Fruits of neotropical species of the tribe Malveae (Malvoideae – Malvaceae): macro- and micromorphology

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ABSTRACT

Fruit morphology of the tribe Malveae has been discussed since the first taxonomic classifications of Malvaceae. The fruits are schizocarps, with some genera possessing an endoglossum. Besides morphological variation in the endoglossum, other differences include the number seeds per locule and ornamentation of the exocarp. An in-depth study of the fruit morphology of Malveae is essential to gain insight into the relationships among taxa of the tribe. Therefore, the present study aimed to describe the fruit morphology of Malveae, including micromorphology, variation in endoglossum structure and arrangement of seeds in the locule, to comprehensively evaluate the systematic relationships among its contained taxa. The results indicate morphological variation in fruit of various genera with regard to the number of mericarps, degree of dehiscence, relationship between calyx and fruit and their relative sizes, number and morphology of spines, number of seeds per locule, presence or absence of an endoglossum, presence and types of trichomes in exocarp and endocarp, and shape and presence of trichomes in the testa of seeds. Despite the morphological proximity of taxa, there are distinct combinations of characters that define some genera, and when one or more characters overlap, joint analysis makes it possible to clarify existing relationships.

Keywords: endoglossum, mericarps, pericarp, schizocarp, seeds

Introduction

Malvaceae is widely distributed around the world, and its occurrence in tropical regions is numerous and diverse. The family is composed of about 4,465 species (The Plant List 2013), the taxa of which present several types of fruits, such as capsules, follicles, nuts, and, rarely, samaras. At least two thirds of species in the family are characterized as schizocarps (Areces-Berazain & Ackerman 2017). The tribe Malveae, which includes the major morphological and taxonomic diversity of Malvoideae, has about 70 genera and 1,000 species (Tate *et al*. 2005), and most species in the tribe have schizocarp fruits. Studies indicate that schizocarp fruits have evolved from capsules with more efficient adaptations for seed dispersal and that the transition from capsule fruit to the schizocarp in Malveae is evident (Areces-Berazain & Ackerman 2017).

Analyses of reproductive structures in phylogenetic studies are essential, as observed by Ray (1995), García *et al*. (2009) and Areces-Berazain & Ackerman (2017). In these studies, the molecular phylogenies were confirmed through the morphological analysis of Malveae fruits. More specifically, from the phylogenetic reconstruction of Malvoideae the capsular fruit was defined as the ancestral condition (Areces-Berazain & Ackerman 2017). Besides

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this type of fruit the schizocarp fruit evolved three times during the diversification of the subfamily, twice in Hibisceae tribe and once at the base of Malveae tribe, a structure that circumscribes the tribe. In addition, there was also an increase in the number of carpels in the subfamily, which duplicate in Malveae. The increase in the number of carpels is a derived condition in Malvoideae, which occur at the base of Malveae. There is a strong relationship between the type of fruit and diversification. Lineages of schizocarp fruits exhibit high rates of speciation and diversification, higher than capsular fruits. The presence of schizocarp fruits and increase in the number of carpels are positively correlated in Malvoideae, ensuring greater success in the dispersion of Malveae (Areces-Berazain & Ackerman 2017).

Some fruits of Malveae present an endoglossum. This structure was identified by Hochreutiner (1920), who defined it as 'an appendix found inside the mericarps' and further considered it to be an exclusive character of the tribe. When comparing the endoglossum in genera of the alliances *sensu* Bayer & Kubitzki (2003), we clearly see the variation in size and arrangement of this structure. In the genus *Gaya*, for example, the endoglossum appears as prominent (Masullo *et al.* 2019), originating from the basal dorsal portion of carpels, diverging from the assessment of this structure by Takeuchi & Esteves (2017), who described it as originating from the ventral portion of the mericarp. In *Wissadula*, according to Barroso *et al.* (1999), this structure is extremely reduced, being characterized only by a scar. Bovini & Baumgratz (2016), for the same taxon, consider the endoglossum as a thick line that surrounds the mericarp.

In addition to variable descriptions of endoglossum in the fruits of Malveae, other variations in the fruits are observed for their shape, size and position, ornamentation of exocarp surface, and number of seeds, among other descriptors (Schumann 1890; Krapovickas 1970; Fryxell

1976; Bovini 2015; Bovini & Baumgratz 2016). These variable descriptions of fruit morphology are a strong indication that consensus remains out of the reach of investigators. Therefore, we undertook a systematic approach involving additional morphological examination of Malveae fruits. Specifically, in the present study, we aimed to analyze exocarp micromorphology, structural variations of the endoglossum and seed arrangement in the loci in species of the tribe, including the following genera: *Abutilon*, *Briquetia*, *Briquetiastrum*, *Gaya*, *Malvastrum*, *Monteiroa*, *Sida*, *Sidastrum* and *Wissadula*. In addition, we added data to the phylogenetic discussion of the tribe, preferentially approaching the Neotropical clade *sensu* Tate *et al.* (2005).

Materials and methods

We selected 16 Neotropical species of Malveae clades as proposed by Tate *et al.* (2005) and the alliances *sensu* Bayer & Kubitzski (2003) (Tab. 1).

Until five to eight fruits at different stages of development, of about five individuals, were fixed in 2.5 % glutaraldehyde in 0.1 M sodium phosphate buffer pH 7.2 (Gabriel 1982) immediately after collection. Observations and dissections were performed with an Olympus SZ61 stereomicroscope coupled with an Olympus SC-30 digital camera. Fertile branches were collected from all individuals and deposited in the herbarium of the Rio de Janeiro Botanical Garden Herbarium Collection (RB) (Tab. 1).

For scanning electron microscopy (SEM), the already fixed samples were dehydrated in ethyl alcohol and acetone (Gabriel 1982). After this procedure, the samples were submitted to critical point drying (Bal-Tec Critical Point Dryer CPD 030) in order to complete the dehydration. The samples were then fixed with carbon adhesive tape on stubs and covered with a thin layer of gold of about 20 nm (Emitech K550X Sputter Coater). These samples were

Table 1. Malveae species used in the present study and their vouchers in the RB herbarium. Clades according to Tate *et al.* (2005) and Alliances according to Bayer & Kubitsky (2003). The samples marked with asterisk were also in spirit collection.

