

Morphology of fruits, seeds, seedlings and saplings of three species of *Macrolobium* Schreb. (Leguminosae, Caesalpinioideae) in the Brazilian Amazon floodplain¹

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ABSTRACT

The evaluation of the post-germination phases of plants allows the recognition of transitional structures that support the relationships among taxa and their establishment. Together with fruit and seeds, seedlings and saplings provide useful characters for identifying many species. This study aimed to describe and characterize the morphology of the fruits, seeds, seedlings and saplings of *Macrolobium acaciifolium*, *M. bifolium* and *M. pendulum*, as well as to evaluate the ecological, taxonomic and phylogenetic value of the structures identified. In this work, the seeds were sown in plastic trays with sterilized sand and sawdust, without pre-germination treatment. The fruits of the three species are woody legumes, dehiscent fruit or indehiscent fruit. The seeds have seed coats with or without venation and variable embryos, with plumules differing among the three species; this trait can be helpful in distinguishing among the species studied. The seedlings are of the cryptocotylar-hypogeal-reserve or phanerocotylar-epigeal-reserve type. *Macrolobium bifolium* and *M. pendulum* are similar species, differing in only a few characters. These characters have taxonomic value and aid species identification. The characteristics of *M. pendulum* are described here for the first time.

Key words: Detarieae, embryo, Fabaceae, plumule, post-germination development

Introduction

The morphological aspects of the initial stages of plant development have been poorly investigated in various families, principally when compared with the structure of mature vegetative organs. The study of the initial morphology provides knowledge about transitional or ephemeral structures that can supply relevant insights into phylogenetic relationships (Moreira-Coneglian & Oliveira 2006). Likewise, the morphological characters of fruits and seeds constitute highly reliable criteria for botanical identification, because they normally have little phenotypic plasticity and are therefore good taxonomic characters (Oliveira & Pereira 1984; Oliveira 1999a). In addition, data about seedlings, fruits and seeds can contribute information that is valuable for analyzing the systematics and ecology of various groups of tropical plants (Garwood 1995).

Morphological studies of fruits, seeds, seedlings and saplings have helped the characterization of several taxonomic groups in Leguminosae. In Caesalpinioideae, details have been presented for *Copaifera* (Gurgel 2009). In Mimosoideae, *Calliandra* and *Mimosa* have been evaluated (Parra 1984). In Papilionoideae, there have been studies of Phaseoleae (Baudet 1974); Dalbergieae (Lima 1989-90); Genisteae (López *et al.* 1998); Phaseoleae, Sophoreae, Swartzieae and Tephrosieae (Oliveira 2001); *Vatairea* (Rodrigues & Tozzi 2007a); the genistoid clade (Rodrigues & Tozzi 2007b); *Acosmium, Guianodendron* and *Leptolobium* (Rodrigues & Tozzi 2008); and *Rhynchosia* (Rodrigues *et al.* 2012). The studies of Duke & Polhill (1981), Oliveira (1999a) and Gurgel *et al.* (2012) evaluated various genera within the three subfamilies.

Although Leguminosae is a well-known family, there have been few studies of its representatives in the Amazon, notable exceptions including studies conducted in the Venezuelan Amazon (Ricardi 1996; 1999a; 1999b) and in the Brazilian Amazon (Silva *et al.* 1988; Vieira *et al.* 1996; Aguiar & Mendonça 2000; Gurgel *et al.* 2002; Ramos & Ferraz 2008; and Rodrigues *et al.* 2012). There is also a lack of data on seedlings that occur in specific environments of the Amazon, such as the floodplain forests, where species are subjected to periodic flooding (Silva *et al.* 1988; Moreira &

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Moreira 1996; Gama *et al.* 2003; Maia *et al.* 2005; Schöngart *et al.* 2005). Such knowledge is important to protecting and understanding the regeneration of these ecosystems.

Macrolobium Schreb. (Leguminosae, Caesalpinioideae) is currently included in Detarieae *s.l.* (Bruneau *et al.* 2000; 2001; Herendeen *et al.* 2003). The tribe Detarieae *s.l.*, comprises all of the genera included in Detarieae, Cynometreae and Amherstieae (Léonard 1957); in Detarieae and Amherstieae (Cowan & Polhill 1981); in Detarieae (Polhill 1994); and in Detarieae and Macrolobieae (Breteler 1995), excluding the monotypic genus *Umtiza* Sim, which occurs in Southern Africa (Herendeen *et al.* 2003).

Macrolobium comprises approximately 80 species and is strictly distributed in the tropics (De la Estrella *et al.* 2012). Approximately 40 species occur in Brazil, 15 of which are endemic (Martins-da-Silva & Lima 2013). *Macrolobium* is the second most representative genus of Detarieae *s.l* (Lewis *et al.*, 2005), being used as an ornamental, for timber, to produce fish poison and for lumber in construction (Gama *et al.* 2003; Mackinder 2005; Felix-da-Silva *et al.* 2013). The genus is common in the Brazilian Amazon, mostly in the Negro River Basin, where it constitutes one of the dominant floristic elements of floodplain forests (Ducke 1949).

