

An exploratory study on seed morphology of *Miconia* Ruiz & Pavón (Melastomataceae), with taxonomic and ecological implications

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SUMMARY

The results of an exploratory study on seed morphology of *Miconia* Ruiz & Pavón (Melastomataceae) are presented. Seeds of 75 species, mainly from north-western South America, including representatives of all 12 sections of *Miconia*, were examined, 57 by SEM. *Miconia* shows an appreciable diversity in seed structure. Twelve major seed types are defined and compared with the current sectional division of the genus and with ecological data. The types do not match with the established sections. The defined seed types may well be of importance for phylogenetic classification, because they possibly indicate relationships. In general, variation in seed morphology in *Miconia* largely overlaps with variation found in the tribe *Miconieae* as a whole. Implications for seed dispersal and habitat characteristics are given; the importance of secondary dispersal is discussed. A few species probably are ant-dispersed after having been dropped in vertebrate faeces. Some of the seed types form a species group restricted to certain altitudinal belts and to precipitation zones.

Key-words: seed morphology, *Miconia*, taxonomy, seed dispersal.

INTRODUCTION

The neotropical genus *Miconia* Ruiz & Pavón (*Miconieae*, Melastomataceae) is a very large and polymorphic group of shrubs and trees. It contains about 1000 species, living in an area ranging from southern Mexico to south-eastern Brazil and Bolivia (Wurdack 1980). Species of this taxon have radiated to very different habitat types, and many have a restricted geographical distribution. Different species of *Miconia* are commonly found from lowland rain forests to upper Andean forests and páramos up to 4250 m altitude. Often several species are growing in the same habitat. Therefore, this genus can be regarded as one of the most important neotropical genera.

Miconia plays an important role in various habitat types. In forests, species are mostly understorey inhabitants (Gentry 1983), and usually small trees or shrubs, rarely epiphytes (Renner 1986). Above the upper timber line, in shrub- and grass-páramos, *Miconia* species occur as shrubs and dwarf shrubs. The altitudinally highest growing species, *M. chionophila*, is a tiny, compact prostrate dwarf shrub growing close to moraine boulders in the grass páramo–superpáramo border zones. All species produce

Table 1. Sections of the genus *Miconia* with number of species (estimated by Wurdack, personal communication)

Section	Number of species
I. <i>Jucunda</i> Naud.	c. 30
II. <i>Tamonea</i> Cogniaux	c. 65
III. <i>Adenodesma</i> Naud.	c. 15
IV. <i>Octomeris</i> Triana	c. 40
V. <i>Laceraria</i> Naud.	c. 25
VI. <i>Miconia</i> DC.	c. 230
VII. <i>Glossocentrum</i> Triana	c. 80
VIII. <i>Chaenantha</i> Naud.	c. 25
IX. <i>Amblyarrhena</i> Naud.	c. 175
IXa. <i>Hartigia</i> (Miquel) Gris.	c. 8
X. <i>Cremanium</i> Naud.	c. 175
XI. <i>Chaenopleura</i> Triana	c. 70

berries, which are mostly eaten by a wide range of bird species (e.g. Snow & Snow 1971; Levey 1990; Blake & Loiselle 1992; Stiles & Rosselli 1993). Birds are important seed dispersers for most of the members of the genus (e.g. Gentry 1983). Mammals also disperse seeds of *Miconia* species; *M. dodecandra* and *M. hypoleuca* are dispersed by, among others, the marmoset *Callithrix kuhlii*, and *M. cabuca* and *M. cubatensis* by the howling monkey *Alouatta fusca* (Mittermeier *et al.* 1988). Dispersal by rats was reported by Magnusson & Sanaiotti (1987; see also Renner 1989a). Observations made clear that, in some places, different *Miconia* species living together act as a 'fruiting guild' by having distinct, complementary fruiting periods, thus providing food throughout the year (Hilty 1980; Skutch 1988).

Very little is known of the phylogenetic relationships within the genus. The current sectional division (12 sections, according to Cogniaux (1891)) is based upon flower characteristics (e.g. calyx shape, petal form and anther morphology) and appears to be artificial (Wurdack 1980). Frequent parallel evolution of character states renders the formation of phylogenetic hypotheses difficult.

The history of the taxonomy of *Miconia* species is complicated. Sectional divisions have been made in the 19th century by Naudin (1849–1853), Triana (1871) and Cogniaux (1891). Many earlier described genera were fused by these authors to form *Miconia*. The current division (Wurdack 1980), as shown in Table 1, is a slightly updated version of that made by Cogniaux (1891). Sect. *Hartigia* is regarded a part of sect. *Amblyarrhena*. Type species of the sections have not been designated, except for sect. *Miconia*, which has *M. triplinervis* as type species (automatically, because this species is the generic type species, and placed in sect. *Miconia*). Knowledge of relationships of species is too poor to assign sectional type species for the other sections (Wurdack, personal communication). Also, the genus as a whole is insufficiently characterized and delimited, and apparently is a paraphyletic group (Renner, personal communication). Sect. *Tamonea* probably has a closer relationship with *Clidemia* sect. *Miconiopsis* than with other sections of *Miconia*; sect. *Octomeris* seems to be related with *Clidemia* sect. *Clidemia* and *Capitellaria* (Judd 1986, 1989).

Seed characters, as studied in this paper, have not been used for classification of species of *Miconia* until now. Whiffin & Tomb (1972) provided datasets for tribal

classification of capsular-fruited Melastomataceae by studying seed micromorphology. Renner (1989b) has examined seeds of some baccate-fruited Melastomataceae using SEM.

Seeds of *Miconia* have characteristics typical of Melastomataceae. The testal part has the exotesta differentiated into a mechanical (sclerotic) layer, while in the raphal part a mechanical layer is derived from the endotesta. The cylindrical construction enables the seed to withstand pressure. Due to a weak connection between the testal and the raphal sclerenchyma, the raphal part easily breaks off during germination, thus acting as an operculum, permitting the embryo to emerge (Ziegler 1925; Corner 1976).

This paper aims to give an insight into the usability of seed-morphological data for (sectional) classification of *Miconia* species and to discuss the ecological relevance of seed characters. Comparisons are made between morphological and habitat data and the current sectional division of the genus.

MATERIALS AND METHODS

Seeds of 75 *Miconia* species have been examined. They were collected from the herbaria of the University of Utrecht (U), and of the National Museum of Natural History, Washington DC (US). For some species, treatment of collected fruits with 10% ammonia, followed by ultrasonic cleaning, was necessary to remove the seeds from the berry in an intact state. Dry seed samples of 57 species were gold-palladium-sputtered (for 2 min) in an EM-Scope SC-500 sputter-coater at 20 mA, and studied in an ISI-DS 130 scanning electron microscope (SEM) at 9 kV.

The choice of species was based on habitat (elevation, precipitation) and the country from which the individual plants were collected. We selected species from a wide range of habitats (lowland rainforest to upper páramos), collected in north-western South America (Colombia, Ecuador, Venezuela, Peru). Choice was, at first, random as regards the taxonomic position (section) and seed type of the species. In a later stage of the investigation, missing representatives of sections *Adenodesma*, *Jucunda* and *Octomeris* were collected.

Terminology of seed shape follows Montgomery (1977), that of micromorphology follows Barthlott (1981).

OBSERVATIONS

The fruits of the examined species are baccate (i.e. indehiscent and mostly fleshy) and small. The placentation of the seeds is axillary; the hilum and raphe are always directed inwards. The opposite of the hilar side will be referred to as the chalazal side, the opposite of the raphal part as the antiraphal side. Seeds of *Miconia* in general are anatropous to subcampylotropous, and relatively small.

Variation in seed structure is found in size, shape, ariloid appendages (if present) and testa sculpture. Seed shape can be narrowly to broadly ovoid (to globose) or narrowly to broadly pyramidate. In *M. ternatifolia* and *M. solmsii*, seeds appeared to have a cup-like shape (Fig. 2e, f). Seed size varies from 300 μm (*M. benthamiana*) to about 2250 μm (*M. appendiculata*). Some species have ariloid appendages (for example *M. rupticalyx*, *M. lacera*, *M. lateriflora*, see Fig. 5a).

