophyta*

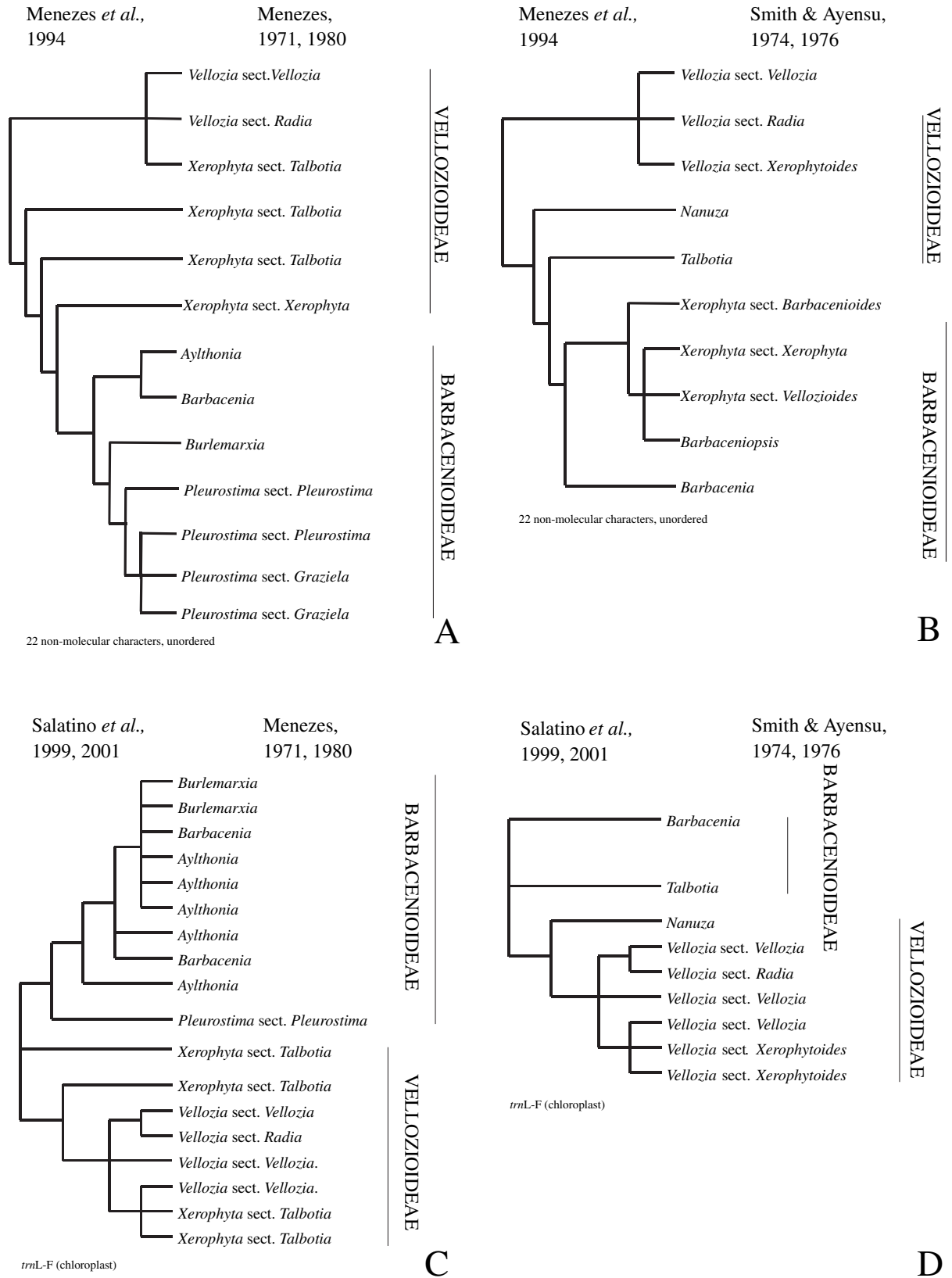


Figure 4. Diagrams of phylogenetic relationship of the Velloziaceae *sensu* Menezes and Smith & Ayensu. A, B, according to Menezes *et al.* (1994). C, D, according to Salatino (1999) and Salatino *et al.* (2001).