Clade	Alliance	Species	Voucher
A	Abutilon	*Abutilon bedfordianum* (Hook.) A. St-Hil & Naud	RB 614245* RB 622248 RB 10809 RB 433933 RB 325652
		Abutilon purpurascens K. Schum.	RB 590795* B 451056 RB 622678 RB 37427 RB 135043
		Pseudabutilon benense (Britton) Fryxell	RB 469370*
		Sida planicaulis Cav.	RB 583010* RB 603508 RB 636577 RB 758578 RB 727171
		Sida santaremensis Monteiro	RB 570257* RB 595559 RB 563612 RB 542019 B 66357
		Sidastrum micranthum (L.) Fryxell	RB 586618* RB 612278 RB 547942 RB 612285 RB 514846
		Wissadula contracta (Link.) R.E.Fries	RB 586615* RB 617861 RB 518767 RB 418486 RB 179340
		Wissadula excelsior (Cav.) C.Presl.	RB 434134* RB 12311 RB 444320 RB 222062 RB 409055
		Wissadula hernandiodes (L'Hér) Garcke	RB 586616* RB 472342 RB 603148 RB 469376 RB 423218
	Batesimalva	*Briquetia denudata* (Nees & Mart.) Chodat & Hassl.	RB 663311*
		Briquetiastrum spicatum (Kunth.) Bovini	RB 586618* RB 790464 RB 660288 RB 514828 RB 33134
	Gaya	*Gaya gaudichaudiana* A.St.-Hil	RB 586615* RB 590797 RB 761138 RB 570257 RB 197413
		Gaya guerkeana K. Schum.	RB 183819* RB 245997
		Gaya pilosa K. Schum.	RB 176503*
A / B	Sphaeralcea	*Monteiroa hatschbachii* Krapov.	RB 605539* RB 406753 RB 788562 RB 730599
B	Malvastrum	*Malvastrum coromandelianum* (L.) Garcke	RB 578478* RB 373300 RB 732613 RB 572528 RB 583047

then observed under the Zeiss EVO 40 scanning electron microscope at a voltage of 15 kV.

For the morphological nomenclature, we used Barthlott & Ehler (1977) and Barthlott & Hunt (2000) for cuticle and cell form; Metcalfe & Chalk (1979) for trichomes; and Barroso *et al.* (1999) for seed format.

Results

The fruits of Malveae species analyzed in the present study are schizocarps with dry pericarp, ranging from brown to dark brown in color after maturation (Fig. 1). They present 4-28 partially or completely dehiscent mericarps
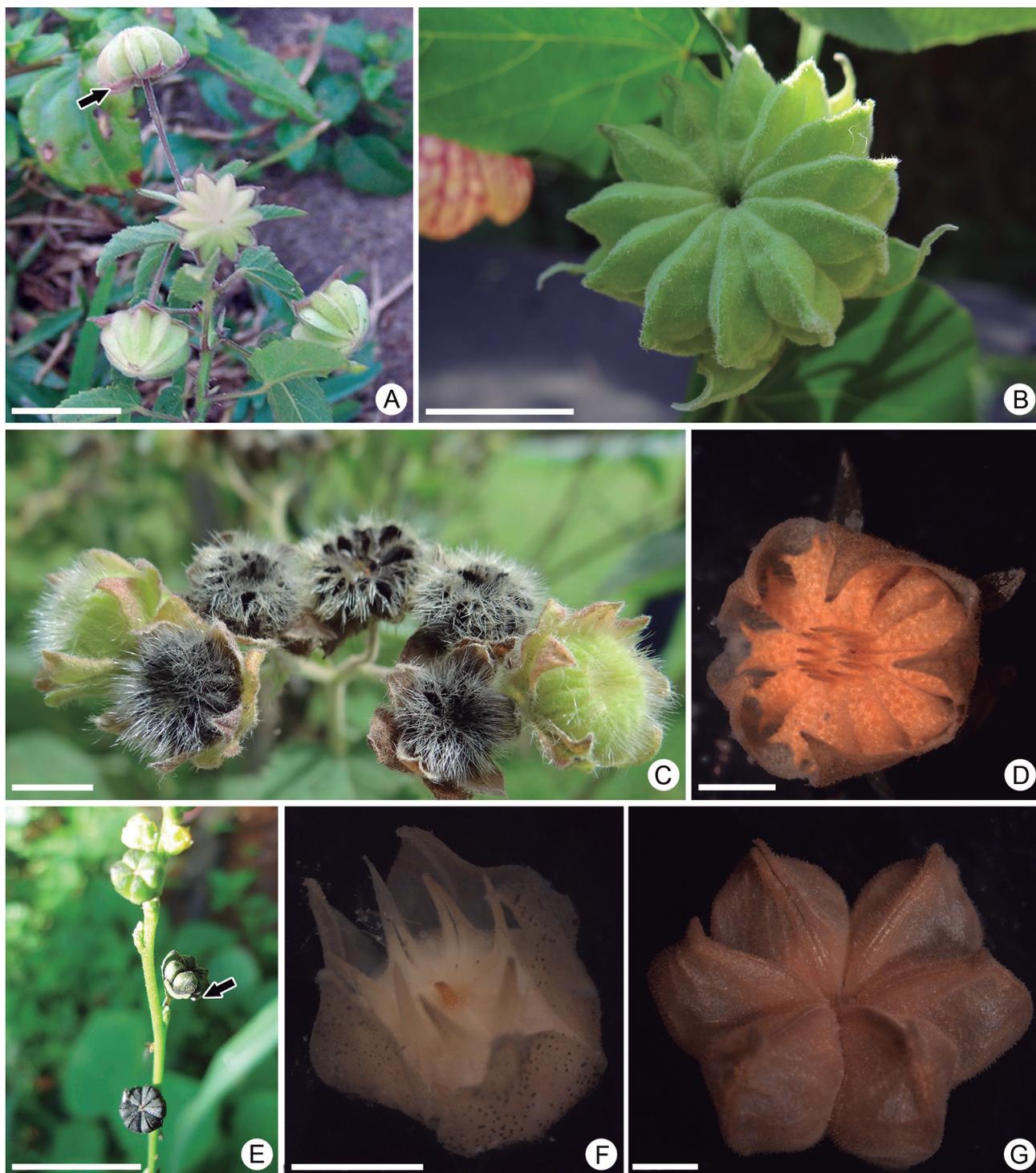
Figure 1. Schizocarps of tribe Malveae. **A** – *Gaya gaudichaudiana*; **B** – *Abutilon bedfordianum*; **C** – *Monteiroa hatschbachii*; **D** – *Malvastrum coromandelianum*; **E** – *Briquetiastrum spicatum*; **F** – *Sida planicaulis*; **G** – *Wissadula contracta*. Arrows indicate the calyx. Scale bar = a – 1 cm; b – 2 cm; c – 1.5 cm; d-f – 2 mm; g – 1mm.