The shape of the seeds is partly determined by contact with neighbouring seeds and with the fruit wall and the placenta during seed development. The lateral sides are

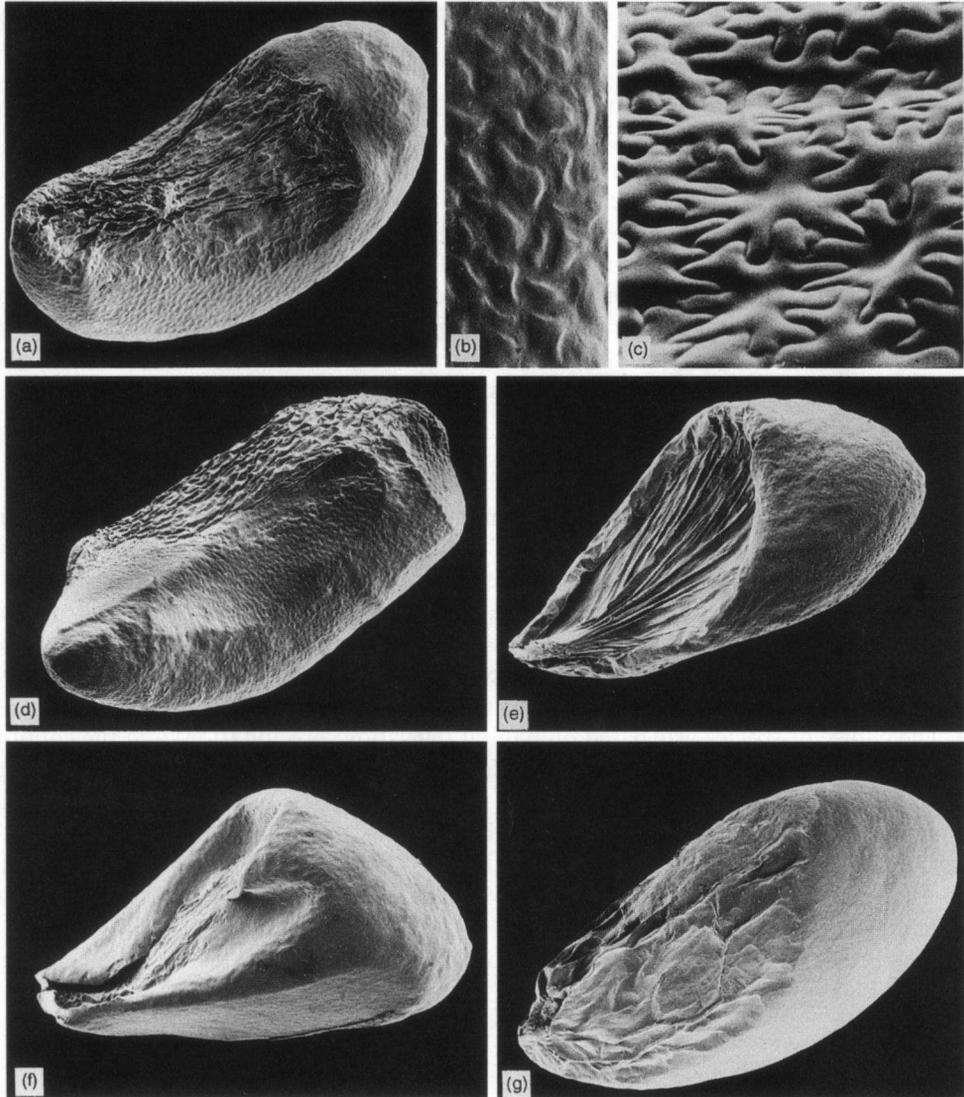


Fig. 1. Scanning electron micrographs of some *Miconia* seeds. (a, b, d): 'Buxifolia'-type; (c, e-g): 'notabilis'-type. (a): *M. buxifolia*, $\times 50$. (b): *M. cf. puracensis*, testa detail, $\times 295$. (c): *M. lasiocalyx*, detail of testa with 'jigsaw'-cells, $\times 860$. (d): *M. squamulosa*, $\times 45$. (e): *M. lasiocalyx*, $\times 90$. (f): *M. notabilis*, $\times 70$. (g): *M. ulmarioides*, $\times 70$.

mostly flattened, the antiraphal ones are commonly rounded. In a number of species, testa sculpture is mainly determined by contact with the internal surface of the pericarp. These species have impressions of the testa caused by the convex walls of turgescient endocarp cells.

The testa sculpture is papillate (*M. chionophila*, Fig. 3a,b), alveolate (with dint-like depressions; *M. oinochrophylla*, Fig. 4a), or smooth (*M. buxifolia*, Fig. 1a). Cell patterns are mostly irregular, seldom forming longitudinal rows (*M. rupticalyx*). The cells are

(commonly) isodiametric or (more or less) elongated (e.g. *M. caudata*, *M. rupticalyx*). Periclinal walls are straight or (often) slightly to strongly convex, sometimes concave (*M. cf. puracensis*). Anticlinal walls are mostly regularly undulated (e.g. *M. oinochrophylla*) or more or less straight (*M. cf. puracensis*). In the latter case, the exotestal cell surface has a polygonal form. Undulation of anticlinal walls gives the outer surface of the testa cell a jigsaw-piece-like appearance. The anticlinal boundaries can be slightly to strongly sunken (e.g., respectively, *M. notabilis*, *M. symplectocaulos*) to flat (*M. solmsii*) or slightly raised (*M. ligustrina*). Cuticular sculptures are mostly smooth, occasionally striate (*M. pseudocapsularis*) or slightly verrucose (*M. mesmeana* ssp. *longepetiolata*).

The cells of seed appendages generally are larger, and polygonal. The outer periclinal walls often were found collapsed, the anticlinals straight and sunken (*M. centrodesma*).

The raphal part often appears as a flattened, ovate surface. Curvature of the raphal part is often found to be very variable; moisture makes it swell. However, seed samples were dry, so the raphal surface mostly appeared flat or sunken. Its length varies from 40% to 100% of the seed length, its width varying from 75% to 100% of that of the seed. The raphe is often clearly visible as a longitudinal vein (see for example Fig. 2c, e and f).

The various species are placed in 12 defined seed types, based on testa sculpture, general appearance and presence of appendages. A number of species have seeds which are so different from others that they could not be placed in our seed types. One type is intermediate between two others. Characteristics of seeds of all species examined, and the distribution of the different sections of *Miconia* over the seed types, are listed in Table 2. The 12 seed types defined below are organized into six 'supertypes', based on testa relief (Table 2).

Descriptions of seed types

Supertype I: seeds with smooth testa surfaces (types 1–4)

1. 'Buxifolia' type (Fig. 1a, b, d)

Berry contains from less than 25 seeds to 50 seeds (rarely 100). Seeds ovoid to ellipsoid, often slightly curved (subcampylotropous in *M. verrucosa*). Lateral sides sometimes flattened. The brown-red colour of the testa is characteristic. The species' mean seed lengths range from 1000 μm to 1700 μm . The raphal part is mostly lateral (subhilar in *M. ligustrina* and *M. oreogena*), large (occupying 50–90% of total length). The testa is smooth or almost so. Cell patterns irregular. Cells more or less elongated. The periclinal walls shallow or straight. Anticlinal walls straight to curved, their boundaries raised. The cuticula is smooth. Ten species were investigated.

2. 'Notabilis' type (Fig. 1c, e–g)

Berry contains 50–100 seeds. Seeds narrowly ovoid to ovoid. The species' mean seed lengths range from 600 μm to 1000 μm . Raphal part straight, subhilar, length occupying 60–80% of total. Testa smooth. Cell pattern irregular. Cells more or less elongated. Periclinal walls straight or convex. Anticlinal walls undulated (S-type), boundaries commonly sunken or flat. Cuticula smooth or slightly striate. Six species were investigated.



Fig. 2. (a–c): ‘*Affinis*’-type; (d): miscellaneous; (e, f): ‘*ternatifolia*’-type. (a): *M. silicicola*, × 15. (b): *M. silicicola*, × 40. (c): *M. splendens*, × 35. (d): *M. smithii*, × 30. (e): *M. solmsii*, × 30. (f): *M. ternatifolia*, × 30.