The phylogenetic relationships of Detarieae s.l. were analyzed by Bruneau et al. (2000; 2001), on the basis of trnL nucleotide sequence data, and by Herendeen et al. (2003), who used morphological data merged with the aligned *trn*L data. Detarieae *s.l.* has a pantropical distribution, approximately 58% of the species being restricted to Africa, including Madagascar, 20% being endemic in the Neotropics; and 12% being endemic in tropical Asia (Mackinder 2005). The genus Macrolobium is at the base of the "higher" Detarieae s.l., constituting a group together with species of the genera Brownea Jacq., Browneopsis Huber, Elizabetha Schomb. ex Benth., Paloue Aubl. and Ecuadendron D.A. Neill. (Herendeen et al. 2003). This underscores the statement made by Bruneau et al. (2000): that the Macrolobium group (sensu Cowan & Polhill 1981) or complex (sensu Léonard 1957) has a complicated history. Bruneau et al. (2000) also stated that the relationships of the Macrolobium group requires a critical evaluation of morphological and anatomical characters in order to examine the possibility of a close affinity between New World Macrolobium and members of the South American Brownea group.

The Environmental Protection Area of Combu Island (EPA of Combu Island), in the state of Pará, Brazil, presents a varied floristic structure and composition (Rodrigues *et al.* 2006). *Macrolobium bifolium* (Aubl.) Pers. is native to the Amazon region and has been recorded for the Combu Island EPA (Maúes *et al.* 2011). *Macrolobium acaciifolium* (Benth.) Benth. has a wide distribution in Brazil, and *M. pendulum* Willd. ex Vogel is endemic in the country, occurring in the states of Amazonas, Pará and Maranhão (Martins-da-Silva & Lima 2013); both species represent new records for the Combu Island EPA. The present study describes the morphology of fruits, seeds and the post-germination phases of *Macrolobium acaciifolium*, *M. bifolium* and *M. pendulum*, aiming to aid the identification of native species of Amazon floodplain forests and to provide a foundation for further phylogenetic and ecological studies involving this complex group.

Material and methods

Fruits and seeds of *Macrolobium acaciifolium*, *M. bifolium* and *M. pendulum* were collected from natural populations in the Combu Island EPA (48°25'W; 1°25'S). The area is entirely constituted of flooded forest (alluvial rain forest) and presents Humic Gleysols, with high percentages of silts and clay and a low percentage of sand (Silva & Sampaio 1998). According to the Köppen classification system, the climate of the region is type Am, with a mean annual rainfall of 2500 mm and a mean annual temperature of 27°C (Jardim & Vieira 2001).

Two matrix trees were selected for each *Macrolobium* species studied. The fruits were collected between January and April 2012, from directly under the trees or with a trimmer. The fruits were packed into polyethylene bags and transported to the Laboratory of Fruit and Seed Morphology of the Museu Paraense Emílio Goeldi for detailed analysis and measurement. Voucher specimens were deposited in the Herbarium of the Museu Paraense Emílio Goeldi, in Belém, Brazil (MG), under the accession numbers MG-204242 (*M. acaciifolium*), MG-204243 (*M. bifolium*) and MG-204244 (*M. pendulum*).

Samples (30 fruits and 50 seeds of each species) were randomly collected and analyzed. The dimensions (length, width and thickness) were measured with an UltraTech[™] digital fractional caliper (0.01 mm accuracy; General Tools, New York, NY, USA). The length was considered the distance from the apex to the base; the width was measured from the dorsal to ventral regions, and the thickness between valves was determined. For observation and illustration of fruits and seeds, we used a stereomicroscope (Motic, SMZ-168 series, Vancouver, Canada) and a camera lucida. The terminology was based on Gunn (1981; 1991), Barroso *et al.* (1999) and Oliveira (1999b).

For the description of plumule development, three embryos of each species were selected and samples of the embryo axis were fixed in 2.5% glutaraldehyde in 0.1 M sodium phosphate buffer pH 7.2 for 24 h. The samples were then dehydrated in a graded ethanol series, dried in a CO₂ critical point dryer, sputter-coated with gold (Robards 1978) and analyzed in a scanning electron microscope (1450VP; LEO Electron Microscopy Ltd, Cambridge, UK). The morphology of each plumule was described according to Oliveira (1999b), considering the types undifferentiated, rudimentary, moderately differentiated and well differentiated.

For the post-germination study, 30 seeds of each matrix tree, without pre-germination treatment, were sown in

plastic trays ($80 \times 40 \times 20$ cm) containing sterilized sawdust and sand (1:1) at a depth of ± 1 cm, maintained at room temperature and in natural light in a greenhouse (average temperature, 26°C). After the expansion of the second eophyll, the saplings were transplanted to polyethylene bags that were filled with a mixture of sand and vermiculite (1:1), after which they were watered once a day.