(Fig. 1A-G); with or without endoglossum, or, rarely, with a constriction in the median region of the mericarp; spines present or not, sometimes muticous; with stellate, simple or glandular trichomes, rarely glabrous. The seeds are reniform, with simple trichomes, rarely glabrous. Morphological data analyzed in the present study, along with similarities and differences among species, are summarized in Table 2.

Differences in size ratio between calyx and fruit are evident. The calyx can either reach the median region of the fruit (Fig. 1B), or not reach the median region (Fig. 1A-E-G). It can partially involve the fruit (Fig. 1C), or completely involve the fruit (Fig. 1D-F).

We observed variations of spines (Fig. 2) including: mericarp without spines, *i.e.*, a muticous mericarp (Figs. 1A, 2A) without edges; conspicuous spine in the dorsal portion of the mericarp (Figs. 1G-2H); inconspicuous spine in the dorsal portion of the mericarp (Figs. 1E, 2B-D); inconspicuous spine at the apex of the mericarp (Figs. 1C, 2C-F); two conspicuous apical spines (Figs. 1F, 2E); and three conspicuous spines, one at the apex and two dorsal spines (Figs. 1D, 2G). In *Briquetia denudata*, despite the

inconspicuous spine in the dorsal portion of the mericarp, two basal hook-shaped projections are observed in the mericarp (Fig. 2D). This species also stands out for its reticulated mericarp (Fig. 2D).

The number of seeds per mericarp varies from one seed (Fig. 2A-C) to three seeds (Fig. 2H-J), up to 4-9 seeds per locule (Fig. 2I).

The endoglossum was observed in several taxa in this study, such as *Gaya*, *Briquetiastrum*, and *Wissadula* (Fig. 2I); otherwise, this structure was not observed in species of *Abutilon*, *Briquetia*, *Malvastrum*, *Monteiroa*, *Sida* or *Sidastrum* (Fig. 2C). This structure, when present, can be prominent or conspicuous, as in *Gaya gaudichaudiana*; reduced, as in *Briquetiastrum spicatum* (Fig. 2K); or vestigial, as in *Gaya guerkeana* (Fig. 2A), *G. pilosa* and in *Wissadula* species (Fig. 2H). In *G. gaudichaudiana*, the endoglossum adheres to the pericarp in its basal ventral portion. In this case, the endoglossum surrounds the seed as a whole, and when the mericarp becomes dehiscent, it is released from the columella. In *B. spicatum*, the endoglossum is only a small structure attached in the median portion of the mericarp, but

Table 2. Morphological characteristics of fruits of Malveae tribe species

	Dehiscence	Mericarps	Calyx	Spine - size	Spine - position	Spine - number	Seeds	Endoglossum
Abutilon bedfordianum	partially dehiscent	8-14	median portion of the fruit	conspicuous	dorsal	one	4-9	absent
Abutilon purpurascens	partially dehiscent	8-14	median portion of the fruit	conspicuous	dorsal	one	4-9	absent
Briquetia denudata	completely dehiscent	6-9	below the median region of the fruit	inconspicuous	two basal hook-shaped projections	one	1	absent
Briquetiastrum spicatum	completely dehiscent	5-7	below the median region of the fruit	inconspicuous	dorsal	one	3	reduced
Gaya gaudichaudiana	completely dehiscent	10-12	below the median region of the fruit	muticous	absent	none	1	conspicuous
Gaya guerkeana	completely dehiscent	13-18	below the median region of the fruit	muticous	absent	none	1	vestigial
Gaya pilosa	completely dehiscent	22-28	below the median region of the fruit	muticous	absent	none	1	vestigial
Malvastrum coromandelianum	partially dehiscent	10-12	involve the fruit	conspicuous	one at the apex and two dorsal	three	1	absent
Monteiroa hatschbachii	partially dehiscent	14-16	partially involve the fruit	inconspicuous	apical	one	1	absent
Pseudabutilon benense	partially dehiscent	5	median portion of the fruit	conspicuous	dorsal	one	3	absent
Sida planicaulis	partially dehiscent	7-10	involve the fruit	conspicuous	apical	two	1	absent
Sida santaremensis	partially dehiscent	10-12	involve the fruit	inconspicuous	apical	two	1	absent
Sidastrum micranthum	partially dehiscent	4-6	median portion of the fruit	inconspicuous	apical	one	1	absent
Wissadula contracta	completely dehiscent	4-6	below the median region of the fruit	conspicuous	dorsal	one	3	vestigial
Wissadula excelsior	completely dehiscent	5-7	below the median region of the fruit	conspicuous	dorsal	one	3	vestigial
Wissadula hernandiodes	completely dehiscent	4-6	below the median region of the fruit	conspicuous	dorsal	one	3	vestigial

it plays an integral role in seed dispersal with the apical seeds released before the basal seeds. The endoglossum in species of *Wissadula* (*W. contracta*, *W. excelsior* and *W. hernandioides*) is a scar around the mericarp, dividing the locule (Fig. 2I).