3. ‘*Affinis*’ type (Fig. 2a–c)

Berry contains from fewer than 25 to 100 seeds. Seeds narrowly to very broadly pyramidate. The species’ mean seed lengths range from 1000 μm to 2100 μm (seeds of *M. silicicola* generally are broad rather than long). Raphal part straight, subhilar to lateral, length occupying 65–95% of total. Testa smooth. Cell pattern irregular. Cells

Table 2. Seed types and characteristics of species examined

Supertype	Type	Species	Section	No. seeds/ berry	Shape	Length range	Testa struct.	Anticl. curv.	Length of raphal part (%)	Remarks		
I. smooth	BUXIFOLIA-type av. l = 1.379 SD = 0.219	<i>M. buxifolia</i>	Cremanium	25-50	ell	0.80-1.00 1.15-1.35 1.20-1.50	sm	s-c	80	Slightly curved		
		<i>M. cundinamarcensis*</i>	Cremanium	25-50	ov-ell	1.00-1.30	sm	—	75	Raphal part subhilar		
		<i>M. ligustrina</i>	Cremanium	25-50	ov-ell	1.20-1.60	sm	c-u	70	Raphal part subhilar		
		<i>M. nitidissima*</i>	Chaenantha	50-100	ov-pyr	1.25-1.45	sm	—	85	Raphal part subhilar		
		<i>M. oreogena</i>	Cremanium	25-50	br ov	0.95-1.10	sm	c	50	Raphal part subhilar		
		<i>M. cf. puracensis</i>	Cremanium	<25	ell	1.50-1.75	sm	s-c	90	Slightly curved		
		<i>M. squamulosa</i>	Cremanium	25-50	ell	1.20-1.80	sm	s-c	80	Slightly curved, laterally flat		
		<i>M. summa*</i>	Cremanium	<25	ov-ell	1.60-1.80	sm	—	80	Slightly curved		
		<i>M. tinifolia*</i>	Cremanium	<25	narr ov-narr ell	1.40-1.60	sm	—	80	Slightly curved		
		<i>M. verrucosa*</i>	Cremanium	25-50	ov-ell	1.20-1.60	sm	—	60	Subcampylotropous		
		NOTABILIS-type	av. l = 0.7924 SD = 0.127	<i>M. biappendiculata</i>	Cremanium	50-100	narr ov-ov	0.85-1.10	sm	u	60	
				<i>M. cf. bracteolata*</i>	Cremanium	50-100	ov	0.75-0.90	sm	—	75	
				<i>M. cf. lasiocalyx</i>	Amblyarrhena	50-100	ov	0.55-0.70	sm	u	70	
<i>M. media</i>	Cremanium			25-50	ov	0.70-0.90	sm	—	60-80			
<i>M. notabilis</i>	Octomeris			200-300	ov	0.80-0.85	sm	u	60			
<i>M. ulmaritoides</i>	Amblyarrhena			± 100	ov	0.65-0.95	sm	u	75			
AFFINIS-type	av. l = 1.473 SD = 0.552	<i>M. affinis*</i>	Miconia	50-100	pyr	0.90-1.10	sm	—	95			
		<i>M. appendiculata*</i>	Miconia	<25	irr pyr-hemisph	1.90-2.25	sm	—	65-95			
		<i>M. silvicola</i>	Adenodesma	25-50	very br pyr	1.10-1.70	sm	c-u	80			
		<i>M. splendens</i>	Miconia	± 30	pyr	1.60-2.10	sm	u	85			
		<i>M. stenostachya</i>	Miconia	± 50	pyr-br pyr	1.00-1.20	sm	u	85			
TERNATIFOLIA-type	av. l = 1.69 SD = 0.165	<i>M. solmsii</i>	Chaenantha	<25	br pyr-br ov	1.30-1.85	sm	u	95	Distinct ridge around raphal part		
		<i>M. spennerostachya</i>	Miconia	<25	br pyr-br ov	1.40-1.80	sm	u	95			
		<i>M. ternatifolia</i>	Glossocentrum	<25	br pyr-br ov	1.75-2.00	sm	c-u	90			

Table 2. Continued

Supertype	Type	Species	Section	No. seeds/ berry	Shape	Length range	Testa struct.	Anticl. curv.	Length of raphal part (%)	Remarks	
II. papillate	CHIONOPHILA-type av. l = 0.758 SD = 0.133	<i>M. chionophila</i>	Chaenopleura	50-100	ov	0.85-1.20	pap	u	65		
		<i>M. chrysocoma</i>	Cremanium	25-50	ov	0.85-1.00	pap	u	75		
		<i>M. elaeoides</i>	Cremanium	50-100	ov	0.70-0.85	pap	u	45	Testa cells elongated, irr. shaped	
		<i>M. elvirae*</i>	Cremanium	25-50	ov	0.50-0.60	pap	—	75		
		<i>M. latifolia</i>	Chaenopleura	50-100	ov	0.70-0.85	pap	u	100	Small ridge at edge of raphal part	
		<i>M. limitaris*</i>	Cremanium	100-200	ov	0.65-0.70	pap	—	75	Cells in longitudinal rows	
		<i>M. cf. ochracea</i>	Cremanium	25-50	ov	0.65-0.80	pap	u	75		
		<i>M. parvifolia</i>	Cremanium	—	ov	± 0.75	pap	—	70		
		<i>M. rotundifolia*</i>	Chaenopleura	50-100	ov	0.95-1.10	pap	—	60-80		
		<i>M. theaezans</i>	Cremanium	50-100	ov	0.60-0.75	pap	u	75		
		<i>M. tricaudata*</i>	Cremanium	25-50	ov	± 0.70	pap	—	85		
		MESMEANA-type av. l = 0.85 SD = 0.147	<i>M. lehmannii</i>	Cremanium	50-100	ov-ell	0.60-0.75	pap	s	50	
			<i>M. mesmeana</i>	Cremanium	25-50	ov-ell	0.85-1.30	pap	s	80	
			<i>ssp. japonensis</i>	Cremanium	25-50	ov-ell	0.70-0.85	pap	s	80	
CENTRODESMA-type av. l = 0.535 SD = 0.142	<i>M. longepetiolata</i>	Cremanium	50	ov	0.85-1.00	pap	s	45			
	<i>M. cleefii</i>	Cremanium	>100	pyr **/cuneate	0.60-0.80	irr pap	u	40			
	<i>M. centrodesma</i>	Laceraria	100-200	ov **	0.40-0.55	pap	u	45	Cuticula striate		
	<i>M. lateriflora</i>	Miconia	50-100	ov **	0.35-0.45	pap	u	85	Cuticula striate		
	<i>M. pseudocapsularis</i>	Miconia	>100	narr ov **	0.55-0.60	sl pap	c-u	85			
III. alveolate	REDUCENS-type av. l = 0.646 SD = 0.263	<i>M. ruplicalyx</i>	Laceraria	>100	ov **	0.55-0.60	sl pap	c-u	85		
		<i>M. acutifolia</i>	Tamonea	25-50	ov-pyr	1.00-1.35	alv	u	85	Smooth at lateral sides	
		<i>M. aponeura</i>	Tamonea	200-300	ov	0.50-0.60	alv	u	50		
		<i>M. caudata</i>	Tamonea	>300	ov	0.40-0.45	alv	u	75	Smooth at lateral sides	
		<i>M. cf. loreyoides</i>	Amblyarthena	50-100	ov	0.55-0.80	alv	u	75		
		<i>M. oinochrophylla</i>	Hartigia	100-200	ov-br ov	0.30-0.40	alv	u	55		
		<i>M. cf. quintuplinerva</i>	Amblyarthena	50-100	ov-pyr	0.60-0.75	alv	u	60		
		<i>M. reducens</i>	Tamonea	200-300	ov-ell	0.55-0.70	alv	u	65		
BENTHAMIANA-type av. l = 0.38 SD = 0.028	<i>M. benthamiana</i>	Octomeris	>300	ov	0.30-0.40	pap-alv	u	60			
	<i>M. porphyrotricha</i>	Octomeris	>300	ov	0.35-0.40	pap-alv	u	95			

Table 2. Continued

Supertype	Type	Species	Section	No. seeds/ berry	Shape	Length range	Testa struct.	Anticl. curv.	Length of raphal part (%)	Remarks
LACERA-type	av. 1=0.53 SD=0.13	<i>M. aspergillaris</i> *	Amblyarrhena	50-100	ov	0.40-0.50	sm	—	50-75	
		<i>M. lacera</i>	Hartigia	100-200	ov	0.40-0.50	sm-alv	u	60	
		<i>M. megalantha</i>	Octomeris	>300	ov-obov	0.60-0.75	sm-alv	c-u	60	
IV.	TRAILLII-type	<i>M. ampla</i>	Jucunda	50-100	irr ov-ell	1.25-1.50	verr	c	70	Pronounced edge of raphal part
		<i>M. barbinervis</i> *	Miconia	25-50	ov	0.85-1.00	verr	—	50-70	
		<i>M. decurrens</i>	Jucunda	50-100	ov	± 1.00	verr	c	80	
V.	TOMETOSA-type	<i>M. holosericea</i>	Jucunda	25-50	br ov	1.20-1.60	verr	c	80	Raphal part lateral
		<i>M. serrulata</i>	Tamonea	100-200	ov	0.50-0.75	irr verr	u	75	Hilum pronounced
		<i>M. stelligera</i>	Miconia	± 100	ov	0.70-0.90	verr	c	80	
		<i>M. cf. traillii</i>	Tamonea	50-100	ov	0.85-1.15	verr	c	45	
		<i>M. jentaculorum</i>	Cremanium	25-50	ov-ell	1.05-1.30	irr verr	—	65	
		<i>M. symplectocaulos</i>	Octomeris	50-100	pyr	0.80-0.95	irr	u	60	
		<i>M. tomentosa</i>	Adenodesma	50-100	pyr	± 1.00	irr	u	80	Raphal appendage
VI.	MISCELLANEOUS group	<i>M. cf. chlorocarpa</i> *	Glossocentrum	25-50	ov	0.70-0.75	pap	—	75	
		<i>M. crocea</i>	Cremanium	50-100	ov	0.60-0.70	± sm	u	10	
		<i>M. insueta</i>	Cremanium	50-100	irr ov	0.70-0.90	± sm	s	50-100	
		<i>M. micropetalata</i> *	Cremanium	25-50	narr ov-ell	0.90-1.05	irr?	—	80	
		<i>M. minutiflora</i>	Glossocentrum	<25	irr pyr-hemisph	0.80-1.00	± sm	u	60-80	
		<i>M. nervosa</i>	Miconia	>100	narr pyr **	0.65-0.75	± sm	c	85	Bladdery elaiosome (Byrne & Levey 1993), not seen
		<i>M. radula</i> *	Amblyarrhena	50-100	irr ov	0.55-0.80	sm	—	75	Cells in longitudinal rows
		<i>M. rigens</i>	Cremanium	50-100	irr ov	0.80-0.95	sm	u	50-90	
		<i>M. salicifolia</i>	Chaenopleura	—	ov	0.50-0.80	sm	u	50	
		<i>M. simplex</i>	Tamonea	± 100	pyr	1.05-1.30	irr	u	100	Pronounced edge of raphal part
		<i>M. smithii</i>	Miconia	<25	irr br ov-br ell	1.70-2.10	sm	—	40-85	