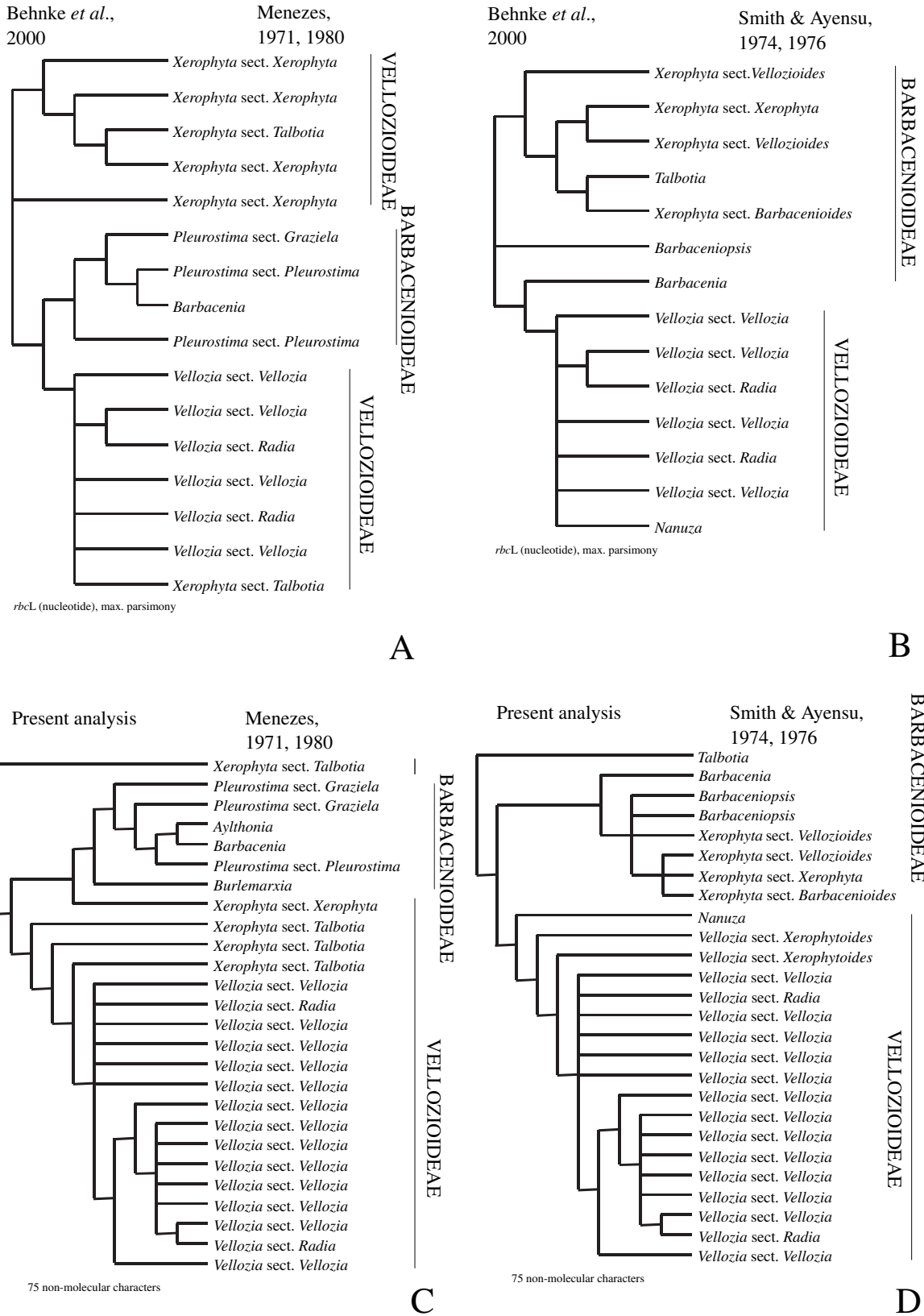


Figure 5. Diagrams of phylogenetic relationship of the Velloziaceae *sensu* Menezes and Smith & Ayensu. A, B, according to Behnke *et al.* (2000). C, D, according to the present analysis.

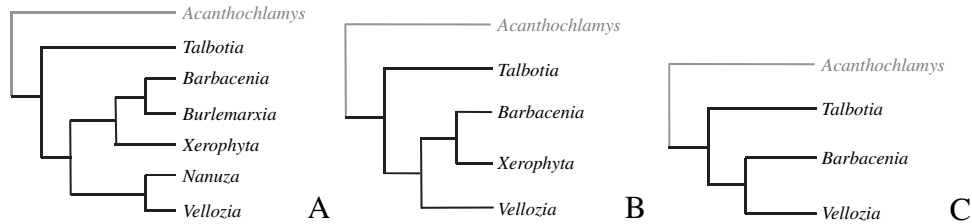


Figure 6. Diagrams of phylogenetic relationship of the Velloziaceae according to different classifications based on the present analysis. A, a splitter choice. B, C, lumper choices.

(Fig. 2A, clade 2), favouring the merging of both genera (Fig. 6C). All other characters that support each of these three disputing taxa are strongly homoplastic and/or do not facilitate identification. The merging of *Barbacenia* with *Burlemarxia* and *Nanuza* with *Vellozia* (Fig. 6B) can be justified by the principles of maximizing phylogenetic information and ease of identification. The clade (*Barbacenia Burlemarxia*) (Fig. 2A, clade 3) is supported by the strong characters listed above. *Barbacenia* alone (including *Aylthonia* and *Pleurostima*) is supported mainly by the anther attachment (character 47). In addition, *Burlemarxia* is a small genus of only three species. *Vellozia* and the monospecific *Nanuza* are mainly characterized by the horizontal stigma lobes (character 59, plesiomorphic), which are also shared with *Talbotia*. Chromosome number $2n = 14$ (character 65), among other characters, supports the clade (*Nanuza Vellozia*) (Fig. 2A, clade 5). On the other hand, the pollen in tetrads (character 56) supports *Vellozia* alone (Fig. 2A, clade 6).

CONCLUSION

None of the proposed phylogenies supports the recognition of two subfamilies of Velloziaceae as delimited in the classifications of either Menezes (1971, 1980a) or Smith & Ayensu (1974, 1976). The results show incompatibility in the support of genera and sections. Only three taxa are supported in all phylogenies, apart from the monospecific *Nanuza* and *Talbotia*: Barbacenioidae *sensu* Menezes (= *Barbacenia sensu* Smith & Ayensu), *Xerophyta* sect. *Barbacenioides* and *Xerophyta* sect. *Xerophyta sensu* Smith & Ayensu. This indicates the need for a rearrangement of the infra-familial classification of Velloziaceae in the context of a more thorough and robust phylogenetic hypothesis, based on a total evidence analysis.

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