REFERÊNCIA

SILVA, Anádria Stéphanie da et al. Micromorphology of the upper anthecium in Mesosetum Steud. and related genera (Poaceae, Arthropogoninae) and its taxonomic applications. **Rodriguésia**, Rio de Janeiro, v. 66, n. 2, p. 645-657, jan./jun. 2015. Disponível em: <http://www.scielo.br/scielo.php?script=sci_arttext&pid=S2175-78602015000200645&lng=en&nrm=iso>. Acesso em: 21 mar. 2018. doi: http://dx.doi.org/10.1590/2175-7860201566227.

Rodriguésia 66(2): 645-657. 2015
http://rodriguesia.jbrj.gov.br
DOI: 10.1590/2175-7860201566227

Micromorphology of the upper anthecium in *Mesosetum* Steud. and related genera (Poaceae, Arthropogoninae) and its taxonomic applications

Anádria Stéphanie da Silva[1,3], *André Rodolfo de Oliveira Ribeiro*[1], *Mayco Werllen dos Santos Sousa*[1], *Christopher William Fagg*[1], *Rosana Falcão*[2] & *Regina Célia de Oliveira*[1]

Abstract

Mesosetum is a Neotropical genus with 25 species, and 21 of them occur in Brazil. *Mesosetum* forms a clade closely related with *Keratochlaena rigidifolia* and *Tatianyx arnacites*. The objective of this work was to establish the taxonomic value of the upper anthecium micromorphology for the group. A total of 96 specimens, representing all *Mesosetum* species (except *M. wrightii*), *K. rigidifolia* and *T. arnacites* were examined under a scanning electron microscope (SEM). PCA and UPGMA analysis were applied using the micromorphological characters. Fifithteen useful taxonomic characters were identified. We highlight the following characters to distinguish the *Mesosetum* species: the presence, type and distribution of papillae on the abaxial surface of the upper lemma; the presence of unicellular macrohairs and bicellular microhairs; presence or absence of silica cells and the structure of the germination lid. The present work shows that the micromorphological characters identified are important taxonomically at the specific level, allowing the species identification in many cases.
Key words: Grass, *Keratochlaena*, *Tatianyx*, PCA, UPGMA.

Introduction

Mesosetum Steud. belongs to the subfamily Panicoideae, tribe Paspaleae. It is inserted in the subtribe *Arthropogoninae*, along with 15 other American genera (Morrone *et al*. 2012). Within *Arthropogoninae, Mesosetum* forms a clade with *Tatianyx* Zuloaga & Soderstr. and *Keratochlaena* Morrone genera, as observed in many phylogenies (Giussani *et al*. 2001; Aliscioni *et al*. 2003; GPWG 2011; Morrone *et al*. 2012).

Swallen (1937) proposed 33 binomials for *Mesosetum*, but only 25 were recognized as valid taxa by Filgueiras (1989). The genus has a predominantly Neotropical distribution, and Brazil is the centre of diversity with 21 species, being 12 endemic to the country (Filgueiras *et al*. 2014). Most of these species occur in Central Brazil, where a total of 16 species occur, being seven endemic to this region (Filgueiras *et al*. 2014).

Mesosetum is characterized by raceme-like solitary terminal inflorescence, spikelets with the first glume adaxial to rachis, glume and lower lemma with tuffs of hairs and caryopsis with linear hilum (Filgueiras 1986, 1989). All these characters are homoplastic because they occur in other genera of the tribe.

There is controversy in the infrageneric classification of the genus *Mesosetum*. Chase (1911) was the first to establish a morphological delimitation of the genus and proposed two sections: *Mesosetum* sect. *Mesosetum* and *M*. sect. *Bifaria* (Hack.) Chase. Swallen (1937) revised the genus and recognized 33 species and added four new sections to those proposed by Chase (1911): *M*. sect. *Annua* Swallen, *M*. sect. *Penicillata* Swallen, *M*. sect. *Loliiformia* Swallen, *M*. sect. *Schlerochloae* Swallen and *M*. sect. *Fulva* Swallen (latter equivalent to *M.* sect. *Mesosetum*). Pilger (1940) partially accepted the work of Swallen, recognizing 30 species and only three sections: *M*. sect. *Bifaria*, *M*. sect. *Eumesosetum* Pilg. and *M*. sect. *Schlerochloae*. Filgueiras (1986,

[1] Universidade de Brasília, Inst. Ciências Biológicas, Programa de Pós-Graduação em Botânica, C.P. 04457, 70910-970, Brasília, DF, Brasil.
[2] Embrapa Recursos Genéticos e Biotecnologia, Parque Estação Biológica, Av. W5 Norte (final), C.P. 02372, 70770-900 Brasília, DF, Brasil.
[3] Author for correspondence: anadriastephanies@hotmail.com

1989) recognized 25 species distributed in five sections. This author included *M*. sect. *Annua* in *M*. sect. *Loliiformia,* and transferred *M*. sect. *Fulva* (containing the type species of the genus) to *M*. sect. *Mesosetum*.

Investigations on the ornamentation of the upper anthecium has revealed important taxonomic information in the Panicoideae (Mejia-Saules & Bisby 2003; Giraldo-Cañas 2004), specially in the delimitation of genera and species phylogenetically related to *Mesosetum,* e.g. *Apochloa* Zuloaga & Morrone, *Canastra aristella* (Döll) Zuloaga & Morrone (under *Panicum aristellum* Döll), *Cyphonanthus* Zuloaga & Morrone, *Homolepis* Chase, *Keratochlaena* (under *Sclerochlamys*, nom. illeg.), *Oncorachis* Morrone & Zuloaga, *Stephostachys* Zuloaga & Morrone, *Streptostachys* Desv., and *Tatianyx* (Zuloaga & Sordestrom 1985, Morrone & Zuloaga 1991; Morrone *et al*. 2007; Sede *et al*. 2008, 2009; Zuloaga *et al*. 2010). Nevertheless, there are no studies on the upper anthecium ornamentation using scanning electron microscopy (SEM) in *Mesosetum* species.

While *Mesosetum* is apparently well circumscribed from the taxonomic and nomenclatural viewpoint, the identification of specimens is difficult. The identification keys and descriptions of many species are based on a small number of specimens available at the time of the last two revisions (Swallen 1937; Filgueiras 1989), which does not represent the range of the morphological variability of the taxa. The present work analyses the upper anthecium micromorphological characters using SEM in *Mesosetum* and related species to verify their taxonomic value, if these characters support the consistency of the *Mesosetum* sections proposed by Filgueiras (1989), and if there are common character states between the clade *Mesosetum-Tatianyx-Keratochlaena.*

Materials and Methods

This work is based on the upper anthecium micromorphology of 24 *Mesosetum* species, with a total of 93 specimens analyzed*,* plus one of *Keratochlaena rigidifolia* (Filg., Morrone & Zuloaga) Morrone & Zuloaga and two of *Tatianyx arnacites* (Trin.) Zuloaga & Soderstr. The samples were obtained from herbarium specimens. The specimens examined are listed in Table 1 and the herbaria acronyms are according to Thiers (2014, continuously updated). The dataset included all the *Mesosetum* species except *M. wrightii* Hitchc., endemic to Cuba, which had very limited collections available, and two other related genera: *Tatianyx* and *Keratochlaena*.