av. 1 = average length (mm); SD = standard deviation. Shape: ell = ellipsoid, ov = ovoid, pyr = pyramidate. Seed length in mm. Testa structure: sm = smooth, pap = papillate, alv = alveolate, verr = verrucose, Anticlinal wall curvature of testa cells: s = straight, c = curved, u = undulated. Length of raphal part in % of total seed length. * = not examined by SEM. ** = appendage disregarded.

more or less elongated. Periclinal walls straight. Anticlinal walls undulated (S-type), flat. Cuticula smooth. Five species were investigated.

4. '*Ternatifolia*' type (Fig. 2e, f)

Berry contains less than 25 seeds. Seeds broadly ovoid to broadly pyramidate, sometimes cyathiform (cup-shaped). The species' mean seed lengths range from 1600 μm to 1900 μm (seeds can be broad rather than long). Raphal part lateral, large (90–95% of total length and width), distinctly sunken, circumfered by a ridge, giving the seed a cup-like appearance (not in *M. spenmerostachya*). Testa smooth. Cell pattern irregular. Cells isodiametric or more or less elongated. Periclinal walls straight to slightly shallow. Anticlinal walls undulated (S-type), boundaries slightly sunken. Cuticula smooth. Three species were investigated.

Supertype II: seeds with papillae consisting of one testa cell each (types 5–7)

5. '*Chionophila*' type (Fig. 3a, b, d)

Berry contains 25 to 100 seeds. Seeds ovoid to broadly ovoid. The species' mean seed lengths range from 550 μm to 1000 μm . Raphal part straight, subhilar, length occupying 45–85% of total (up to 100% in *M. latifolia*). Testa papillate. Cell pattern irregular. Each papilla formed by one, mostly isodiametric cell. Periclinal walls of the testal part always convex. Anticlinal walls undulated (S- to Ω -type), boundaries sunken. Cuticula smooth. Eleven species were investigated.

6. '*Mesmeana*' type (Fig. 3c, e)

Berry contains 25–100 seeds. Seeds ovoid to broadly ovoid. The species' mean seed lengths range from 680 μm to 1100 μm . Raphal part straight, subhilar, length occupying 45–80% of total. Testa papillate. Cell pattern irregular. Each papilla formed by one, mostly isodiametric cell. Periclinal walls locally convex, locally pyramidate to ledge-shaped. Anticlinal walls straight, boundaries sunken. Cuticula smooth. Three species were investigated, one of which divided into two subspecies.

7. '*Centrodesma*' type (Fig. 3f, g)

Berry contains from 50 to more than 100 seeds. Seeds with a chalazal appendage. Shape narrowly pyramidate or narrowly ovoid to ovoid (appendage disregarded). In some species, the appendage makes the general appearance of the seed more or less cuneate (*M. centrodesma*, *M. rupticalyx*). The species' mean seed lengths range from 400 μm to 700 μm . Raphal part straight, subhilar, length occupying 40–85% of total. Testa papillate, but in some species variable within one seed; locally alveolate (*M. lateriflora*) or smooth (*M. nervosa*). Cell pattern irregular or cells in rows. Cells isodiametric to more or less elongated, clearly elongated in *M. rupticalyx*. Periclinal walls mostly convex (locally ledge shaped in *M. centrodesma*) or straight. Anticlinals undulated (S-type to Ω -type), boundaries sunken. Cuticula smooth or striate. Four species were investigated.

Supertype III: seeds with alveolate testae (types 8–10)

8. '*Reducens*' type (Fig. 4a–g)

Berry contains 50 to more than 300 seeds. Seeds ovoid to broadly ovoid. The species' mean seed lengths range from 350 μm to 1200 μm . Raphal part straight to more or less

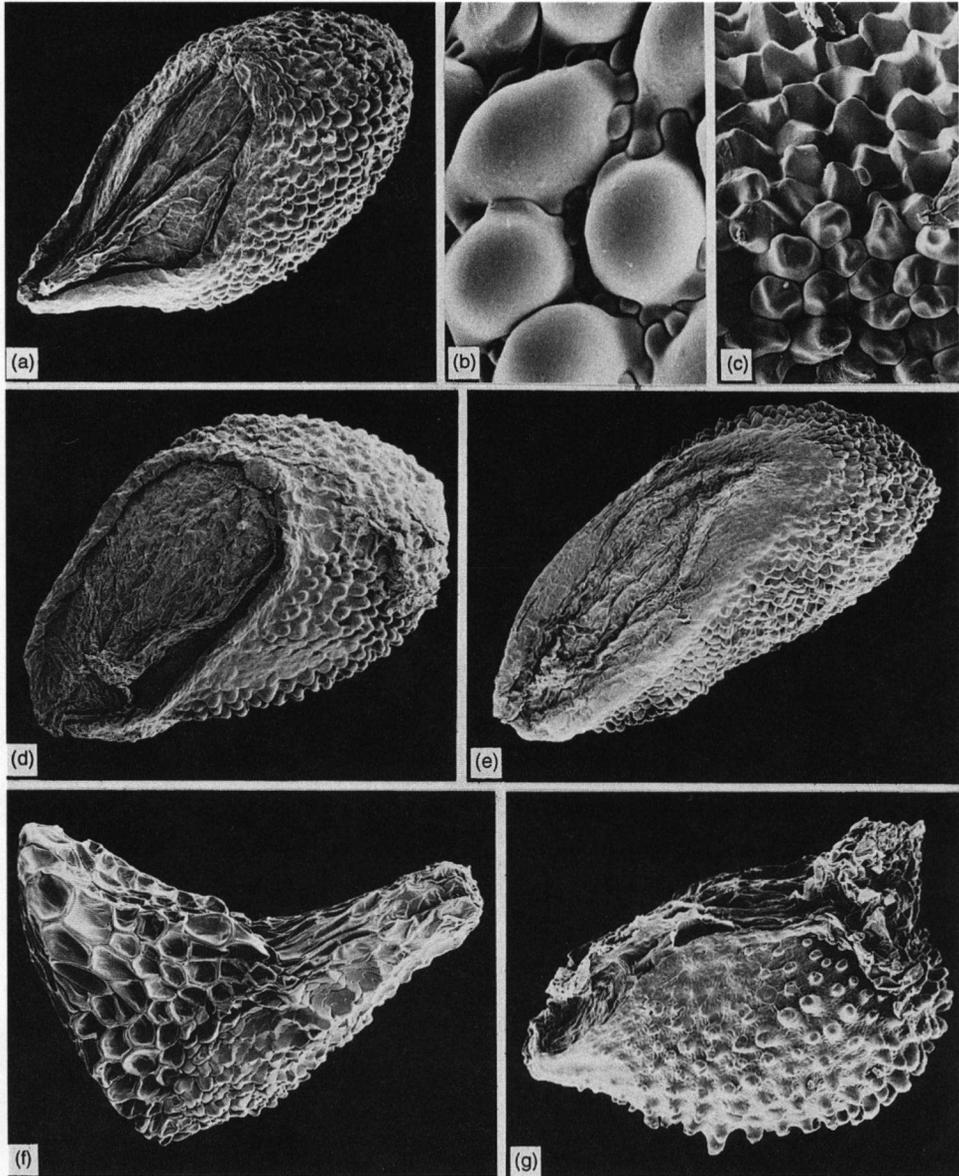


Fig. 3. (a, b, d): 'Chionophila'-type; (c, e): 'mesmeana'-type; (f, g): 'centrodesma'-type. (a): *M. chionophila*, × 55. (b): *M. chionophila*, detail of testa with papillae, × 520. (c): *M. mesmeana* ssp. *jabonensis*, detail of testa with ledge-shaped papillae, × 165. (d): *M. latifolia*, × 75. (e): *M. mesmeana* ssp. *jabonensis*, × 55. (f): *M. centrodesma*, with large eliosome, × 100. (g): *M. pseudocapsularis*, × 145.

convex, subhilar, length occupying 50–85% of total. Testa alveolate at antiraphal side, with irregular relief at lateral sides. Cell pattern irregular. Cells isodiametric or more or less elongated. Periclinal walls following cell pattern of the pericarp. Anticlinal walls undulated (S-type), boundaries sunken. Cuticula irregularly striate (in some species only near anticlinal boundaries of testa cells) or smooth. Seven species were investigated.