The trichomes of exocarp can be seen in Fig. 3. Apart from glabrous fruits, as one can see in *Sida santaremensis* (Fig. 3A), fruits with trichomes uniformly distributed throughout the exocarp were observed *p.ex.* in *Monteiroa hatschbachii*, *Sidastrum*
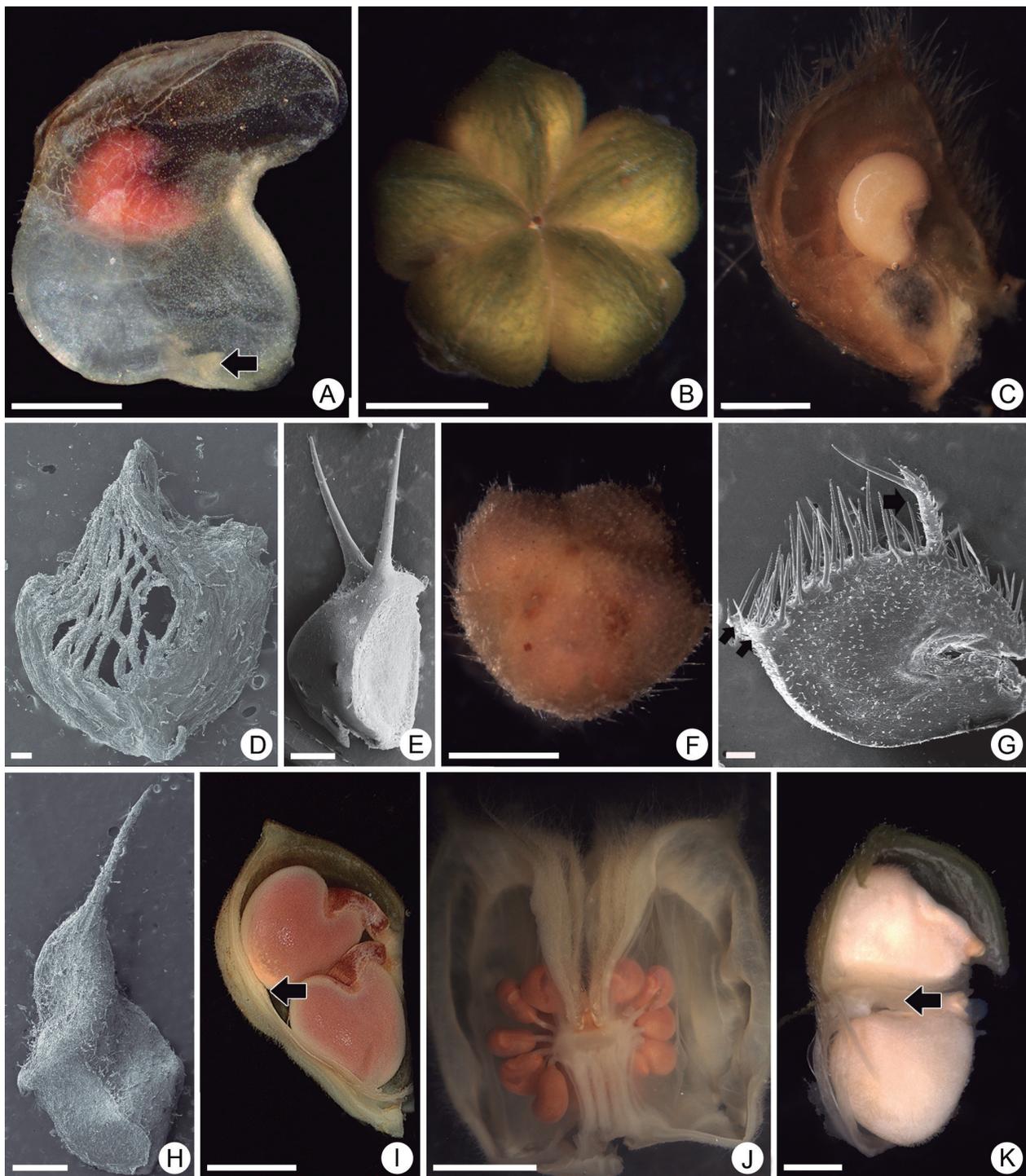
Figure 2. Schizocarps and mericarps of the tribe Malveae. **A** – *Gaya pilosa*, mericarp, lateral view, with seed, with arrow indicating endoglossum; **B** – *Briquetiastrum spicatum*, schizocarp frontal view; **C** – *Monteiroa hatschbachii*, mericarp, internal view, with seed; **D** – *Briquetia denudata*, external view of the pericarp; **E** – *Sida planicaulis*, mericarp; **F** – *Sidastrum micranthum*, schizocarp frontal view; **G** – *Malvastrum coromandelianum*, mericarp, lateral view; **H** – *Pseudoabutilon benense*, mericarp, lateral view; **I** – *Wissadula hernandioides*, mericarp, lateral view, with seeds, with arrow indicating endoglossum; **J** – *Abutilon purpurascens*, schizocarp, lateral view, with seeds; **K** – *Briquetiastrum spicatum*, mericarp, lateral view, with seeds; arrow indicating the endoglossum. Scale bar = a-c, f – 2 mm; e, g-h – 1 mm; d, g – 200 μm; i-k – 2cm.

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micranthum, and *Pseudoabutilon benense* (Fig. 2C-F-H). In *Malvastrum coronandelianum*, trichomes were only recorded in the apical portion of the mericarps (Fig. 2G). Intraspecific variations of trichomes were observed in the fruits such that the same species present different types of trichomes, such as multiangulate stellate sessile trichomes (Fig. 3B-C), trichomes with two to four arms (Fig. 3D-F), simple short (Fig. 3G) or long trichomes (Fig. 3H), and glandular trichomes (Fig. 3C-F).

The cells of the exocarp are polygonal (Fig. 4), and the cuticle may vary by the slightly oblique striae (Fig. 4A), parallel striae (Fig. 4B-D), cuticle without ornamentation in periclinal outer surface and raised corners in anticlinal walls (Fig. 4C), and cuticle without definite orientation (Fig. 4E).