We defined the seedling phase as that occurring between the protrusion of the primary root and the full expansion of the eophylls of the first node (sensu Oliveira 2001). Voucher specimens of *Macrolobium* saplings collected at 40 days after germination were prepared and deposited in MG under the accession numbers MG-204245 (*M. acaciifolium*), MG-204246 (*M. bifolium*) and MG-204247 (*M. pendulum*). Some specimens were preserved in 70% ethanol to show the different stages of post-germination development.

To describe the morphology of seedlings and saplings, we selected 20 samples of each species and we photographed each sample with a digital camera (FinePix S4500; FUJIFILM do Brazil, São Paulo, Brazil). The structure of the hypocotyl, epicotyl, cotyledons, cataphylls and eophylls was described. The terminology for the seedling morphological types—crypto-cotylar-hypogeal-reserve (CHR) and phanerocotylar-epigeal-reserve (PER)—followed Garwood (1996), and descriptive terms were based on Radford *et al.* (1974) and Harris & Harris (2001). We also employed the terminology established by Camargo *et al.* (2008), describing seedlings according to the unipolar or bipolar emergence of the root and epicotyl. The saplings were evaluated until the complete expansion of the third eophyll, as adopted for other Leguminosae species by Rodrigues & Tozzi (2008) and Rodrigues *et al.* (2012).

Results

The quantitative and qualitative data related to fruits, seeds and seedlings are summarized in Tab. 1 and 2, respectively. The fruits of *Macrolobium acaciifolium* (Fig. 1 and 2), *M. bifolium* (Fig. 3 and 4) and *M. pendulum* (Fig. 5 and 6) are woody legumes, dehiscent fruit or indehiscent fruit (Tab. 2), all of which are subapiculate and substipitate. The funiculus is flattened, and the seeds are transversally disposed (Fig. 2, 4 and 6).

The seeds are brownish and laterally compressed, variable in form (Fig. 7-9, Tab. 2), with or without conspicuous venation; the micropyle is inconspicuous and the hilum is basal and elliptical. The endosperm is absent, and the cotyledons are storage organs that are juxtaposed, symmetric or asymmetric, and plano-convex, the abaxial surface being sinuate or entire (Fig. 7-9, Tab. 2). The embryos are investing, and the embryo axis is straight or oblique, oblong or conical (Fig. 10-12, Tab. 2). Among the three species, plumules vary from well differentiated, to moderately differentiated and undifferentiated (Fig. 13-15).

All of the seeds we tested germinated. The morphological aspects of seedlings and saplings of *Macrolobium*

acaciifolium, M. bifolium and M. pendulum can be seen in Fig. 16-21, Fig. 22-29 and Fig. 30-35, respectively. The germination of all species began with the rupture of the seed coat in the hilum-micropyle region and the emergence of the primary root, which is whitish, non-tuberose and cylindrical (Fig. 16, 22 and 30). The hypocotyl is cylindrical or quadrangular (Fig. 28). The seedlings are type CHR (Fig. 16-19) or PER (Fig. 22-26 and 30-33). The emergence of the primary root and epicotyl is unipolar. The vegetative axis is lateral to the cotyledons (Fig. 17) or between them (Fig. 24 and 32). All three species presented an alternate arrangement of the eophylls (Fig. 21, 29 and 35). In all three species, the eophylls of the three first nodes were very similar, occurring as even-pinnate (Fig. 20 and 21) or bifoliolate (Fig. 27, 29 and 35) and variable in form. In young eophylls, we observed pairs of stipules that are axillary, filiform and free between them; the stipules are caducous (Fig. 21 and 29) or persistent (Fig. 35). Nyctinastic movement is observed in all species, in which the leaflets are "forward-folding".

Macrolobium acaciifolium (Benth.) Benth.-The fruit is indehiscent, woody, oblong to oval, flattened, sparsely pilose at the margins, without constrictions, substipitate, with an oblique base, apex obtuse and rounded with a short apiculus (Fig. 1-2). The pericarp is externally shiny and slightly rough, with red-brown to brown dots, and internally spongy and brown. The seed is oblong to elliptical (Fig. 2), laterally compressed (Fig. 7), red-brown, with smooth surface (Fig. 2 and 7), radicular lobe poorly pronounced, without seed appendages; micropyle, lens and raphe inconspicuous. The embryo is cream-colored, with symmetrical storage cotyledons that are sinuate, juxtaposed (Fig. 7) and strongly adhered to each other. There is no endosperm; only residues can be seen around embryo axis, which is conical, two-thirds exposed and oblique to the cotyledons (Fig. 10). The plumule is well differentiated (Fig. 13), and the seedling is type CHR (Fig. 16-20). The germination is unipolar, and the vegetative axis is lateral to the cotyledons (Fig. 17). The hypocotyl is cylindrical, whitish and glabrous. The epicotyl is cylindrical, light green and glabrous. The axillary buds are inconspicuous; the first three eophylls are alternate, even-pinnate, with glabrous pulvini, petioles and rachises. Leaflets are oblong, with oblique bases, retuse to emarginate apices, entire margin; a small pulvinule occurs at the base of each leaflet.