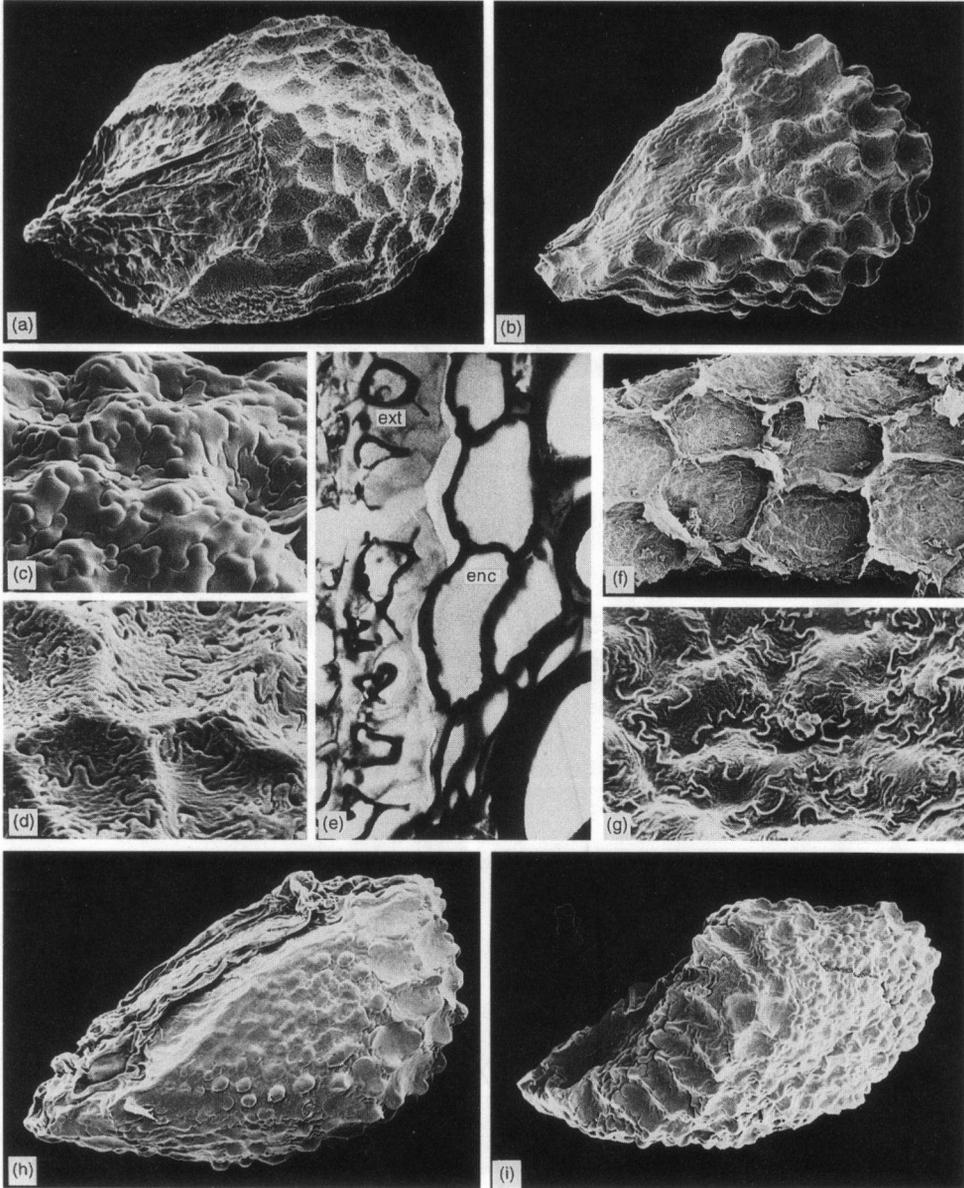


Fig. 4. (a–g): ‘*Reducens*’-type; (h, i): ‘*benthamiana*’-type. (a): *M. oinochrophylla*, $\times 180$. (b): *M. reducens*, $\times 90$. (c): *M. aponeura*, detail of testa with impressions, $\times 260$. (d): *M. oinochrophylla*, detail of testa with impressions, $\times 685$. (e): light-microscope picture of *M. cf. loreyoides*, illustrating impressions of endocarp (enc) into exotesta (ext), $\times 390$. (f): inner side of endocarp of *M. oinochrophylla*, $\times 65$. (g): detail of inner side of endocarp of *M. oinochrophylla*, $\times 470$. (h): *M. porphyrotricha*, $\times 180$. (i): *M. benthamiana*, $\times 175$.

9. ‘*Benthamiana*’ type, intermediate between types 5 and 8 (Fig. 4h, i)

Berry contains more than 300 seeds. Seeds ovoid. The species’ mean seed lengths range are $\pm 350 \mu\text{m}$. Raphal part straight, 60–95% of total length. Testa papillate and locally alveolate (at antihilar side in *M. porphyrotricha*, at hilar side in *M. benthamiana*). Papillae developed at places without impressions; mostly lateral and between dints. Cell

pattern irregular. Cells isodiametric to more or less elongated. Periclinal walls locally following patterns of cells responsible for impressions, locally convex (papillae). Anticlinal walls undulated (mostly Ω -type), boundaries sunken. Cuticula smooth. Two species were investigated.

10. 'Lacera' type (Fig. 5a, b)

Berry contains 50 to more than 300 seeds. Seeds ovoid, with raphal appendage at hilar side. The species' mean seed lengths range from 450 μm to 680 μm . Raphal part swollen, subhilar to hilar, length 50–75% of total. Testa alveolate at antiraphal side, smooth at the lateral sides. Cell pattern irregular. Cells more or less elongated. Periclinal walls straight. Anticlinal walls undulated (S-type), boundaries flat or sunken and then locally flat. Cuticula smooth or almost smooth. Three species were investigated.

Supertype IV: seeds with verrucose testae (type 11 only)

11. 'Traillii' type (Fig. 5c–e)

Berry contains 25–200 seeds. Seeds ovoid to broadly ovoid. The species' mean seed lengths range from 630 μm to 1400 μm . Raphal part straight, subhilar to lateral, length 45–80% of total. Testa verrucose. Cell pattern irregular. 'Warts' consisting of several cells. Cells isodiametric to more or less elongated. Periclinal walls straight or almost straight. Anticlinal walls irregularly curved, boundaries flat or sunken. Cuticula smooth. Seven species were investigated.

Supertype V: pyramidate, coarsely shaped seeds (type 12 only)

12. 'Tomentosa' type (Fig. 5f, g)

Berry contains 50–100 seeds. Seeds pyramidate, coarsely shaped, with distinct facets. Sides are clearly formed by contact with pericarp and neighbouring testae and raphal parts. The species' mean seed lengths range from 880 μm to 1000 μm . Raphal part convex, lateral, with appendage in *M. tomentosa*. Length of raphal part 60–80% of total. Testa with irregular, coarse relief. In *M. tomentosa*, the antiraphal side locally has imprints from the raphal appendage cells of the neighbouring seed. Cell pattern irregular. Cells isodiametric to more or less elongated. Periclinal walls convex. Anticlinal walls undulated, boundaries sunken. Cuticula smooth. Two species were investigated.

Supertype VI: miscellaneous group

13. Miscellaneous group

Seeds not resembling seeds of types 1–12. In Fig. 2d, a SEM picture of a *M. smithii* seed is shown. Eleven species were investigated.