In the endocarp (Fig. 5), trichomes were only found in *Abutilon berfordianum* (Fig. 5A). In this species, the sparsely
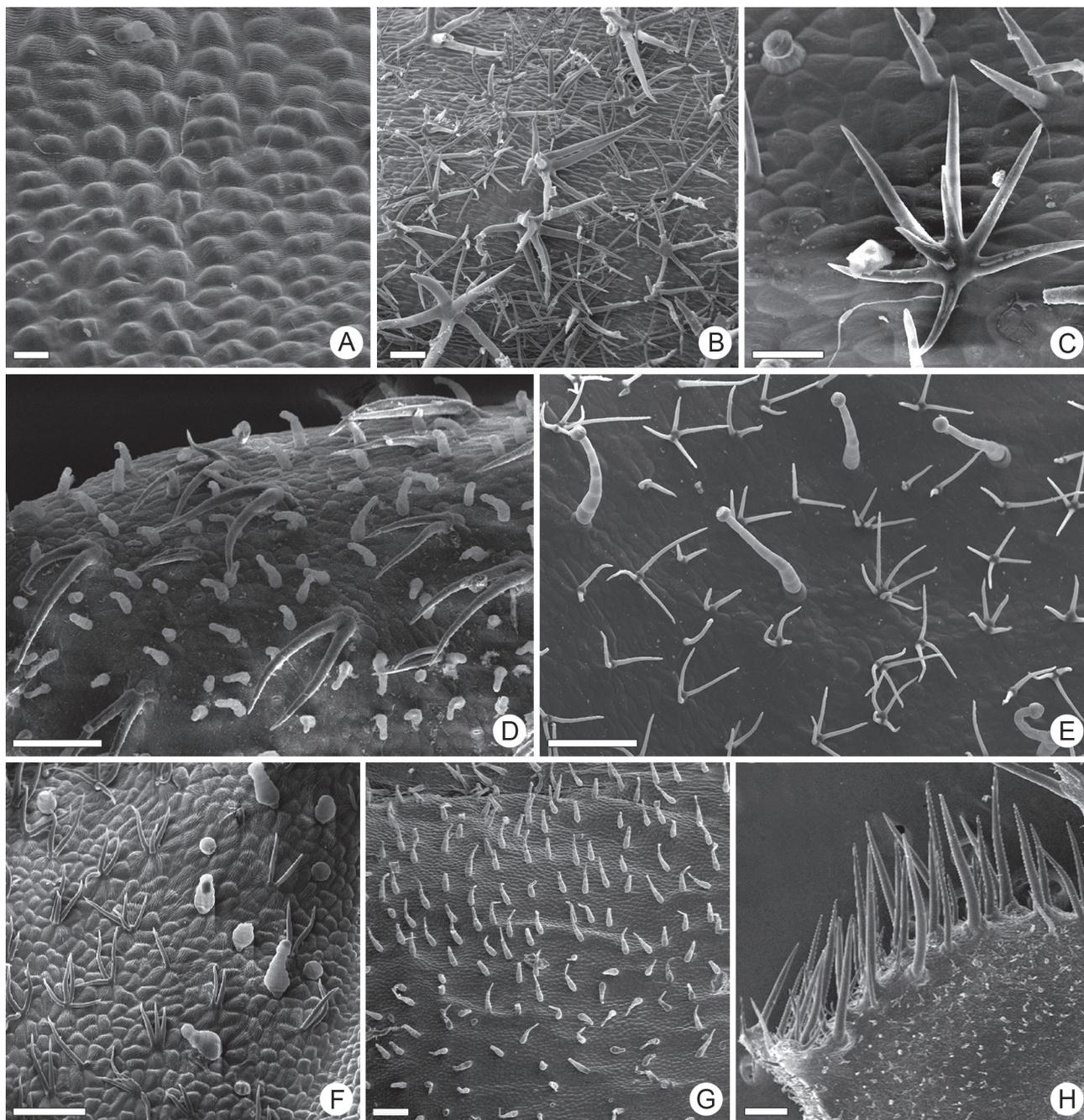
Figure 3. Micromorphology of exocarp of the tribe Malveae, under SEM, evidencing the trichomes. **A** – *Sida santaremensis*, exocarp glabrous; **B** – *Abutilon bedfordianum*, multiangulate stellate sessile trichomes; **C** – *Wissadula contracta*, multiangulate stellate sessile and glandular trichomes; **D** – *Briquetiastrum spicatum*, **E** – *Gaya gaudichaudiana* and **F** – *S. planicaulis*, trichomes with two to four arms and glandular trichomes; **G** – *W. hernandioides*, simple trichomes; **H** – *Malvastrum coromandelianum*, simple long trichomes. Scale bar = a – 20 µm; b, e, g – 100 µm; c – 50 µm; d, f – 10 µm; h – 200 µm.

distributed trichomes can be simple and glandular. The cells of the endocarp can be considered elongated with parallel cuticle striations (Fig. 5A-B-E-F). In *Sida santaremensis*, endocarp cells present random orientations of cuticle (Fig. 5C).

In *Wissadula hernandioides*, projections can be seen at the ends of cells, which overlap (Fig. 5D). No ornamentation of the cuticle was observed in the endocarp of any analyzed species (Fig. 5A-F).
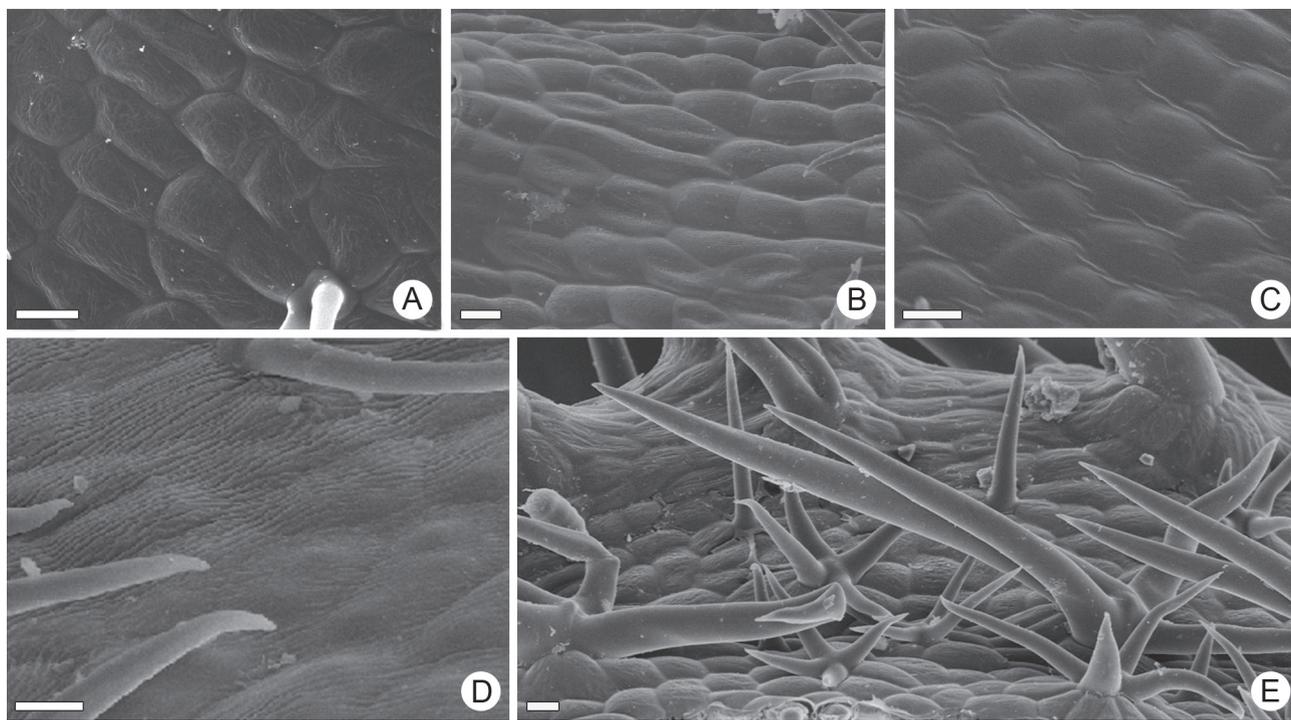
Figure 4. Detail of exocarp cells in the tribe Malveae under SEM. **A** – *Gaya gaudichaudiana*, slightly oblique striae ornamentation; **B** – *Abutilon bedfordianum*, parallel striae; **C** – *Wissadula hernandioides*, no ornamentation; **D** – *Sida planicaulis*, parallel striae; **E** – *Malvastrum coromandelianum*, cuticle without definite orientation. Scale bar = a-b, e – 20 μm; c – 10 μm; d – 5 μm.
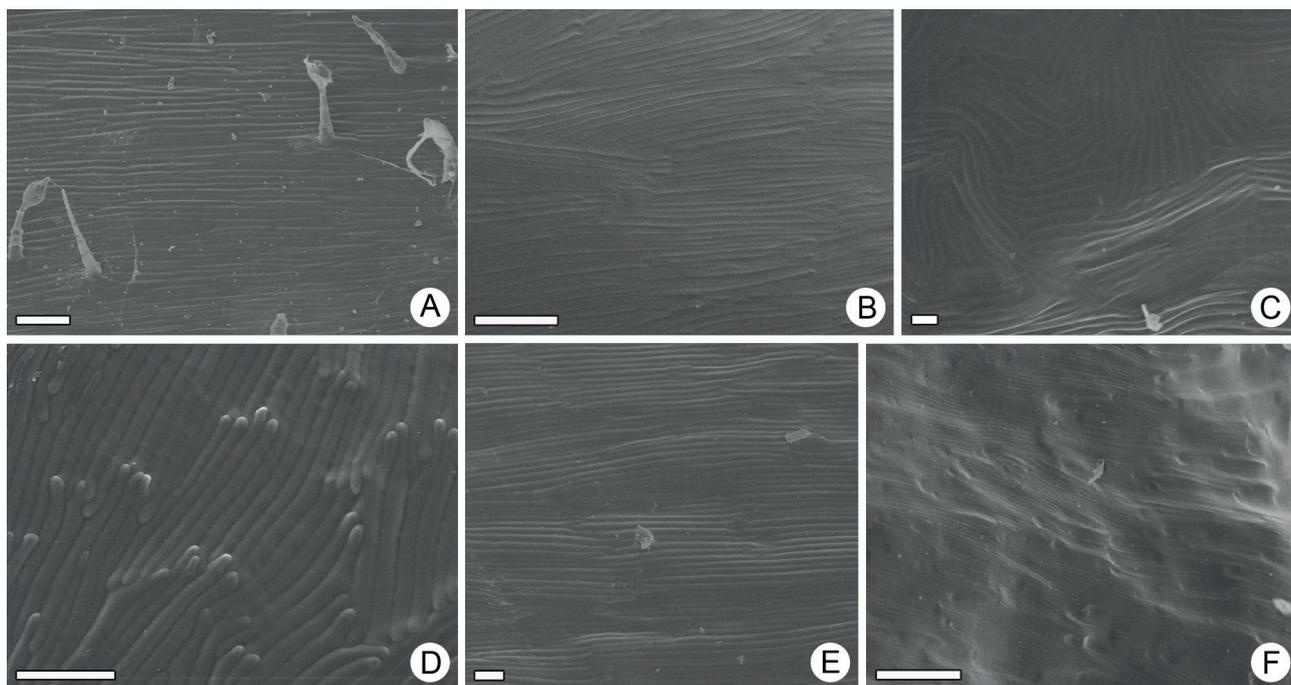
Figure 5. Detail of endocarp cells of the tribe Malveae under SEM. **A** – *Abutilon bedfordianum*, simple and glandular trichomes. Glabrous endocarp in **B** – *Malvastrum coromandelianum*; **C** – *Sida santaremensis*; **D** – *Wissadula contracta*; **E** – *W. hernandioides*; **F** – *Monteiroa hatschbachii*. Scale bar = a, f – 100 μm; b-c – 20 μm; d-e – 50 μm.