The mature anthecia were mounted onto aluminum metal stubs using carbon double-stick tape and sputter-coated with platinum without pretreatment. The material was carried out on SEM (Jeol JSM 7001S) at 15 KV, at the Electronic Microscope Laboratories of the University of Brasilia, and "Embrapa Recursos Genéticos e Biotecnologia". Deformed and flaccid immature anthecia were not considered. The terminology followed Ellis (1979), Sordestrom & Zuloaga (1989) and Giraldo-Cañas (2004).

Table 2 shows the descriptors used in the present work. Significant differences were not found between the lemma and palea, which presented similar ornamentation.

Each specimen measured was considered an operational taxonomic unit (OTU), following (Rohlf 2000). Cluster analysis was carried out to analyze the taxonomic value of the micromorphological characters in the genus. The similarity matrix was based on Jaccard´s coefficient and then unweighted pair group method with arithmetic averages (UPGMA) applied in the dendrogram. A cophenetic matrix was computed from the clustering matrix in order to assess the correlation between the matrix of similarity and the dendrogram. Principal component analysis (PCA) was used based on the correlation matrix (Tab. 3). All these analyses were undertaken using the software NTSYS–PC 2.0 (Rohlf 2000).

Results

Micromorphology Characterization

Our results are new to *Mesosetum* species. The anthecia can be elliptic, lanceolate or ovate (*M. pappophorum* (Nees) Kuhlm.) and the apex acute to acuminate (*M.* sect *Sclerochloae*). The anthecia vary from glabrous to hairy, with bicellular microhair and unicellular macrohair short or long. The surface of anthecia is quite variable, can be totally smooth (*M. pappophorum*) to completely covered by papillae and silica cells. The epidermal cells vary into shape and size. Stomata (Fig. 1a) were seen in 16 species, however difficulties in the technique could hide their presence in the other species, hence they were not analyzed.

Simple and compound papillae (Fig. 1a,c,e-g) were found on short and long cells, generally with

Table 1 – Specimens examined for micromorphological characters from upper anthecium. * According to Filgueiras (1989).

Species	**Section***	**Collection Site**	***Voucher***	Herbarium
Mesosetum agropyroides Mez	*Penicillata*	*s.l.* - GO	*Glaziou s.n.*	K
Mesosetum alatum Filg.	*Bifaria*	Água Boa - MT	*R.C. Oliveira et al. 2765*	UB
		Novo Santo Antonio - MT	*H. Jancoski et al. 444*	UB
		Xavantina - MT	*H.S. Irwin et al. 16467*	UB
Mesosetum annuum Swallen	*Loliiformia*	Flores de Goiás - GO	*A.S. Silva et al. 269*	UB
		Jerumenha - PI	*A.S. Silva et al. 270*	UB
		Campo Maior - PI	*M.S.B. Nascimento 103*	K
Mesosetum ansatum (Trin.) Kuhlm.	*Bifaria*	Poconé - MT	R.C. Oliveira et al. 2766	UB
Mesosetum arenarium Swallen	*Loliiformia*	Diamantina - MG	*T.S. Filgueiras et al. 11321*	IBGE
		Diamantina - MG	*T.S. Filgueiras et al. 1101*	IBGE
		Cristalina - GO	*H.S. Irwin et al. 13337*	IBGE
Mesosetum bifarium (Hack.) Chase	*Bifaria*	Teresina de Goiás - GO	*A.S. Silva et al. 235*	UB
Mesosetum blakei Swallen	*Penicillata*	Zelaya, Nicarágua	*W.D. Stevens 8188–a*	K
Mesosetum cayennense Steud.	*Mesosetum*	Alto Paraíso - GO	*R.C. Oliveira et al. 2744*	UB
		Cachoeira Paraíso - TO	*R.C. Oliveira et al. 2848*	UB
		Mineiros - MT	*G.H. Rua 940*	UB
		La Paz, Bolívia	R. Haase 630	K
		La Paz, Bolívia	*C.E. White 2318*	K
		Santa Cruz, Bolívia	*B. Bruderreck 70*	K
		Santa Cruz, Bolívia	*J.R.I. Wood et al. 20791*	K
		Santa Cruz, Bolívia	*J.R.I. Wood et al. 20006*	K
		Santa Cruz, Bolívia	J.R.I. Wood et al. 17248	K
		Santa Cruz, Bolívia	*J.R.I. Wood et al. 25982*	K
		Santa Cruz, Bolívia	*J.R.I. Wood et al. 13516*	K
		Santa Cruz, Bolívia	*J.R.I. Wood et al. 26130*	K
Mesosetum chaseae Luces	*Bifaria*	Poconé - MT	*R.C. Oliveira et al. 2772*	UB
		Corumbá - MS	*A. Allem et al. 1152*	CEN
		Corumbá - MS	*A. Allem et al. 1397*	CEN
		Corumbá - MS	*A. Pott et al 1771*	CEN
		Furnas - MG	*S.C. Pereira et al. 7178*	IBGE
		Boa Vista - RR	*L. Coradin et al. 871*	CEN
		Boa Vista - RR	*L. Coradin et al. 909*	CEN
		Bolivar, Venezuela	*G. Davidse 22876*	K
Mesosetum chlorostachyum (Döll) Chase	*Loliiformia*	Rio Negro - AM	*Spruce 1310*	K
		Rio Negro - AM	*Spruce s.n.*	K
		Atabapo, Venezuela	*G. Davidse 16863*	ESA