DISCUSSION

The variation in seed morphology within the genus *Miconia* is very wide. We defined 12 major types of seeds, but not all seeds could be assigned to these types. Of 1000 described species we only examined 75. Further studies on seeds of other species of *Miconia* might result in more types than described in this paper, but also in a more solid circumscription of the types. More insight is also needed in intraspecific variation. We have found intraspecific variation in shape (especially *M. rigens*, within one individual),

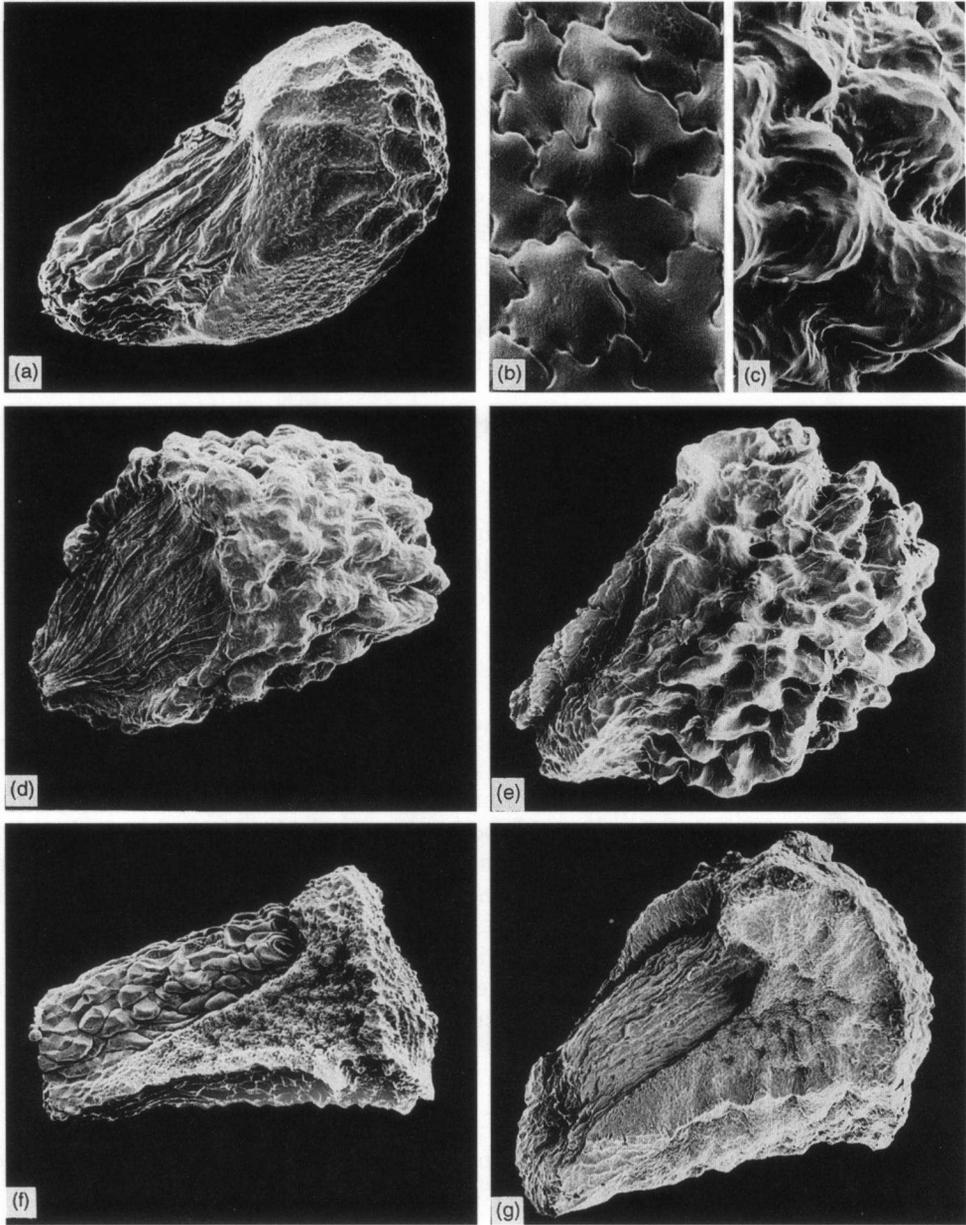


Fig. 5. (a, b): 'Lacera'-type; (c–e): 'trailii'-type; (f, g): 'tomentosa'-type. (a): *M. lacera*, $\times 150$. (b): *M. lacera*, detail of testa, $\times 930$. (c): *M. trailii*, detail of verrucose testa, $\times 120$. (d): *M. trailii*, $\times 55$. (e): *M. stelligera*, $\times 80$. (f): *M. tomentosa*, with raphal appendage, $\times 50$. (g): *M. symplectocaulos*, $\times 75$.

seed size (*M. buxifolia*) and size of arilloid appendages (in *M. affinis*, presence of a bladderly appendage is mentioned by Byrne & Levey (1993), but not seen in our study).

Testa sculpture is likely to be a result of competition between testa and carpel cell growth and development (see also Whiffin & Tomb 1972). We suppose that antiraphal alveolate testae are the result of impressions of carpel cells, as shown in Fig. 4e.

Interaction in testal cell development between neighbouring seeds could cause the impressions and flattenings in testal surfaces at the lateral sides. Intermediates between seeds of '*chionophila*' type and '*reducens*' type support this hypothesis; development of testal papillae is locally suppressed by turgorescent carpel cells. This might be an indication of phylogenetic relationship between species of '*chionophila*' and '*reducens*' type.

Taxonomic implications

The wide variation in seed morphology, as shown in this paper, might indicate a large flexibility of characters. This hypothesis is supported by the fact that species of *Miconia* have radiated into a polymorphic group with often several species coexisting in the same habitat. It should be kept in mind, however, that this genus is very large, and probably has a long evolutionary history. The taxonomic status of the taxon is also unclear. The genus is poorly characterized and delimited, and some sections are thought to be related to extrageneric groups (Judd 1986, 1989).

Some character states found in *Miconia* seeds are also found in seeds of related genera. *Clidemia*, *Leandra*, *Loreya*, *Macairea*, *Myriaspora* and *Pleiotrichon* have species with papillate seeds (Wijninga 1996), alveolation (resembling that of seeds of *Miconia reducens*) is found in species of *Bellucia* (Renner 1989b). In general, variation in seed morphology of *Miconia* largely overlaps with variation found in the tribe *Miconieae* as a whole.

We have found some distinct types of seeds. The types '*buxifolia*', '*ternatifolia*' and '*chionophila*' are the best examples of types with small ranges of character states. Seeds of these groups are resembling in shape, size, position and length of the raphe part and testal sculpture. This is obviously of considerable value for classification of species.

Thirty-one of the collected species appeared to be placed in sect. *Cremanium*, 10 species are placed in sect. *Miconia*. From other sections less than 10 species were studied. If we compare seed types versus sectional division (see Table 2), it becomes clear that only two small types are completely homogenous considering section representatives: type '*mesmeana*' has members of sect. *Cremanium* only, the intermediate type '*benthamiana*' has its two only members placed in sect. *Octomeris*. Types '*buxifolia*' and '*chionophila*' are dominated by sect. *Cremanium*, type '*affinis*' is dominated by sect. *Miconia*, and type '*reducens*' by sect. *Tamonea*. All members (three species) of sect. *Jucunda* are placed in the '*traillii*'-type. The two examined species of sect. *Laceraria* both were placed in type '*centrodesma*'.

Papillae are found mostly in sections *Cremanium* and *Chaenopleura*. Sect. *Chaenopleura* is regarded as a modern group within the genus *Miconia* and sect. *Cremanium* has phylogenetic relations with sect. *Chaenopleura* (Wurdack, personal communication). Therefore, possession of papillae might be a derived character within the genus. Sect. *Tamonea* is considered primitive on morphological characters (Solt & Wurdack 1980).

Little is known of the evolutionary history of the genus *Miconia*. It is reasonable to assume that the uplift of the Andes has had a great impact; montane biotas (higher than 3000 m alt.) have developed from the Middle-Miocene (17–12 Ma BP) until the end of the Tertiary (± 3 Ma BP) (Kroonenberg *et al.* 1990), presumably within the development time range of *Miconia*. The modern sections *Chaenopleura* and *Cremanium* occur largely at high altitudes, while the primitive section *Tamonea* lives at low altitudes (Fig. 6). Apparently, the species number of the genus was able to grow due to the formation of the Andes.

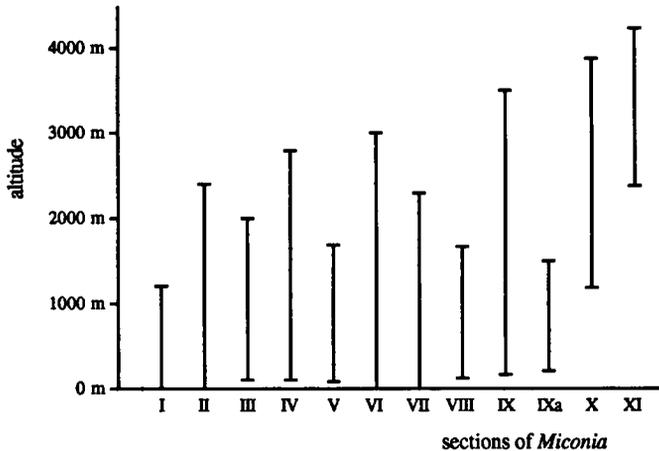


Fig. 6. Altitudinal ranges of sections of *Miconia*. Numbers of sections conform to Table 1. Data from Wurdack (1973; 1980).