Macrolobium bifolium (Aubl.) Pers.—The fruit is dehiscent, woody, oblong to spatulate, flattened, glabrous, without constrictions, substipitate, with an oblique base, truncate to obtuse apex with a short apiculus (Fig. 3 and 4). The pericarp is externally opaque, reticulate, light brown to brown; internally spongy, cream-colored to brown. The seed is oval to orbicular (Fig. 4), laterally compressed (Fig. 8), light brown, symmetric, with evident seed coat venation;

Character	Statistic	M. acaciifolium	M. bifolium	M. pendulum
Fruit length	minimum	50.00	91.08	64.40
	maximum	62.00	108.10	80.79
	average	55.09	100,35	73.45
	standard deviation	3.76	5.96	6.50
Fruit width	minimum	36.00	54.55	38.00
	maximum	41.47	62.71	55.00
	average	39.14	57.63	49.43
	standard deviation	1.82	2.94	6.14
Fruit thickness	minimum	8.00	13.15	5.00
	maximum	10.14	14.58	8.30
	average	9.31	13.95	6.51
	standard deviation	0.70	0.51	1.17
Seeds per fruit		1	1 (2-3)	1-2
Seed length	minimum	23.25	31.18	24.38
	maximum	32.28	47.69	38.62
	average	26.51	36.66	31.79
	standard deviation	2.53	4.97	4.59
Seed width	minimum	29.66	33.86	36.80
	maximum	40.44	47.00	51.00
	average	33.14	37.31	42.71
	standard deviation	3.04	3.97	5.30
Seed thickness	minimum	4.95	4.69	4.78
	maximum	7.18	11.40	7.30
	average	5.58	7.33	5.73
	standard deviation	0.61	1.89	0.92
Embryo axis length	minimum	3.97	8.18	3.86
	maximum	5.48	14.28	5.72
	average	2.67	11.12	4.81
	standard deviation	0.66	2.02	0.65
Embryo axis width	minimum	1.91	2.79	2.17
	maximum	3.26	5.38	2.76
	average	1.99	3.77	2.46
	standard deviation	0.45	0.67	0.13

Table 1. Quantitative data* related to samples of fruits (n = 30) and seeds (n = 50) of *Macrolobium acaciifolium* (Benth.) Benth., *Macrolobium bifolium* (Aubl.) Pers. and *Macrolobium pendulum* Willd. ex Vogel.

*All measurements are expressed in millimeters.

seed appendages are not found, and micropyle, lens and raphe are inconspicuous. The embryo is cream-colored with two plano-convex, storage, symmetrical cotyledons (Fig. 8). The endosperm is absent and the embryo axis is oblong and straight (Fig. 11). The plumule is moderately differentiated (Fig. 14). The seedling is type PER (Fig. 22-26), and germination is unipolar with the vegetative axis between the cotyledons (Fig. 24). The hypocotyl is quadrangular (Fig. 28) and glabrous. The epicotyl is cylindrical, dark-green and glabrous. The axillary buds are inconspicuous. The three first eophylls are alternate (Fig. 26-27 and 29), bifoliolate, with oblong to falcate leaflets (Fig. 27), with oblique bases, acute to acuminate apices and entire margins, showing glabrous pulvini and petioles; a small pulvinule occurs at the base of each leaflet.

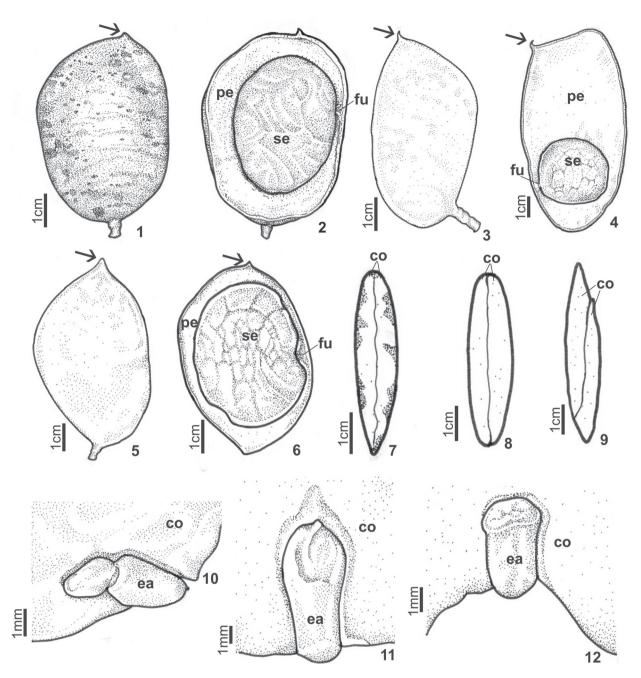
Macrolobium pendulum Willd. ex Vogel.—The fruit is dehiscent, woody, D-shaped (Fig. 5), flattened, glabrous, without constrictions, substipitate, with oblique base and obtuse apex (Fig. 5 and 6). The pericarp is externally shiny and smooth, without apparent venation, and dark-brown; internally, it is light brown. The seed is oval to reniform (Fig. 6), laterally compressed (Fig. 9), dark brown and asymmetrical, with evident seed coat venation; without seed appendages; funicular residue is adhered to the hilum region; the micropyle, lens and raphe are inconspicuous. The embryo is light brown with two storage cotyledons, plano-convex and asymmetrical (Fig. 9). The endosperm is absent, and the embryo axis is oblong and straight (Fig. 12). The plumule is undifferentiated (Fig. 15). The seedling is type PER, and the germination is unipolar with the vegetative axis