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About the seeds (Fig. 6), trichomes can be seen (Fig. 6A-F), and they differ in type and arrangement among species. Simple trichomes were observed on the testa (Fig. 6A-C) and/or hilum of the seed (Fig. 6D-F). Simple, multiangulate stellate or bi-armed trichomes (Fig. 6G-H) were seen on the testa, or even glabrous seeds. The cells of the testa are polygonal (Fig. 6H) and may have sinuous walls (Fig. 6H). In all cases, the cuticle has no ornamentation (Fig. 6H).

Discussion

The Malveae tribe has schizocarp fruits with dehiscent mericarps, which present morphological variations, mainly in relation to dehiscence (Spjut 1994; Barroso *et al*. 1999), which agrees with the results obtained herein. Dehiscent mericarps release or expose the seeds at the opening of the pericarp (Roth 1977). This characteristic
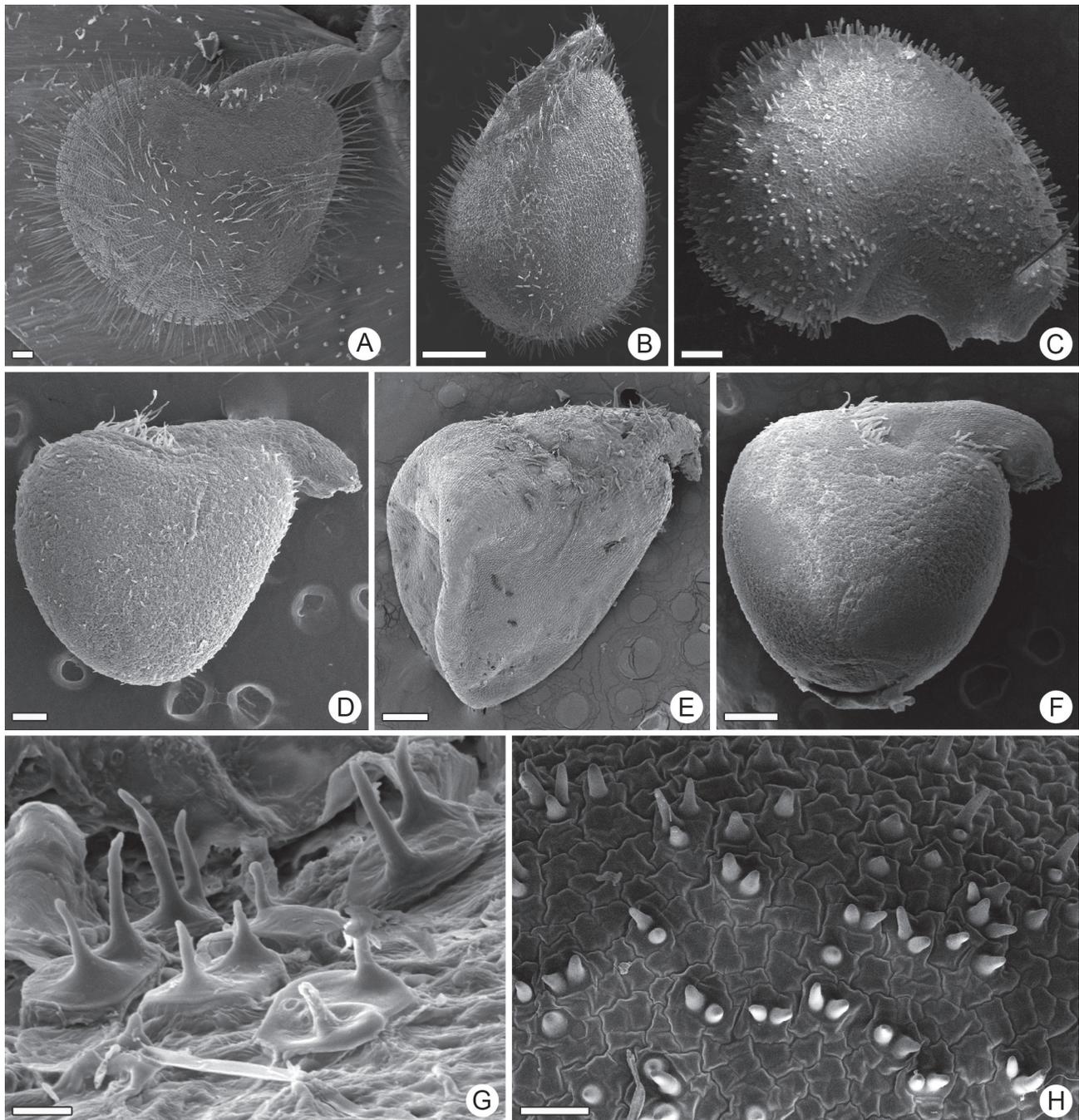
Figure 6. Seeds of the tribe Malveae under SEM. **A** – *Abutilon bedfordianum*; **B** – *Gaya gaudichaudiana*; **C**, **H** – *Monteiroa hatschbachii*; **D** – *Wissadula excelsior*; **E** – *Sida santaremensis*; **F** – *W. hernandioides*; **G** – *Pseudoabutilon benense*. **A** and **C** – simple trichomes in testa and hilum; **D** and **F** – simple trichomes in hilum; **G** and **H** – detail of seed coat, with multiangulate stellate in G and bi-armed trichomes in H. Scale bar = a, c, e-f – 200 μm; b – 500 μm; d, g-h – 50 μm.