The types defined in this paper do not match with the current sectional division of the genus. The results presented in this paper demonstrate the necessity of a thorough study on seed (micro)morphology of *Miconia*, since that can be of great help—together with the study of other characters—in solving the uncertainties concerning the taxonomy of this genus.

Ecological implications: seed dispersal

Seeds of *Miconia* species primarily are dispersed by vertebrates. Birds are the most common dispersers of seeds, but occasionally mammals and reptiles also transport *Miconia* seeds. Seeds are dropped with the faeces (e.g. Snow & Snow 1971; Levey 1990; Blake & Loiselle 1992; Stiles & Rosselli 1993).

Post-dispersal survival of seeds is considered to be very important for establishment and competitive power of seedlings (Loiselle 1990). Variation in morphology of endozoochorously dispersed seeds indicates selective pressure on structures important to post-dispersal survival within species of *Miconia*.

Seeds of some of the species studied in this paper are likely to be dispersed by ants after having been dropped by birds. Collection of seeds of *M. centrodesma*, *M. affinis* and *M. nervosa* by ants is reported by Byrne & Levey (1993). Also Kaspari (1993) has observed ants taking away seeds of *M. affinis*. SEM-examination showed the firm appendage of *M. centrodesma* (Fig. 3f). A relative of this species, *M. rupticalyx*, appeared to have the same kind of appendage. Appendages with the same type of large, collapsed, polygonal cells (which, therefore, might be elaiosomes too) were also found in *M. lacera*, *M. megalantha* and *M. lateriflora*. We hypothesize that the seeds of these species have a large chance of being post-dispersed by ants. Like Levey (1988), we suggest that for these species dispersal is 'fine-tuned' to favourable microsites by myrmecochory.

Two species, *M. ternatifolia* and *M. solmsii*, have seeds which have the ability to float on water due to their cup-shape. In a floating experiment, seeds of these species floated with the hollow side downwards, thus keeping air in the 'cup'. The importance of rain-wash for seed dispersal in humid tropical forests has been mentioned before by

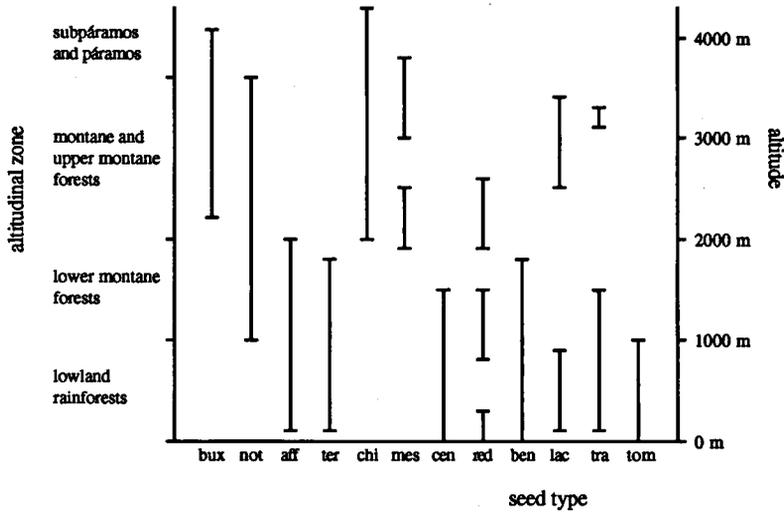


Fig. 7. Altitudinal ranges of seed types. Data of elevation derived from herbarium sheet labels, and from Wurdack (1973; 1980) and Uribe Uribe (1972).

Bouman & Deventer (1986). This mechanism of dispersal might also play a role for *M. ternatifolia* and *M. solmsii*, but we lack habitat data of these species to confirm this. Hydrochloric dispersal has also been suggested for cup-shaped seeds of several taxa of Cactaceae by Bregman (1988).

We suppose other morphological characteristics of the seeds (seed size and shape and testa relief) to have a considerable influence on their post-dispersal fate. The possession of papillae for example must be of benefit for either protection, dispersal or establishment of the seed. However, until fieldwork is done, the presence of papillae and alveolation, and shape and size of seeds will largely be of interest for taxonomists.

Ecological implications: habitat characteristics

Restriction to certain altitudinal zones is found in some of the seed types. Figure 7 gives altitudinal ranges of the specimen vouchers for each seed type. Types '*buxifolia*', '*chionophila*' and '*mesmeana*' (10, 11 and three species sampled, respectively) clearly are types found at elevations above 2000 m; from montane forests to páramos. The '*notabilis*' type has most species (five out of six) living in lower to upper montane forests, with only *M. biappendiculata* growing above the upper forest line. Types '*affinis*', '*ternatifolia*', '*centrodesma*' and '*benthamiana*' (five, three, four and two species sampled, respectively) represent species groups of lower montane forests and lowland rain forests.

Explanations of these results in ecological terms are hard to give. Seed types may, in some cases, be restricted to certain altitudinal belts, but characters like papillate testae are not. Also, sizes of seeds in this genus do not seem to be correlated with elevation. Phylogenetic restriction might have had a greater impact on evolution of seeds of *Miconia*.

We compared the annual precipitation ranges of the species' habitats (put together in an interval for each seed type) with our seed types (Fig. 8). A clear overlap is present; all seed types have species living in habitats with 2–3 m of precipitation, except the '*tomentosa*' type, of which the precipitation interval is 3000–4000 mm. Difference seems

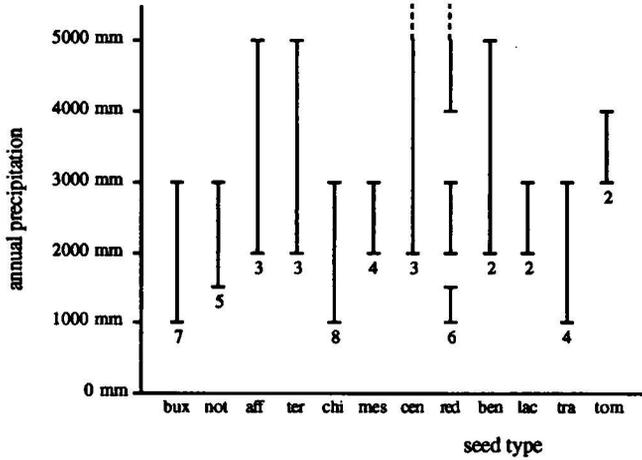


Fig. 8. Intervals of annual precipitation for each seed type. Numbers below the intervals indicate the number of species from which precipitation ranges in their habitats could be determined. Data derived from Latorre (1977), Renner *et al.* (1990) and Tosi (1960).

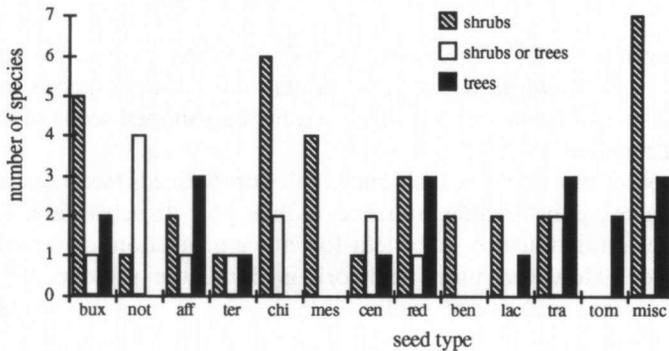


Fig. 9. Numbers of species of shrubs, shrubs or trees and trees for each seed type. None of the seed types has a shrub/tree species ratio significantly different from that of another type (*G*-tests, adjusted to a significance level of $\alpha=0.000777$ (for series of tests), as suggested by Sokal & Rohlf (1981)).

to exist between types ‘*affinis*’, ‘*ternatifolia*’, ‘*centrodesma*’ and ‘*benthamiana*’ on one side, and types ‘*buxifolia*’ and ‘*chionophila*’ on the other side; the first four types represent species groups which also live in wetter habitats, while the latter two mainly contain species living in drier habitats.

A comparison of seed length data by means of the *G*-test showed that seed lengths of tree species and shrub species do not differ significantly. If the significance level would not be adapted for series of *G*-tests (Sokal & Rohlf 1981), i.e. when the comparisons are made separately, significant differences are found between the types ‘*tomentosa*’ and ‘*benthamiana*’, ‘*tomentosa*’ and ‘*chionophila*’ ($P < 0.05$) and between ‘*tomentosa*’ and ‘*meseana*’ ($P < 0.01$). In Fig. 9, numbers of species for each growth form are shown for each seed type. The predominantly montane seed types ‘*buxifolia*’, ‘*chionophila*’ and ‘*meseana*’ are mostly found in shrubby species, and species growing either as shrubs or as trees. No seed types appear to be typical of species only growing as trees.