Component	Character	M. acaciifolium	M. bifolium	M. pendulum
	Consistence	woody	woody	woody
	Dehiscence	indehiscent	dehiscent	dehiscent
	Туре	indehiscent legume	typical legume	typical legume
	Transversal contour	flattened	flattened	flattened
Fruits	Longitudinal contour	oblong to oval	oblong to spatulate	D-like
	Apex	obtuse and rounded	truncate to obtuse	obtuse
	Apiculus	subapiculate	subapiculate	subapiculate
	Base	oblique	oblique	oblique
	Stipe	substipitate	substipitate	substipitate
Seeds	Transversal contour	compressed	compressed	compressed
	Longitudinal contour	oblong to elliptical	oval to orbicular	oval to reniform
	Seed coat venation	inconspicuous	conspicuous	conspicuous
	Micropyle	inconspicuous	inconspicuous	inconspicuous
	Hilum	elliptical	elliptical	elliptical
	Lens	inconspicuous	inconspicuous	inconspicuous
	Raphe	inconspicuous	inconspicuous	inconspicuous
	Appendages	absent	absent	absent
	Endosperm	absent	absent	absent
	Embryo type	investing	investing	investing
	Consistence of the cotyledons	storage	storage	storage
	Cotyledons in cross section	plano-convex	plano-convex	plano-convex
	Symmetry of the cotyledons	symmetric	symmetric	asymmetric
	Abaxial surface of cotyledons	sinuate	entire	entire
	Embryo axis position	oblique	straight	straight
	Shape of embryo axis	conical	oblong	oblong
	Plumule development	well differentiated	moderately differentiated	undifferentiated
Seedlings and saplings	Туре	CHR	PER	PER
	Hypocotyl shape	cylindrical	quadrangular	cylindrical
	Root and epicotyl emergence	unipolar	unipolar	unipolar
	Vegetative axis position	lateral to cotyledons	between cotyledons	between cotyledons
	Epicotyl shape	cylindrical	cylindrical	cylindrical
	Axillary buds	inconspicuous	inconspicuous	inconspicuous
	Eophylls arrangement	alternate	alternate	alternate
	Eophylls division	even-pinnate	bifoliolate	bifoliolate
	Leaflets shape	oblong	oblong to falcate	oblong to falcate
	Leaflets apex	retuse to emarginate	acute to acuminate	<u>obtuse a attenuate</u>
	Leaflets base	oblique	oblique	oblique
	Leaflets margin	entire	entire	entire
	Persistence of stipules	caducous	caducous	persistent
	Nyctinasty	"forward-folding"	"forward-folding"	"forward-folding"

Table 2. Qualitative data* related to the fruits, seeds, seedlings and saplings of *Macrolobium acaciifolium* (Benth.) Benth., *Macrolobium bifolium* (Aubl.) Pers. and *Macrolobium pendulum* Willd. ex Vogel.

CHR – cryptocotylar-hypogeal-reserve; PER – phanerocotylar-epigeal-reserve. *Bolded states are shared by two species; underlined states segregate the three species.

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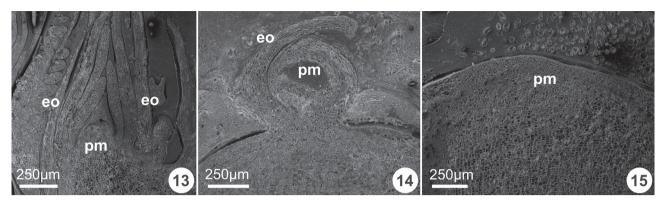


Figures 1-12. Fruits and seeds: *Macrolobium acaciifolium* (Benth.) Benth. (Fig. 1, 2, 7 and 10); *Macrolobium bifolium* (Aubl.) Pers. (Fig. 3, 4, 8 and 11); and *Macrolobium pendulum* Willd. ex Vogel (Fig. 5, 6, 9 and 12). Fig. 1-6: Entire fruits (odd numbered) and without a valve (even numbered); arrows indicate the apiculus. Fig. 7-9: Seeds in cross section. Fig. 10-12: Details of the embryo, showing the embryo axis. co – cotyledon; ea – embryo axis: fu – funiculus; pe – pericarp; se – seed.