Species	Section*	Collection Site	*Voucher*	Herbarium
Mesosetum comatum Swallen	*Loliiformia*	Missiones, Argentina	*M. Crovetto 8241*	BAA
		Missiones, Argentina	*M. Crovetto 9533*	BAA
		Missiones, Argentina	*M.E. Mulgura 3461*	BAA
Mesosetum compressum Swallen	*Bifaria*	Pesqueira - PE	*D. Andrade-Lima et al. 9438*	UB
		Brejo da Madre de Deus - PE	L.M. Nascimento et al. 393	HUEFS
		Estreito, Marabá - PA	*G.S. Pinheiro et al. 68*	IAN
		Estreito, Marabá - PA	*G.S. Pinheiro et al. 495*	IAN
Mesosetum elytrochaetum (Hack.) Swallen	*Bifaria*	Alto Paraíso - GO	*R. C. Oliveira et al. 2722*	UB
		Alto Paraíso - GO	*H.M. Longhi-Wagner 3934*	IBGE
		Teresina de Goiás - GO	*T. S. Filgueiras et al. 3229*	SP
Mesosetum exaratum (Trin.) Chase	*Penicillata*	Jaguariaíva - PR	*J.F.M. Valls et al. 11260*	CEN
		Jaboticatubas - MG	*T. Sendulski 443*	CEN
		São José do Barreiro - SP	*L. Freitas 753*	CEN
Mesosetum ferrugineum (Trin.) Chase	*Mesosetum*	São João del Rei - MG	*Glaziou 17385*	P
Mesosetum filifolium F.T. Hubb.	*Penicillata*	Parauapebas, Pará	*C.R. Martins 998*	UB
		Atabapo, Venezuela	*G. Davidse et al. 17209*	K
		Trinidad, Belize	*G. Davidse et al. 32780*	K
		San Luis, Honduras	*R.R. Innes 19*	K
Mesosetum gibbosum Renvoize & Filg.	Loliiformia	Rio de Contas - BA	*S. Atkins et al. 14783*	ESA
		Lençóis - BA	*J.R. Pirani et al. 7238*	K
		Abaíra - BA	*R.M. Harley et al. 50772*	K
		Palmeiras - BA	*V.C. Souza et al. 5238*	K
Mesosetum loliiforme (Hochst. ex Steud.) Chase	*Loliiformia*	Niquelândia - GO	*A.S. Silva et al. 247*	UB
		Brasília - DF	*M.W.S. Souza 62*	UB
		St. Ignatius, Guiana	*R. Goodland 226*	K
		Pakaraima, Guiana	*T.W. Henkel 5820*	K
		Kayserberg, Suriname	*K.U. Kramer et al. 3003*	K
Mesosetum longiaristatum Filg.	*Bifaria*	Teresina de Goiás - GO	*R.C. Oliveira et al. 2816*	UB
		São Domingos - GO	*J.F.M. Valls et al. 15812*	CEN
		São Domingos - GO	*J.F.M. Valls et al. 15841*	CEN
Mesosetum pappophorum (Nees) Kuhlm.	*Loliiformia*	Flores de Goiás - GO	*A.S. Silva et al. 267*	UB
		Flores de Goiás - GO	*J.F.M. Valls et al. 15949*	CEN
		Flores de Goiás - GO	J.F.M. Valls et al. 15953	CEN
		Serra Negra do Norte - RN	*M.F. Simon 498*	HUEFS
		Serra Negra do Norte - RN	*C.G.T. Ferreira 254*	UFRN
Mesosetum penicillatum Mez	*Penicillata*	Xavantina - MT	*G. Eiten & L.T. Eiten 8541*	K
		Xavantina - MT	*G.D. Smith 81*	K
		Beni, Bolívia	*G. Beck 20682*	K
		La Paz, Bolívia	*R. Haase 122*	K
Mesosetum pittieri Hitchc.	*Sclerochloae*	Chepo, Panamá	*H. Pittier 4516*	K

Species	Section*	Collection Site	*Voucher*	Herbarium
Mesosetum rottboellioides (Kunth) Hitchc.	*Mesosetum*	Grão Mogol - MG	*P.A. Reis et al. 331*	UB
		Cristália - MG	*Hatschbach 55064*	ICN
		Buíque - PE	*D.N. Silva et al. 36*	UB
		Serra Branca - PB	*M.C. Pesssoa et al. 477*	UB
		Atures, Venezuela	*G. Davidse 15250*	K
		Atures, Venezuela	*G. Davidse 15428*	K
		Atures, Venezuela	*O. Hubber 2335*	K
		Atures, Venezuela	*O. Hubber 5207*	K
		Atures, Venezuela	*O. Hubber 5259*	K
		Atabapo, Venezuela	*J.J. Wurdack 43753*	K
		Bolivar, Venezuela	*J.J. Wurdack 39762*	K
		Piar, Venezuela	*O. Hubber 12154*	K
		Santa Barbara, Venezuela	*M.J. Eden 224*	K
Mesosetum sclerochloa (Trin.) Hitchc.	*Sclerochloae*	Flores de Goiás - GO	*A.S. Silva et al. 266*	UB
		Flores de Goiás - GO	*J.F.M. Valls et al. 15937*	CEN
		Flores de Goiás - GO	*J.F.M. Valls et al. 15947*	CEN
		Flores de Goiás - GO	*J.F.M. Valls et al. 15954*	CEN
Keratochlaena rigidifolia (Filg., Morrone & Zuloaga) Morrone & Zuloaga	-	Loreto - MA	*J.F.M. Valls et al. 8432*	CEN
Tatianyx arnacites (Trin.) Zuloaga & Soderstr.	-	Abaíra - BA	*W. Ganev 2728*	K
		Guiratinga - MT	*S.S. Silva 133*	IBGE

1–3 papillae per cell. In *M. loliiforme* (Hochst. ex Steud.) Chase, *M. annuum* Swallen, *M. arenarium* Swallen, *M. chlorostachyum* (Döll) Chase, *M. chaseae* Luces, and *M. ansatum* (Trin.) Kuhlm., coalescence between the larger papillae occurs in the basal and distal portions of the anthecium, forming cells with two to six coalescent papillae (Fig. 1e, g).

The silica cells were found in the cross form (Fig. 1b). They were registered in *M. alatum* Filg., *M. bifarium* (Hack.) Chase, *M. compressum* Swallen, *M. elytrochaetum* (Hack.) Swallen, *M. exaratum* (Trin.) Chase, *M. longiaristatum* Filg., *M. blakei* Swallen, and *M. filifolium* F.T. Hubb.

The germination lid in the anthecium basal portion is very conspicuous in all species, and differences were observed in these structures (Fig. 1h, i). We identified two new character states. Unilobed germination lid is present in *Mesosetum alatum* (Fig. 1h), *M. agropyroides* Mez, *M. chlorostachyum*, *M. ferrugineum* (Trin.) Chase, *M. filifolium*, *M. gibbosum* Renvoize & Filg., and *M. pappophorum*. This is the typical form found in Paniceae (Rost & Simper 1975; Johnston & Watson 1981; Giraldo-Cañas 2004), but bilobed germination lid was observed in the other 17 species (e.g. *M. elytrochaetum*, Fig. 1i).

In the third distal portion, the presence or absence of long macrohairs aided in the distinction of the *Mesosetum* species. Only five species analyzed did not show a conspicuous hairy anthecium apex. This character contributed to distinguish *M. exaratum* from *M. filifolium*.

Bicellular microhairs were found in *M. cayennense* Steud., *M. rottboellioides* (Kunth) Hitchc., *M. filifolium* and *M.* sect. *Bifaria*. Only the panicoid type was registered (Zuloaga & Soderstrom 1985), with the basal cell smaller than the lanceolate apical cell with an acute apex (Fig. 1d, arrow).

Table 2 – Micromorphological characters and character states of the upper anthecium of *Mesosetum*, *Keratochlaena*, and *Tatianyx* species used in the PCA and UPGMA analyses.