is not considered homologous during the evolution of the tribe, as it appears several times throughout the phylogeny (Tate *et al*. 2005). In particular, this characteristic was found in *Briquetiastrum spicatum*, *Gaya gaudichaudiana*, and in the species of *Wissadula* studied here. The presence of schizocarp fruits with complete dehiscence of mericarps was observed, whereas in the studied species of *Abutilon*, *Malvastrum coromandelianum*, *Monteiroa hatschbachii*, and species of *Sida* and *Sidastrum micranthum*, the opening of the mericarp is just partial.

Several proposals, such as Spjut (1994), Barroso *et al*. (1999) and Souza (2006) classify schizocarp fruits. According to Spjut (1994), schizocarp fruits of the Malvaceae include Achenarium, Camarium, Coccarium, and Druparium, and for Malveae, he includes Camarium and Coccarium (Spjut 1994). They differ by number of seeds and type of dehiscence of the mericarp. The fruits of Malveae herein analyzed represent the Coccarium type. This classification agrees with that of Muneratto & Souza (2013) for *Sida rhombifolia*, *S. regnelli* and *S. urens*, as well as *Wissadula* by Spjut (1994).

The size of calyx of the species studied is directly related to the size of the fruits and presence, or not, of the epicalyx, and it is extremely relevant to circumscriptions of the genera. The presence of epicalyx is fundamental in the recognition of *Malvastrum coromandelianum* and *Monteiroa hatschbachii*. Bello *et al*. (2016) demonstrate that such structure can provide ovary protection, pollinator attraction and / or seed dispersal. Tate *et al*. (2005) suggest segregation into two monophyletic clades, depending on the absence or presence of the epicalyx. The results presented here also highlighted the lack of morphological characters to support the relationships among alliances (*sensu* Tate *et al*. 2005), indicating that more research is needed.

In the dehiscence of a schizocarp into mericarps, only parts of the fruit are separate from each other so that no total opening takes place (Roth 1977). This morphological characteristic was observed in the species herein analyzed. In these fruits, a portion of the mericarp (usually apical) separates, then the total dehiscence of the mericarps is unnecessary. However, in *Sida* species, the dehiscence of the mericarp does not allow for seed dispersal; therefore, the mericarp itself functions as a diaspora (Barroso *et al*. 1999). No total opening has been confirmed here for *Malvastrum coromandelianum* and *Sidastrum micranthum*. In *Gaya gaudichaudiana*, seed dispersal is closely related to the endoglossum, which is prominent. In this species, the mericarp as a whole (pericarp and seed) acts as a unit of dispersion (Masullo *et al*. 2019). According to Bovini & Baumgratz (2016), the dehiscence of the mericarp in *Wissadula* occurs in the apical-basal direction, first releasing the two collateral seeds and later the basal seed, only after the total opening of the mericarps. For Areces-Berazain & Ackerman (2017), these dehiscence characteristics may confer additional protection against seed desiccation and

predation, being modified to facilitate dispersion by different vectors as also observed here in *Briquetiastrum spicatum*.

Besides the absence of endoglossum and one seed per mericarp in *Briquetia*, Bovini (2015) bases the difference between *Briquetiastrum* and *Briquetia* on the presence of hook-shaped structures at the basal portion of the mericarp in relation to seed dispersal and diaspora. In addition, the reticulated mericarp is established as an exclusive feature of *Briquetia*, which has been confirmed here.

For the genus *Wissadula*, each mericarp usually presents a well-developed spine. Rare species show muticous mericarps, and according to Bovini & Baumgratz (2016), the size of the spine has diagnostic value for species distinction (Bovini & Baumgratz 2016). In addition, studies of Monteiro (1936), Fryxell (1992), Esteves (2001) and Krapovickas (2007, 2014) have already demonstrated spines as an important structure for the delimitation of Malvaceae species *sensu stricto*.