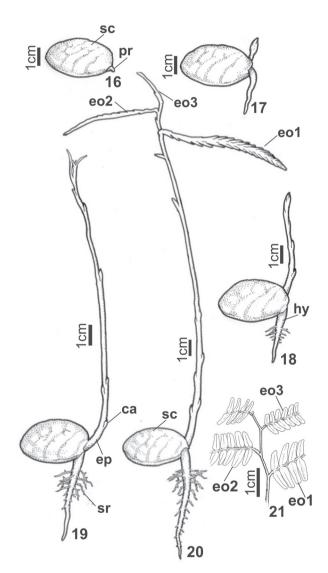
between cotyledons (Fig. 32). The hypocotyl is cylindrical and glabrous. The epicotyl is cylindrical, dark-green and glabrous. The axillary buds are inconspicuous. The three first eophylls are alternate and bifoliolate, showing oblong to falcate leaflets, with oblique bases, obtuse to attenuate apices and entire margins; the pulvini and petioles are glabrous, and a pair of persistent stipules can be seen at the leaf base; a small pulvinule occurs at the base of each leaflet.

Discussion

According to Cowan (1953), the species of *Macrolobium* can present dehiscent fruits, as in *M. acaciifolium*, or indehiscent ones, as in *M. bifolium* and *M. pendulum*. The fruits of this genus are lateral flattened legumes, varying from suborbicular to oblong or spatulate (Cowan 1953). These forms were found for the fruits of *M. acaciifolium* Gildo Vieira Feitoza, João Ubiratan Moreira dos Santos, Ely Simone Cajueiro Gurgel and Denise Maria Trombert Oliveira



Figures 13-15. Plumule of *Macrolobium*. Fig. 13: Well differentiated plumule of *Macrolobium acaciifolium* (Benth.) Benth. Fig. 14: Moderately differentiated plumule of *Macrolobium bifolium* (Aubl.) Pers. Fig. 15: Undifferentiated plumule of *Macrolobium pendulum* Willd. ex Vogel. eo – eophyll; pm – promeristem.



Figures 16-21. Seedlings and saplings of *Macrolobium acaciifolium* (Benth.) Benth. Fig. 16: Seedling at post-germination day 5. Fig. 17: Seedling at post--germination day 10. Fig. 18: Seedling at post-germination day 15. Fig. 19: Seedling at post-germination day 18. Fig. 20: Sapling at post-germination day 22. Fig. 21: Detail of leaf arrangement after complete eophyll expansion. ca – cataphyll; eo1-eo3 – sequence of eophylls; ep – epicotyl; hy – hypocotyl; pr – primary root; sc – seed coat; sr – secondary root.

and *M. bifolium*, but not for *M. pendulum*, in which fruits were D-shaped, as was also reported by Kirkbride *et al.* (2003). The dehiscence, shape and pericarp traits, as well as other fruit characters, can help recognize the groups in Caesalpinioideae (Gunn 1991, Barroso *et al.* 1999).

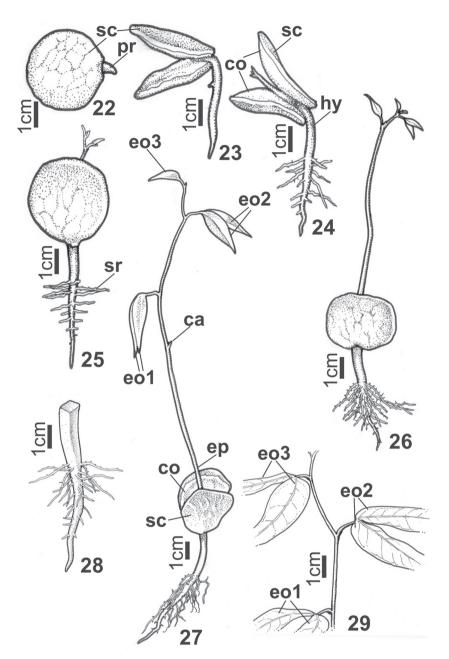
In the present study, the measurements of fruits were consistent with those described for *Macrolobium* by Gunn (1991), Barroso *et al.* (1999) and Kirkbride *et al.* (2003). The analysis of the dimensions of the fruits demonstrated that *M. bifolium* had the largest fruits and *M. acaciifolium* had the smallest fruits.

Although the size and shape of the seeds were similar among the species studied, the values of seed length and thickness were highest for *Macrolobium bifolium*, as were the dimensions of the embryo axis. In *M. bifolium* and *M. pendulum*, the venation of seed coat is a notable trait that can be useful in identifying certain *Macrolobium* species; this feature was previously reported by Cowan (1953) in the last revision of the genus. Apparently, there are different patterns of seed coat venation, although only anatomical studies could describe and discuss those. For the seeds of *M. acaciifolium*, our data corroborate those of Cowan (1935), who described the crustose testa, and of Gunn (1991), who reported the intrusion of the testa into the corrugate cotyledons.