1. Papilla on the abaxial surface: absent(0), present(1)
2. Papilla on the germination lid surface: absent(0), present(1)
3. Papilla on the median surface: absent(0), present(1)
4. Papilla on the distal surface: absent(0), present(1)
5. Simple papilla: absent(0), present(1)
6. Compound papilla: absent(0), present(1)
7. Number of papilla per epidermical cell: one per cell(0), more than one per cell(1)
8. Coalescence between the larger papillas: absent(0), present(1)
9. Bicellular microhairs: absent(0), present(1)
10 Unicellular macrohairs: absent(0), present(1)
11. Unicellular macrohairs on the median surface: absent(0), present(1)
12. Unicellular macrohairs on the distal surface: absent(0), present(1)
13. Cruciform silica cells: absent(0), present(1)
14. Germination lid: bilobed(0), unilobed(1)
15. Germination lid lobe width/dorsal spikelet width: narrow(0), equal(1)

Table 3 – Data matrix used in the cluster analysis of *Mesosetum* and related genera. Character states according to Table 2

Species/ Character states	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
Mesosetum agropyroides Mez	1	0	1	1	1	1	1	0	0	1	0	1	0	1	0
Mesosetum alatum Filg.	1	0	0	1	1	0	0	0	1	1	1	1	1	1	1
Mesosetum annuum Swallen	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
Mesosetum ansatum (Trin.) Kuhlm.	1	0	0	1	1	1	1	1	1	1	0	1	0	0	0
Mesosetum arenarium Swallen	1	1	1	1	1	1	1	1	0	1	0	1	0	0	0
Mesosetum bifarium (Hack.) Chase	1	0	0	1	1	0	1	0	1	1	1	1	1	0	0
Mesosetum blakei Swallen	1	1	1	1	1	0	1	0	0	1	0	1	1	0	1
Mesosetum cayennense Steud.	1	1	1	1	0	1	0	0	1	1	1	1	0	0	0
Mesosetum chaseae Luces	1	0	1	1	1	1	1	1	1	1	0	1	0	0	0
Mesosetum chlorostachyum (Döll) Chase	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
Mesosetum compressum Swallen	1	0	0	0	1	0	0	0	1	1	1	1	1	0	0
Mesosetum elytrochaetum (Hack.) Swallen	1	0	0	1	1	1	1	0	1	1	1	1	1	0	0
Mesosetum exaratum (Trin.) Chase	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Mesosetum ferrugineum (Trin.) Chase	1	1	1	1	0	1	0	0	1	1	1	1	0	1	1
Mesosetum filifolium F.T. Hubb.	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0
Mesosetum gibbosum Renvoize & Filg.	1	0	1	1	1	1	1	0	0	1	0	1	0	1	1
Mesosetum loliiforme (Hochst. ex Steud.) Chase	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
Mesosetum longiaristatum Filg.	1	0	0	1	1	1	1	0	1	1	1	1	1	0	0
Mesosetum pappophorum (Nees) Kuhlm.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Mesosetum penicillatum Mez	1	1	1	1	0	1	0	0	0	1	0	1	0	1	0
Mesosetum pittieri Hitchc.	1	1	1	1	1	1	0	0	0	1	0	1	0	1	0

Species/ Character states	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Mesosetum rottboellioides (Kunth) Hitchc.	1	1	1	1	0	1	0	0	1	1	1	1	0	0	0
Mesosetum sclerochloa (Trin.) Hitchc.	1	1	1	1	1	1	0	0	0	1	0	1	0	1	0
Mesosetum comatum Swallen	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
Keratochlaena rigidifolia (Filg., Morrone & Zuloaga) Morrone & Zuloaga	1	1	1	1	0	1	0	0	0	0	0	1	0	0	0
Tatianyx arnacites (Trin.) Zuloaga & Soderstr.	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0

Numerical Analysis

Figures 2 and 3 show the relationship between the analyzed species and the micromorphological characters of the upper anthecium. The UPGMA dendrogram shows three clearly separated groups (Fig. 2). A high correlation of 0.91 was found between cophenetic matrix and similarity matrix. These major groups have no correspondence to taxonomic clades, nor genera or sections of *Mesosetum*.

The first three axes of PCA (Fig. 3) explained 71.74% of the total variation (50.95% for axis 1, 12.60% for axis 2 and 8.17% for axis 3). The characters that contributed more to the formation of the four groups were: presence or absence of papillae, quantity of papillae per epidermal cell, presence of hairs on the apex and presence of silica cells.

The absence of papillae was the most important character to distinguish *M. pappophorum, M. exaratum,* and *M. filifolium* from the other species (Fig. 2, 3). However, these species did not group.

Group 1 was composed by species of *M. sect. Bifaria* (Fig. 2, 3): *M. alatum*, *M. bifarium, M. compressum, M. elytrochaetum,* and *M. longiaristatum*. This group shares many characters, e.g. absence of papillae on the median surface, unicellular macrohairs on the median and distal surface, bicellular microhairs and silica cells.

Group 2 is comprised of *M. arenarium, M. annuum, M. chlorostachyum, M. comatum* Swallen*, M. loliiforme, M. ansatum*, *M. chaseae,* and *Tatianyx arnacites* (Fig. 2, 3). It has more than one papilla per cell, compound papillae, coalescence between the larger papillae, and hairy anthecium apex.

Group 3 is characterized by one papilla per epidermal cell and is composed of *M. cayennense, M. ferrugineum, M. rottboellioides, M. agropyroides, M. gibbosum, M. penicillatum* Mez*, M. pittieri* Hitchc.*, M. sclerochloa* (Trin.) Hitchc., and *Keratochlaena rigidifolia* (Fig. 2, 3).

Discussion

Micromorphological characters of the upper anthecium have recognized taxonomic value and are widely used in the taxonomy of the Poaceae (Thompson & Estes 1986; Filgueiras 2001; Giraldo-Cañas 2001; Oliveira *et al*. 2008). Our results reinforce the importance of such characters, but after analyzing several specimens some of the characters are more variable than previously expected and should be used carefully.

Sede *et al*. (2009) segregated the genera *Oncorachis* and *Keratochlaena* (under *Sclerochlamys* nom. illeg.) based on molecular data, and anatomical, morphological, and micromorphological characters. In their study, *Mesosetum* was reported to have a smooth anthecium, i.e. without papillae and open at the apex, based on *M. cayennense* and *M. loliiforme*. However, our results differ significantly. We analyzed populations of each of these *Mesosetum* species, from distinct localities (Tab. 1) and the upper anthecia was closed at the apex and covered by abundant verrucose papillae (Fig. 1j). Unfortunately, Sede *et al*. (2009) did not cite vouchers.

Sede *et al*. (2009) also reported the apex of the upper anthecium as glabrous in *Keratochlaena rigidifolia* (under *Sclerochlamys*) supporting the segregation of this species into a new genus *Keratochlaena*. However, we recorded prickly hairs on the upper anthecium apex in one voucher (Fig. 4a). On the other hand, a voucher of *Tatianyx arnacites* analyzed by Zuloaga & Sorderstrom (1985) had prickly hairs on the upper anthecium, differing from the two specimens analyzed in this current study which had a glabrous upper anthecium apex (Fig. 4d).