Furthermore, mericarp dehiscence and morphology, as well as position and number of seeds, can be considered diagnostic for genera circumscription, as observed for *Wissadula* (Bovini & Baumgratz 2016), *Briquetia* and *Briquetiastrum* (Bovini 2015). These characteristics have remained frequent among species of the same genus and even for similar genera, as observed here for *Briquetiastrum* and *Wissadula*, which have three seeds, two apical collateral and one basal. However, in *W. stipulata*, a species not analyzed in this study, the mericarp possesses a single seed, which includes species in another taxonomic section in the same genus (Bovini 2009; Bovini & Baumgratz 2016). Bovini (2009) comments that species with only one seed results from the existence of an abortion in the collateral ovules, developing only the basal seed. Between *Sida* and *Sidastrum*, each present a single seed occupying the entire loci of the mericarp, and this close relationship was indicated in the phylogeny of Tate *et al*. (2005).

To understand evolution in the number of seeds per mericarp, uniseminated versus multiseminated divergences were observed in Malveae. Multiseminated mericarps are predominant in the Gossypieae and Hibisceae tribes, and uniseminated mericarps in the Malvavisceae and Decaschistieae tribes (Bates 1968). However, in Malveae, multi-and uniseminated mericarps with about one to five seeds are observed, as seen herein for *Wissadula*, which has three seeds, two are apical collateral, and one is basal. *Sida* and *Sidastrum* present a single seed occupying the entire locule of the mericarp. According to Bates (1968), the uniseminated condition in Malveae derives from multiseminated fruits. According to Aguilar *et al*. (2003), in the phylogeny constructed from ITS fragment, the number of seeds per mericarp is an important condition for the circumscription of genera in Malveae, indicating that fruits with many seeds have evolved several times in Malveae. The high number of carpels, also common in this tribe, may be correlated with speciation (Areces-Berazain & Ackerman 2017). However, according to Heel (1978), in some genera,

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such as *Pavonia*, *Malvaviscus* and *Urena*, the low number of carpels may be related to their abortive state during their development, presenting 10 carpels at the beginning of the development. However, five carpels are aborted with only five carpels remaining.

The morphology of fruits and seeds is extremely relevant for *Wissadula* (Bovini & Baumgratz 2016) because the genus can be circumscribed by the combination of a small constriction in the mericarp and the positioning and arrangement of the seeds. However, such constriction in the fruit is not exclusive to *Wissadula*. It is also found in *Allowissadula*, *Bastardiastrum*, *Briquetia*, *Briquetiastrum*, *Phragmocarpidium*, *Pseudabutilon* and *Tetrasida*, e.g., (Bovini & Baumgratz 2016). This constriction can divide the mericarp into two parts. This internal structure has already been described historically as an internal appendage in the mericarp and defined as endoglossum by Hochreutiner (1920). According to Fryxell (1988), this structure is considered as a protrusion of the inner wall of the mericarp, a term also recognized by Krapovickas (1970) and Barroso *et al.* (1999). The presence or absence of this structure and its size, as well as the arrangement of the seeds in the mericarp, define genera in Malveae (Bovini & Baumgratz 2016). In *Gaya gaudichaudiana*, for example, the endoglossum is prominent, according to the descriptions of Takeuchi & Esteves (2017) and Masullo *et al.* (2019), but this structure is vestigial in *Gaya guerkeana* and *G. pilosa*, as presented here and according to Takeuchi & Esteves (2017). In *Briquetiastrum spicatum*, it is reduced (Bovini & Baumgratz 2016). According to these authors, for *Wissadula*, the presence of the endoglossum cannot be considered because it only appears as a continuous thickened line surrounding the mericarp. Takeuchi *et al.* (2018) agree with Bovini & Baumgratz (2016) and mention that the genus *Wissadula* does not present an endoglossum, but only a constriction in its mericarp. In the present study, we propose that the presence of constriction is a character related to the existence of a vestigial endoglossum. This condition was also observed here for *W. contracta*, *W. excelsior* and *W. hernandioides*, and it is therefore considered as a reduced, *i.e.*, vestigial, endoglossum. This suggestion agrees with the proposal of Barroso *et al.* (1999).

Seeds and fruits provide characters with taxonomic value because they have both morphological and micromorphological complexity (Carvalho *et al.* 1999; Lange & Bouman 1999; Plaza *et al.* 2004; Ritter & Miotto 2006; Guimarães *et al.* 2007; Mostafavi *et al.* 2013). In the species analyzed here, simple trichomes, multiangulate stellate sessile, trichomes with two to four arms, and glandular trichomes were all observed. The main variations observed here were found among the *Abutilon* and *Sida* species, and no uniformity was observed for the types of interspecific trichomes. Among the species analyzed in this study, the presence of trichomes in endocarp was not observed, except in *Abutilon bedfordianum*. The presence of trichomes in

the endocarp was recorded in the literature for species of *Oncidium* (Mayer *et al.* 2011). In *Crotalaria*, this character has value in systematics of the group (Roux *et al.* 2011).

The presence of trichomes in the seeds can be found in such groups as Malvaceae (Malveae), Apocynaceae (Asclepiadaceae) and Salicaceae (Werker 1997). Thus, for Malveae, in general, the presence of single and long trichomes in the hilum and / or seed coat was shown to be a persistent character in the group (Werker 1997). This characteristic was also observed for most species studied here, except for *Briquetiastrum spicatum*, which presents, in addition to simple trichomes, multiangulate stellate sessile trichomes on the seed coat, and for *Malvastrum coromandelianum* and *Sidastrum micranthum*, which have glabrous seeds. Variations in seed trichomes were also recorded for *Sida* by Muneratto & Souza (2013). These authors consider micromorphological characteristics of the seeds as potentially valuable for characterization of *S. rhombifolia*, *S. regnelli* and *S. urens*. In order to confirm the relevance of the results of Muneratto & Souza (2013), we also observed significant differences in relation to the types of trichomes in the seeds in *S. planicaulis* and *S. santaremensis*. More specifically, we noted simple trichomes in the hilum of *S. planicaulis*, and simple and bi-armed trichomes in *S. santaremensis*.

From our study, some morphological characters were shown as potential contributors to systematics or phylogenetic studies for Malveae. These characters include morphology and quantity of the spines, number and position of seeds per mericarp, as well as the presence and type of trichomes in exocarp and seeds. In addition, the presence or absence of the endoglossum, which, when present, may be conspicuous (occupying the whole locule of the mericarp), reduced (separating the mericarp in two) or vestigial (like a scar that separates). This structure proved to be one of the most striking characters, indicating its systematic and phylogenetic potential since it is useful in the circumscription of the genera based on its relevance to the study of the ontogeny of this structure to verify the homologies between the genera.

The combination of fruit and seed characters determines the generic limits since the taxa have morphological vegetative proximity. At times, one or more characters may overlap, and only the overlapping set may clarify the existing relationship.

Acknowledgements

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