Gunn (1991) stated that the embryo axis is straight in 98% of Caesalpinioideae genera. *Macrolobium acaciifolium* is one of the exceptions in the subfamily, presenting a clearly oblique embryo axis, as documented in the present work. The asymmetry of the cotyledons of *M. pendulum*, a state not shared by the other species studied, is noteworthy. Cowan (1953) and Gunn (1991) did not highlight this trait for *Macrolobium* species. According to Smith (1983) and Duke & Polhill (1981), all of the Amherstieae (sensu Cowan & Polhill 1981) have storage cotyledons, constituting exalbuminous seeds. Our data support that statement, because all three of the species studied showed fleshy cotyledons and only remains of the endosperm were found.

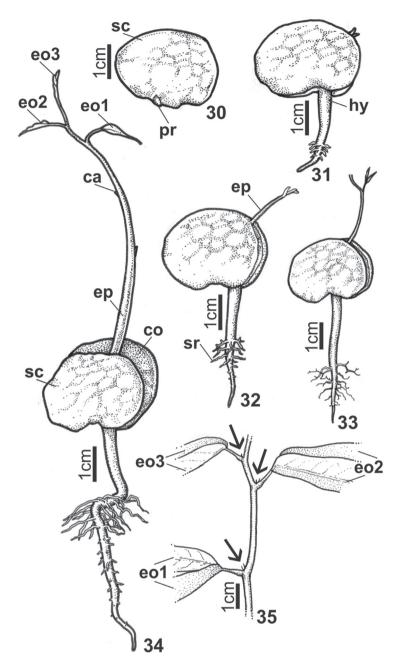
The evaluation of embryo structure of the studied species revealed many distinctive characters (see Tab. 2).

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Figures 22-29. Seedlings and saplings of *Macrolobium bifolium* (Aubl.) Pers. Fig. 22: Seedling at post-germination day 5. Fig. 23: Seedling at post-germination day 7. Fig. 24: Seedling at post-germination day 10. Fig. 25: Seedling at post-germination day 12. Fig. 26: Seedling at post-germination day 17. Fig. 27: Sapling at post-germination day 25. Fig. 28: Detail of the hypocotyl showing the quadrangular cross-section. Fig. 29: Detail of leaf arrangement after complete eophyll expansion. ca – cataphyll; co – cotyledon; eo1-eo3 – sequence of eophylls; ep – epicotyl; hy – hypocotyl; pr – primary root; sc – seed coat; sr – secondary root.

Considering the embryo axis of Leguminosae species, the plumule is recognized as one of the most variable traits. In fact, the plumule development was a determinant in the separation of some groups in this family, such as *Poecilanthe* (Meireles & Tozzi, 2008) and *Copaifera* (Gurgel, 2009), at the infrageneric and interspecific levels respectively. Caesalpinioideae presents all types of plumules, as observed in the work of Oliveira (1999b), in which the plumule was found to be well differentiated in *Caesalpinia leiostachya* (Benth.) Ducke; moderately differentiated in *Cassia ferruginea* (Schrad.) Schrad. ex DC. and *Peltophorum dubium* (Spreng.) Taub.e; rudimentary in *Dimorphandra mollis* Benth.; and undifferentiated in *Senna multijuga* (Rich.) Irwin & Barn. Gunn (1991) observed none of the variation reported here, reporting that the plumule of *Macrolobium* is rudimentary. In our results, the three *Macrolobium* species evaluated presented distinct patterns of plumule development, showing that detailed studies of this character can be relevant for species identification. These findings underscore the need for further studies of *Macrolobium* species in order to clarify



Figures 30-35. Seedlings and saplings of *Macrolobium pendulum* Willd. ex Vogel. Fig. 30: Seedling at post-germination day 5. Fig. 31: Seedling at post-germination day 10. Fig. 32: Seedling at post-germination day 15. Fig. 33: Seedling at post-germination day 20. Fig. 34: Sapling at post-germination day 25. Fig. 35: Detail of leaf arrangement after complete eophyll expansion (arrows indicate the persistent pairs of stipules).

ca - cataphyll; co - cotyledon; eo1-eo3 - sequence of eophylls; ep - epicotyl; hy - hypocotyl; pr - primary root; sc - seed coat; sr - secondary root.

aspects of circumscription and phylogeny, exploring the morphological diversity of the genus (Bruneau *et al.* 2001; Herendeen *et al.* 2003; Mackinder 2005).