Another major divergence was found in our study with that of Zuloaga & Sorderstrom (1985). In our study, *T. arnacites* has simple papillae, and they are localized in depressions on the epidermis surface of the anthecium (Fig. 1f). In Zuloaga & Soderstrom (1985) the papillae are compound and

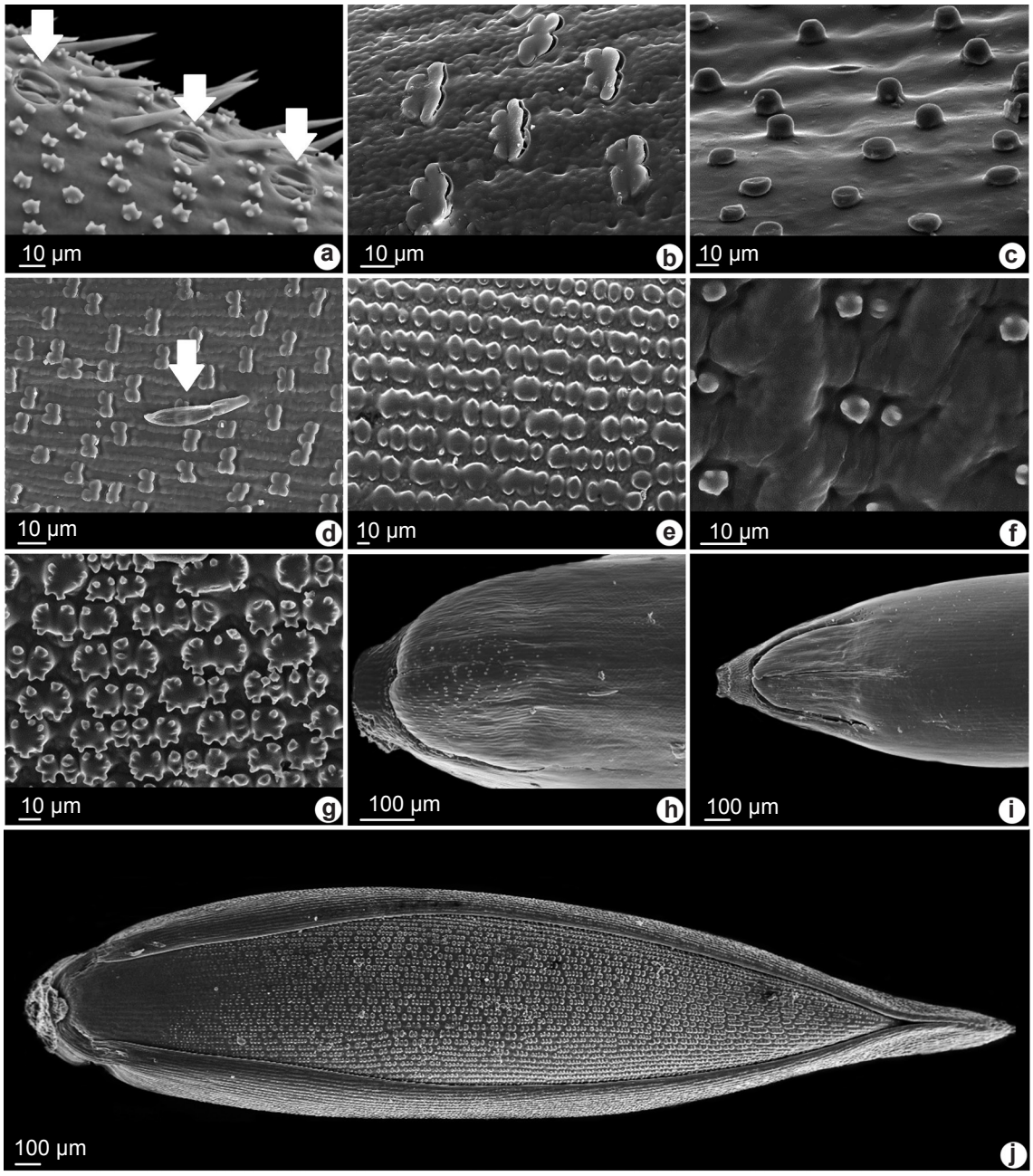

Figure 1 – a-g. Detail of the upper anthecium in some of the species analyzed. a. *Mesosetum cayennense* (*R. Haase 630*) - stomata (arrow). b. *M. filifolium* (*R.R. Innes 19*) - silica cells. c. *M. pittieri* (*H. Pittier 4516*) - papillae. d. *M. filifolium* (*C.R. Martins 998*) - bicellular microhairs (arrow). e. *M. annuum* (*A.S. Silva et al. 270*) - papillae. f. *Tatianyx arnacites* (*W. Ganev 2728*) - papillae. g. *M. chaseae* (*A. Pott et al 1771*) - papillae. h. *M. alatum* (*H. Jancoski et al. 444*) - unilobed germination lid. i. *M. elytrochaetum* (*R. C. Oliveira et al. 2722*) - bilobed germination lid. j. upper anthecium of *M. loliiforme* (*T.W. Henkel 5820*).

not included in depressions. We have observed a wide morphological variation in *Tatianyx* and found distinct micromorphological characters of the upper anthecium, requiring reevaluation of this species.

In *Arthropogoninae*, the bicellular microhairs were observed only in species of *Altoparadisium* Filg., Davidse, Zuloaga & Morrone, *Canastra* Morrone, Zuloaga, Davidse & Filg. and *Homolepis*