Concluding remarks

In this paper, we have shown a wide variety in seed morphology of *Miconia*. The micromorphology of seeds supports the idea that the current sectional division and delimitation of *Miconia* does not reflect phylogenetic relationships. The different seed types defined in this paper can very well be of importance for phylogenetic analysis. For a complete set of seed micromorphological data, more studies on this topic are necessary. This study is meant to serve as a pilot to a thorough investigation of seed morphology of *Miconia* and its relatives.

The ecological implications given above should be tested by fieldwork.

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APPENDIX I: LIST OF EXAMINED SPECIES WITH SECTIONAL DIVISION

<i>Sections with species examined</i>	<i>Country; specimen collector, herbarium</i>
I. JUCUNDA	
<i>Miconia ampla</i> Triana	Jamaica; Proctor 11345, U
<i>M. decurrens</i> Cogn.	Venezuela; Huber & Colchester 8422, U
<i>M. holosericea</i> (L.) DC.	Venezuela; Steyermark 104097, U
II. TAMONEA	
<i>M. acutifolia</i> Ule	Venezuela; Holst 3644, U
<i>M. aponeura</i> Triana	Colombia; Idrobo & Schultes 1301, U
<i>M. caudata</i> (Bonpl.) DC.	Colombia; Uribe Uribe 2800, U
<i>M. reducens</i> Triana	Colombia; Alston 4896, U
<i>M. serrulata</i> (DC.) Naud.	Venezuela; Breteler 3789, U
<i>M. simplex</i> Triana	Panama; de Nevers <i>et al.</i> 3474, U
<i>M. cf. traillii</i> Cogn.	Venezuela; Liesner 25740, U
III. ADENODESMA	
<i>M. silicicola</i> Gleason	Venezuela; Steyermark 109291, U
<i>M. tomentosa</i> (L. C. Rich.) D. Don ex DC.	Colombia; Schultes 12673, U
IV. OCTOMERIS	
<i>M. benthamiana</i> Triana	Ecuador; Øllgaard <i>et al.</i> 34744, U
<i>M. megalantha</i> Gleason	Colombia; Lawrence 456, U
<i>M. notabilis</i> Triana	Colombia; Wijninga 477, U
<i>M. porphyrotricha</i> (Markgraf) Wurdack	Ecuador; Holguer Lugo 1870, U
V. LACERARIA	
<i>M. centrodesma</i> Naud.	Colombia; Maas 1985, U
<i>M. rupticalyx</i> Wurdack	Bolivia; Solomon 9555, U
VI. MICONIA	
<i>M. affinis</i> DC.	Venezuela; Breteler 3794, U
<i>M. appendiculata</i> Triana	Ecuador; Berg & Akkermans 1025, U
<i>M. barbinervis</i> (Benth.) Triana	Peru; Croat 18811, U
<i>M. lateriflora</i> Cogn.	Colombia; Callejas 2407, U
<i>M. nervosa</i> (Smith) Triana	Peru; Schunke 9996, U
<i>M. pseudocapsularis</i> Wurdack	Venezuela; Liesner & Holst 21522, U
<i>M. smithii</i> Cogn. ex Gleason	Colombia; Jaramillo 5302, 5344, U
<i>M. spennerostachya</i> Naud.	Bolivia; Solomon 14797, U
<i>M. splendens</i> (Sw.) Griseb.	Peru; Plowman & Schunke 11483, U
<i>M. stelligera</i> Cogn.	Peru; Belshaw 3510, U
<i>M. stenostachya</i> DC.	Bolivia; Solomon 8875, U
VII. GLOSSOCENTRUM	
<i>M. cf. chlorocarpa</i> Cogn.	Colombia; Luteyn 12945, US
<i>M. minutiflora</i> DC.	Colombia; Callejas 2312, U
<i>M. ternatifolia</i> Triana	Colombia; Vogelmann <i>et al.</i> 1271, U
VIII. CHAENANTHERA	
<i>M. nitidissima</i> Cogn.	Venezuela; Steyermark 56593, US
<i>M. solmsii</i> Cogn.	Venezuela; Steyermark 104627, U
IX. AMBLYARRHENA	
<i>M. aspergillaris</i> Naud.	Ecuador; Harling <i>et al.</i> 8288, US
	Ecuador; Hutchinson & K. Wright 6643, US
<i>M. cf. lasiocalyx</i> Cogn.	Ecuador; Øllgaard 35855, U

APPENDIX I: *Continued**Sections with species examined**Country; specimen collector, herbarium*

<i>M. cf. loreyoides</i> Triana	Colombia; León 1586, U
<i>M. cf. quintuplinerva</i> Cogn.	Colombia; Juncosa & Misas 1008, U
<i>M. radula</i> Cogn.	Peru; Boeke 2038, US
<i>M. ulmarioides</i> Naud.	Venezuela; Barclay & Juajibioy 10287, US
IXa. HARTIGIA	
<i>M. lacera</i> Naud.	Colombia; Uribe Uribe 2919, U
<i>M. oinochrophylla</i> Donn. Sm.	Colombia; Callejas 2342, U
X. CREMANIUM	
<i>M. biappendiculata</i> (Naud.) Uribe	Colombia; Cleef 7387, U
<i>M. cf. bracteolata</i> DC.	Colombia; Cuatrecasas 11871, U
<i>M. buxifolia</i> Naud.	Colombia; Cleef 9164, U
	Colombia; U. Uribe & Jaramillo 2667, U
	Colombia; Cuatrecasas <i>et al.</i> 12631, US
<i>M. chrysocoma</i> Gleason	Colombia; Cuatrecasas 12251, U
<i>M. cleefii</i> Uribe	Colombia; Cleef 7880, U
<i>M. crocea</i> Naud.	Ecuador; Hekker & Hekking 10357, U
<i>M. cundinamarcensis</i> Wurdack	Colombia; Orozia 2665, US
<i>M. elaeoides</i> Naud.	Colombia; Rangel & Aguirre 409, U
<i>M. elvira</i> Wurdack	Venezuela; Wurdack 2767, US
<i>M. insueta</i> Wurdack	Colombia; Jaramillo 5443, U
<i>M. jentaculorum</i> Wurdack	Colombia; Cuatrecasas & G. Boerriga 9925, US
<i>M. lehmannii</i> Cogn.	Colombia; Uribe Uribe 2801, U
<i>M. ligustrina</i> (Smith) Triana	Ecuador; Brandbyge 42118, U
<i>M. limitaris</i> Wurdack	Venezuela; Tillett 747, US
<i>M. media</i> Naud.	
ssp. <i>borealis</i> Wurdack	Peru; Wurdack 1438, US
<i>M. mesmeana</i> Gleason	
ssp. <i>jabonensis</i> Wurdack	Colombia; Cleef 10113, U
ssp. <i>longepetiolata</i> Wurdack	Venezuela; Wessels Boer 1716, U
<i>M. micropetala</i> Cogn.	Peru; Smith 2763, US
<i>M. cf. ochracea</i> Triana	Colombia; Beukema 19, US
<i>M. oreogena</i> Wurdack	Colombia; Krikbride & Forero 1769, US
<i>M. parvifolia</i> Cogn.	Colombia; Cleef 6953, U
<i>M. cf. polyneura</i> Triana	Colombia; Ellenberg 988, US
<i>M. cf. puracensis</i> Wurdack	Colombia; Cleef 480, U
<i>M. rigens</i> Naud.	Colombia; Cleef 9759, U
<i>M. squamulosa</i> Triana	Colombia; Cleef 2747, U
<i>M. summa</i> Cuatrec.	Colombia; Phillip 34140, US
<i>M. symplectocaulos</i> Pilg.	Peru; Smith <i>et al.</i> 647, U
<i>M. theaezans</i> Cogn.	Bolivia; Solomon 8623, U
<i>M. tinifolia</i> Naud.	Colombia; Cuatrecasas 2015, US
<i>M. tricaudata</i> Wurdack	Colombia; Rangel & Cleef 953, US
<i>M. verrucosa</i> Cogn.	Colombia; Barclay & Juajibioy 10429, US
XI. CHAENOPLEURA	
<i>M. chionophila</i> Naud.	Colombia; Cleef 3128, U
<i>M. latifolia</i> Naud.	Colombia; Cleef 9619, U
	Venezuela; Luteyn 6133, U
<i>M. rotundifolia</i> Naud.	Peru; Sagastegui 7478, Wurdack 1199, US
<i>M. salicifolia</i> Naud.	Colombia; Breteler 4461, U