Hypogeal germination, as we observed in *Macrolobium acaciifolium*, is considered a derived condition for Leguminosae (Moreira & Moreira 1996). The CHR morphological type exhibited by *M. acaciifolium* was also reported by Silva *et al.* (1988) and Moreira & Moreira (1996). Although Maia *et al.* (2005) classified the seedlings of this species as the phanerocotylar-hypogeal-reserve type, there seems to be some discrepancy regarding this point. Analyzing the figure of *M. acaciifolium* in Maia *et al.* (2005), we see that seeds were germinated within the indehiscent fruits, which opened during the process, thus inducing the misconception; in the referred figure, authors also drew the typical rugose seed coat of *M. acaciifolium*, confirming our interpretation. In the present study, *Macrolobium bifolium* and *M. pendulum* showed the PER morphological type, in agreement with the results of Gates (1951). Léonard (1957) made a brief description of the germination and seedling type of *M. bifolium*, which is also in agreement with our data.

Some connections can be established between Leguminosae subfamilies and seedling or germination types. According to Gates (1951), seedlings of Caesalpinioideae and Mimosoideae are usually epigeal, differing from Papilionoideae, in which they are cryptocotylar or phanerocotylar. Duke & Polhill (1981) stated that, in Caesalpinioideae alone, there are three groups with respect to the seedling type, in which the consistency and exposure of the cotyledons, as well as the structure of eophylls and metaphylls, can be variable. Gurgel et al. (2012) stated that Caesalpinioideae and Mimosoideae seedlings are considered epigeal with foliar cotyledons, and that hypogeal species with storage cotyledons predominate in the Papilionoideae. Oliveira (1999a) presented data for 30 leguminous tree species that corroborated the statements of Gates (1951), Duke & Polhill (1981) and Gurgel et al. (2012). Examples of hypogeal species in Caesalpinioideae are very rare, and the results of the present study illustrate this pattern in Macrolobium acaciifolium.

When the ecological aspects are considered, the current knowledge about seedlings allows interesting evaluations to be performed. According to Lima (1989-90), the CHR morphofunctional type is normally found for species occurring in periodically flooded environments. This was confirmed by the Ressel et al. (2004), who identified CHR seedlings in species occurring in temporarily flooded areas; the authors also correlated CHR seedlings with the climax species. According to Felix-da-Silva et al. (2013), Macrolobium bifolium and M. pendulum (both having PER seedlings) occur only in flooded environments, as is the case for M. acaciifolium (which has CHR seedlings). It is possible that the occurrence in flooded environments was related to the presence of fleshy cotyledons, which supply the initial requirement of reserves for the establishment of the plant. It is also necessary to emphasize that, although producing phanerocotylar seedlings, M. bifolium and M. pendulum have seed coats that remain adhered to the abaxial face of the cotyledons, exposing only their adaxial face. Thus, the seed coat is partially responsible for the protection of cryptocotylar seedlings, exposing only part of the cotyledon surface.

The stipules observed for the studied taxa were persistent only in *Macrolobium pendulum*. Cowan (1953) stated that stipules are more frequently caducous in *Macrolobium* species but are persistent, which is a useful trait, in *M. huberianum* Ducke and *M. pendulum*. According to Cowan (1953), the persistence of stipules in *M. pendulum* is an important state distinguishing *M. pendulum* from its relatives *M. palustre* Ducke and *M. savannarum* R.S.Cowan when specimens are adults and not in the reproductive phase. Duke (1965) demonstrated that the presence or absence of stipules is a useful criterion for interspecific differentiation within a given genus. The occurrence of stipules in seedlings has also been described in other species of Caesalpinioideae, such as *Apuleia leiocarpa* (Vog.) Macbr., *Senna macranthera* (Collad.) H.S. Irwin & Barneby (Finger *et al.* 1979) and *Senna multijuga* var. *lindleyana* (Amorim *et al.* 2008).

Typical of the legumes, the foliar nyctinasty is still scarcely described for seedlings of the Leguminosae family. The "forward-folding" nyctinasty found in the present study for the leaves of the *Macrolobium* species is probably related to the asymmetrical leave base, similar to what occurs in the *Dalbergia* clade (Lavin *et al.* 2001) and in the genus *Acosmium* (Rodrigues & Tozzi, 2008).

As can be inferred from the data shown in Tab. 2, *Macrolobium bifolium* and *M. pendulum* are closely related species, sharing 10 character states, compared with only three shared by *M. acaciifolium* and *M. bifolium*, whereas *M. acaciifolium* and *M. pendulum* have no character states in common. These data corroborate the relationships within the genus *Macrolobium* described by Cowan (1953). According to that author, despite being in the same section (*Vouapa*), *M. bifolium* and *M. pendulum* are more closely related to each other than to *M. acaciifolium*, a species with more ancestral traits.

The data presented in this work underscore the relevance of detailed morphological studies (especially of seeds and seedlings) to understanding the ecological and phylogenetic aspects of leguminous species. Structural information about *Macrolobium pendulum* is provided here for the first time, contributing interesting knowledge for recognizing this species in the natural environment.

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