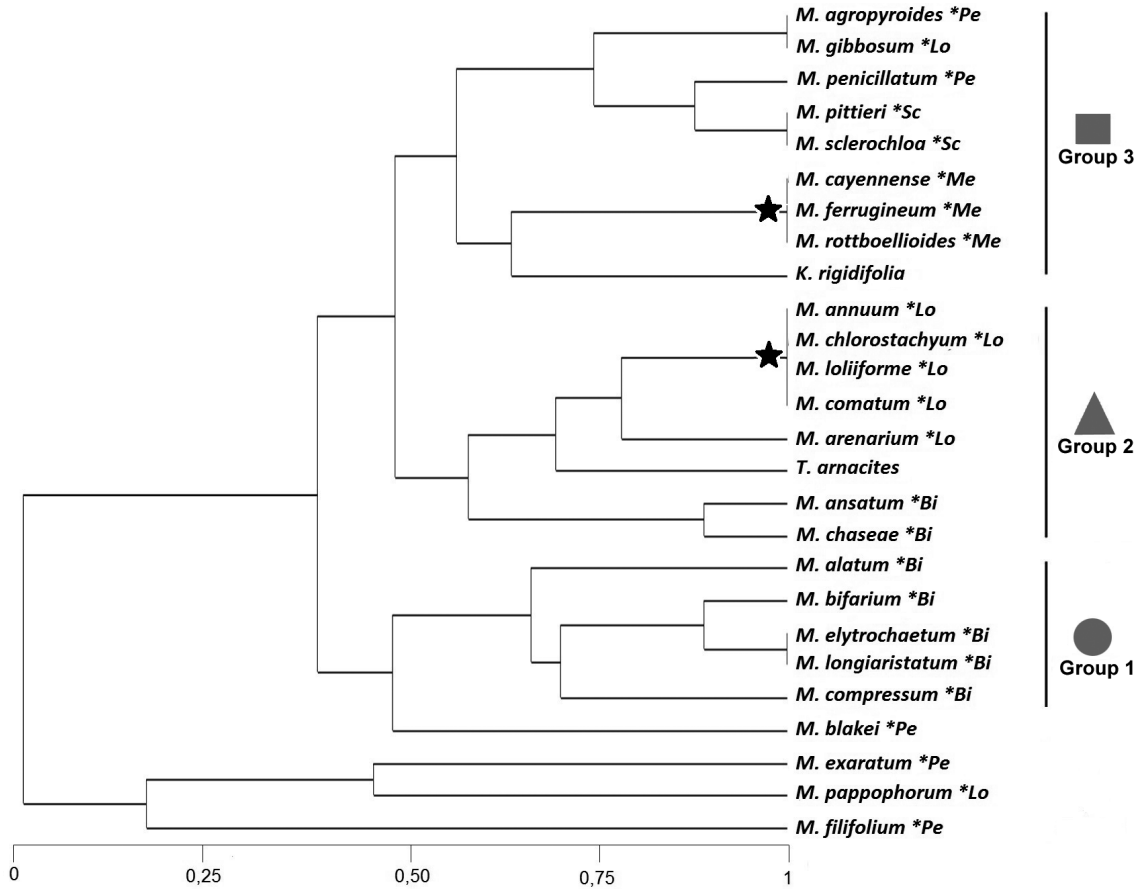

Figure 2 – UPGMA dendrogram based on Jaccard's similarity using micromorphological characters of the upper anthecium for *Mesosetum*, *Tatianyx*, and *Keratochlaena* species. **Bi*. *Mesosetum* sect *Bifaria*. **Lo*. *Mesosetum* sect *Loliiformia*. **Me*. *Mesosetum* sect *Mesosetum*. **Pe*. *Mesosetum* sect *Penicillata*. **Sc*. *Mesosetum* sect *Sclerochloae*. *The classification of sections follows Filgueiras (1989). ●. Group 1. ▲. Group 2. ■. Group 3. ★. Subgroups corresponding exactly to sections proposed by Filgueiras (1989).

(Zuloaga & Soderstrom 1985; Filgueiras *et al*. 2001; Sede *et al*. 2008). Silica cells in *Mesosetum* have the form of crosses, with a minimum of two grooves (Fig. 1b), differing from those encountered in other members of *Arthropogoninae* whose silica cells has a dumbbell (halteriform) shape (Zuloaga & Sorderstrom 1985; Filgueiras *et al*. 2001).

The germination lid is reported as little evident or conspicuous in Paniceae (Giraldo-Cañas 2004; Filgueiras *et al.* 2001). In *Mesosetum* all the species had a conspicuous germination lid, and we proposed two new character states for this structure, i.e. unilobed or bilobed.

According to Zucol (1998, 2000), the form of silica cells can show a minimum of two grooves, but it is more like lobes than grooves. They were mainly found in the distal portion of the abaxial surface of fertile lemma, like in the majority of Paniceae (Hsu 1935; Zuloaga & Soderstrom 1985; Giraldo-Cañas 2004).

The SEM analyses helped to distinguish between the closely related taxa. *Mesosetum annuum* and *M. pappophorum*, were previously distinguished by the length of spikelet hairs, according to Swallen (1937) and Filgueiras (1989). However, this character is variable between populations, and sometimes the overlapping of the hair length brings doubts if the species are indeed distinct. The micromorphology of the upper anthecium showed in the present study, supports the separation of these species with more certainty. *Mesosetum annuum* has papillae on all surfaces and a few hairs at the apex (Fig. 4b), while *M. pappophorum* shows a totally smooth and glabrous upper anthecium (Fig. 4e).

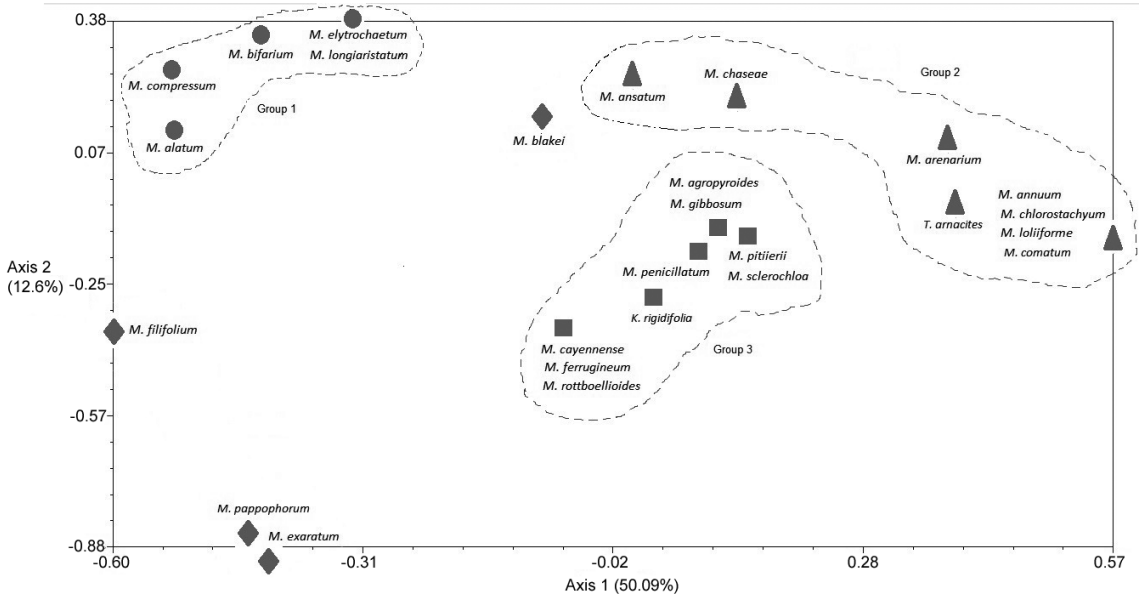

Figure 3 – PCA using micromorphological characters of the upper anthecium for *Mesosetum*, *Tatianyx*, and *Keratochlaena* species. ●. Group 1. ▲. Group 2. ■. Group 3. ◆. Species not grouped.

The character used by Filgueiras (1989) to separate *M. alatum* from *M. bifarium* (upper glume with tufts of hairs) is also inconsistent (Ribeiro 2013), when more samples are analyzed. Our results show that the best character is the germination lid. *Mesosetum alatum* is the only species in *M.* sect. *Bifaria* that has a unilobed germination lid and the width of this structure is equal to the dorsal spikelets, while in *M. bifarium* it is narrower. In addition, the anthecium has one papilla per cell in *M. alatum*, while it has at least three or more papillae per cell in *M. bifarium* (Tab. 2).

Another case where the morphological distinction was also supported by unstable characters is that of *M. exaratum* and *M. filifolium*. Swallen (1937) used the pilosity of the second glume to support their distinction, while Filgueiras (1989) put more value on the plant height and leaf blade length. *Mesosetum filifolium* shows silica cells and bicellular microhairs all over the upper anthecium surface, and a few macrohairs on the distal portion, while *M. exaratum* is glabrous and showed one silica cell in the three examined specimens.

There are two subgroups of species within the major groups of the dendrogram (Fig. 2, star) that coincide with the sections suggested by Filgueiras (1989). The species that compose the section *Mesosetum* adopted by this author include *M. cayennense*, *M. rottboellioides*, and *M. ferrugineum* and it corresponds to the subgroup identified by one compound papillae per cell. This section is characterized by spikelets with ferruginous indumentum, which is an exclusive character (Filgueiras 1989). Species of this same group are associated with *Keratochlaena rigidifolia*, that is the sister group of *Mesosetum* genus. Similarities in chromosome size and number of species from *M.* sect. *Mesosetum* were also found by Sousa (2014).

Another subgroup found in the dendrogram using the upper anthecium micromorphological characters (Fig. 2, star) corresponds to the very homogenous *M.* sect. *Loliiformia*: *M. annuum*, *M. arenarium*, *M. chlorostachyum*, *M. loliiforme* and M. *comatum*. This section is characterized by spikelets with an inflated asymmetric lower glume and the second glume triangular (Filgueiras 1989). The upper anthecium of this group has more than one papilla per cell and coalescent papillae.

This study endorses the importance of the upper anthecium micromorphological characters for delimitation of *Mesosetum* species, but the taxonomic value of these characters are reduced for higher hierarchical levels. Also a new character is described, the germination lid bilobed, which has never before been mentioned. The lack of

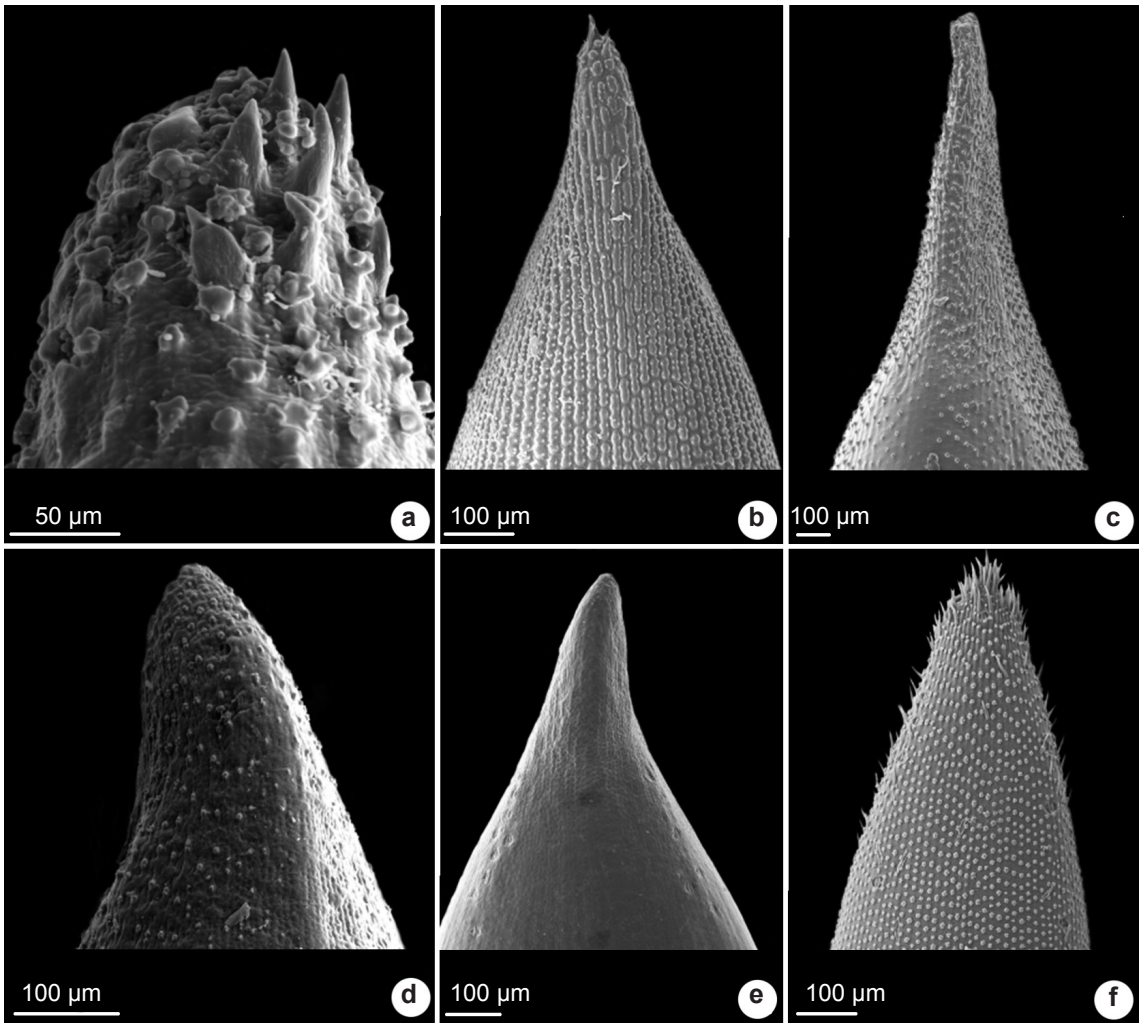

Figure 4 – Apex of the upper anthecium in some of the species analyzed. a. *Keratochlaena rigidifolia* (*J.F.M. Valls et al. 8432*). b. *Mesosetum annuum* (*A.S. Silva et al. 270*). c. *M. pittieri* (*H. Pittier 4516*). d. *Tatianyx arnacites* (*W. Ganev 2728*). e. *M. pappophorum* (*A.S. Silva et al. 267*). f. *M. cayennense* (*R. Haase 630*).

standard descriptive terms in Poaceae and the lack of correspondence between vouchers examined and the description morphological in SEM studies are still problematic, whereas it brings difficulties to compare species and their structures. More studies that include SEM additional character are needed to achieve a stronger systematic study of this group, accurate species identification, and more comprehensive biogeographical relationships.

Acknowledgements

This study was supported in part by Protax (562340/2010-6), Reflora and CNPq Edital Universal (474880/2012-5) and Capes for the doctorate grants to the first two authors. We are grateful to Sueli Maria Gomes for her assistance with the anatomy descriptions and help during revision of this paper.

References

Aliscioni, S.S.; Giussani, L.M.; Zuloaga, F.O. & Kellogg, E.A. 2003. A molecular phylogeny of *Panicum* (Poaceae: Paniceae): tests of monophyly and phylogenetic placement within the Panicoideae. American Journal of Botany 90: 793-821.

Chase, A. 1911. Notes on genera of Paniceae 4. Proceedings Biological Society of Washington 24: 103-159.

Ellis, R. 1979. A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view. Bothalia 12: 641-671.

Filgueiras, T.S. 1986. O gênero *Mesosetum* Steudel (Gramineae: Paniceae). Tese de Doutorado. Universidade Estadual de Campinas, Campinas. 344p.

Filgueiras, T.S. 1989. Revisão de *Mesosetum* Steudel (Gramineae: Paniceae). Acta Amazônica 19: 47-114.

Filgueiras, T.S.; Davidse, G.; Zuloaga, F.O. & Morrone, O. 2001. The establishment of the new genus *Altoparadisium* and a reevaluation of *Arthropogon* (Poaceae, Paniceae). Annals of the Missouri Botanical Garden 88: 351-372.

Filgueiras, T.S.; Silva, A.S. & Oliveira, R.C. de. 2014. *Mesosetum. In*: Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro. Available at <http://floradobrasil.jbrj.gov.br/jabot/floradobra.sil/FB13355>. Access on 23 August 2014.

Giraldo-Cañas, D. 2001. Estudios micromorfológicos y anatómicos en el género Neotropical *Axonopus* (Poaceae: Paniceae). II. Antecio superior. Caldasia 24: 293-316.

Giraldo-Cañas, D. 2004. Características micromorfológicas y anatómicas de la espiguilla y el antecio superior del género *Digitaria* (Poaceae: Panicoideae: Paniceae). Caldasia 26: 1-35.

Giussani, L.M.; Cota-Sanchez, H.; Zuloaga F.O. & Kellogg, E.A. 2001. A molecular phylogeny of the grass subfamily Panicoideae (Poaceae) shows multiple origins of C4 photosynthesis. American Journal of Botany 88: 1993-2012.

Grass Phylogeny Working Group (GPWG). 2011. New grass phylogeny resolves deep evolutionary relationships and discovers C_4 origins. New Phytologist 193: 304-312.

Hsu, C. 1935. The classification of *Panicum* (Gramineae) and its allies, with special reference to the characters of lodicule, style-base and lemma. Journal of the Faculty of Science University of Tokyo 9: 43-150.

Johnston, C. & Watson, L. 1981. Germination flaps in grass lemmas. Phytomorphology 31: 78-85.

Mejia-Saules, T. & Bisby, F.A. 2003. Silica bodies and hooked papillae in lemmas of *Melica* species (Gramineae: Pooideae). Botanical Journal of the Linnean Society 141: 447-463.

Morrone, O. & Zuloaga, F.O. 1991. Revision del género *Streptostachys* (Poaceae–Panicoideae), su posicion sistematica dentro de la tribu Paniceae. Annals of the Missouri Botanical Garden 78: 359-376.

Morrone, O.; Scataglini, A.M. & Zuloaga, F.O. 2007. *Cyphonanthus*, a new genus segregated from *Panicum* (Poaceae: Panicoideae: Paniceae) based on morphological, anatomical and molecular data. Taxon 56: 521-532.

Morrone, O.; Aagesen, L.; Scataglini, M.A.; Salariato, D.L.; Denham, S.; Chemisquy, M.A.; Sede, S.M.; Giussani, L.M.; Kellogg, E.A. & Zuloaga, F.O. 2012. Phylogeny of the Paniceae (Poaceae: Panicoideae): integrating plastid DNA sequences and morphology into a new classification. Cladistics 1-24.

Oliveira, R.P.; Longhi-Wagner, H.M. & Leite, K.R.B. 2008. A contribuição da anatomia foliar para a taxonomia de *Raddia* Bertol. (Poaceae: Bambusoideae). Acta Botanica Brasilica 22: 1-19.

Pilger, R. 1940. Gramineae. In: Engler, A & Prantl, K. Die Natürlichen Pflanzenfamilen. 2ed, 14e. Wilhelm Engelmann, Leipzig. 208p.

Ribeiro, A.R.O. 2013. Citogenética, reprodução e variabilidade morfológica de espécies de *Mesosetum* sect. *Bifaria* (Hack.) Chase (Poaceae: Paspaleae). Dissertação de Mestrado, Universidade de Brasília, Brasília. 111p.

Rohlf, F. J. 2000. NTSYS-pc: numerical taxonomy and multivariate analysis system. Verion 2.1, Exeter Software, New York. 38p.

Rost, T.L. & Simper, A.D. 1975. The germination lid: A characteristic of the lemma in the Paniceae. Madroño 23: 68-72.

Sede, S.M.; Morrone, O.; Giussani, L.M. & Zuloaga, F.O. 2008. Phylogenetic studies in the Paniceae (Poaceae): a realignment of section Lorea of *Panicum*. Systematic Botany 33: 284-300.

Sede, S.M.; Morrone, O.; Aliscioni, S.S.; Giussani, L.M. & Zuloaga, F.O. 2009. *Oncorachis* and *Sclerochlamys*, two new segregated genera from *Streptostachys* (Poaceae, Panicoideae, Paniceae): a revision based on molecular, morphological and anatomical characters. Taxon 58: 365-374.

Soderstrom, T.R. & Zuloaga, F.O. 1989. A Revision of the Genus *Olyra* and the New Segregate Genus *Parodiolyra* (Poaceae: Bambusoideae: Olyreae). Smithsonian Contributions to Botany 69: 1-79.

Sousa, M.W.S. 2014. Citogenética e morfologia de espécies de *Mesosetum* Steud. (Poaceae, Paspaleae). Dissertação de Mestrado. Universidade de Brasília, Brasília. 61p.

Swallen, J.R. 1937. The grass genus *Mesosetum*. Brittonia 2: 363-392.

Thiers, B. (continuously updated). Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. Available at <http://sweetgum.nybg.org/ih/>. Access on 17 August 2014.

Thompson, R. & Estes, J. 1986. Anthecial and foliar micromorphology and foliar anatomy of *Brachiaria*. American Journal of Botany 73: 398-408.

Zucol, A. 1998. Microfitolitos de las Poaceae argentinas: II. Microfitolitos foliares de algunas especies del género *Panicum* (Poaceae, Paniceae) de la provincia de Entre Ríos. Darwiniana 36: 29-50.

Zucol, A. 2000. Fitolitos de Poaceae de Argentina. III. Fitolitos foliares de especies del género

Paspalum (Paniceae) en la provincia de Entre Ríos. Darwiniana 38: 11-32.

Zuloaga, F.O. & Soderstrom, T.R. 1985. Classification of the outlying species of New World *Panicum* (Poaceae: Paniceae). Smithsonian Contributions to Botany 59: 1-63.

Zuloaga, F.O.; Scataglini, M.A. & Morrone, O. 2010. A phylogenetic evaluation of sects. *Agrostoidea*, *Megista*, *Prionitia* and *Tenera* of *Panicum* (Panicoideae, Poaceae): two new genera *Stephostachys* and *Sorengia*. Taxon 59: 1535-1546.

Artigo recebido em 18/09/2014. Aceito para publicação em 27/03/2015.