Short Communication

A morphometric study of early Miocene *Mauritiidites* from Northern South America

Palaeoecological and evolutionary implications

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Palaeo-biogeographical knowledge of the monosulcate Tertiary form-genus *Mauritiidites* can be useful to study important palaeoecological and evolutionary questions in the Neotropical lowlands. However, the lack of taxonomic differentiation within this fossil pollen genus is a handicap, and a broad morphological and morphometric study, both in space and time, is needed to establish a consistent *Mauritiidites* taxonomy. This note shows a morphometric characterisation of early Miocene *Mauritiidites* from western Venezuela, as a first step. Morphologically, the specimens studied are consistent with the description of *Mauritiidites franciscoi* (van der Hammen) van der Hammen & García de Mutis 1966. Light microscope measurements show little variability in most of the parameters, except for the aperture width. However, this is considered part of the natural variability within a single pollen type, which is commonly found in the pollen of several modern palm genera and species. As a result, a single morphological and morphometric pollen type is proposed for the specimens studied. Future studies should characterise more *Mauritiidites* specimens from other regions and time slices, to found taxonomically-meaning differences.

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The form-genus *Mauritiidites* van Hoeken-Klinkenberg 1964 is characteristic for the Tertiary of northern South America, where it has been recorded since the Paleocene (Muller 1981). Since that time, its parent pant had been widespread in the region, but its geographical range was notably reduced and fragmented by the Oligo-Miocene Andean orogeny, promoting allopatric speciation and local extinction. During the Quaternary, climate changes related to the glacial/interglacial oscillations drove recurrent expansions and reductions in its aerial distribution, due to the alternation of humid and dry periods in the lowlands (Rull 1998). Based on the presence of the deeply-rooted spines, a unique morphological feature, this pollen type has been considered the fossil equivalent of the extant genera of the palm subfamily Lepidocaryeae: *Mauritia*, *Lepidocaryum* and *Mauritiella* (Muller 1981). Of them, only *Lepidocaryum* has monosulcate pollen, like *Mauritiidites*, while *Mauritia* and *Mauritiella* have monoporate or monoulcerate pollen (Erdtman 1972, Sowunmi 1972, Ferguson 1986, Herrera & Urrego 1996). However, since in the palm pollen, pori and ulci have been interpreted as evolutionary shortened sulci (Sowunmi 1968, Thanikaimoni 1970), it is believed that the parent palm of *Mauritiidites* was an ancestor of the three extant Lepidocaryeae genera. At present, the Lepidocaryeae are almost restricted to wet lowlands of the Orinoco and Amazon basins, except for some representatives in Trinidad and on a narrow fringe along the

Colombian Pacific coasts (Fig. 1). The more characteristic genus (by far, the more extended and abundant) is *Mauritia*, a reliable indicator of warm flooded lowlands (usually below 500 m above sea level), where it develops extensive monotyipical stands along rivers (Rull 1998). Furthermore, it seems to be a successful secondary coloniser of burnt terrains (Rull 1999 *a*). *Lepidocaryum* and *Mauritiella* are similar, but much more restricted. Therefore, using the analogy with present environmental requirements, the study of biogeographical and evolutionary patterns of *Mauritiidites* can contribute to understand important questions, such as for example the debated Pleistocene ecological history of the Amazon plant communities in relation to climate (mainly moisture) and topography (Colinvaux et al. 1999), the assumed Tertiary origin of their diversity (van der Hammen & Hooghiemstra 2000), as well the differentiation of fossil forms into the extant genera (Rull 1998). However, the lack of taxonomic differentiation within *Mauritiidites* prevents this type of studies.

Morphological variation within Neotropical *Mauritiidites* has been noticed but not systematically studied. Its different forms are commonly treated together and included in the generic name (*Mauritiidites* spp), or in the form-species *Mauritiidites franciscoi* (van der Hammen) van der Hammen & Garcia de Mutis (1966). An attempt was done to qualitatively distinguish among three varieties of *Mauritiidites franciscoi* in the Colombian Paleocene (van der Hammen & García

de Mutis 1966), but they have been rarely considered in further literature. In modern pollen taxonomy, it is common to differentiate species and varieties by size and allometric relationships, a poorly developed procedure in fossil pollen and spores, which remains unexplored in the case of *Mauritiidites*. No morphometric studies based on statistically-significant numbers of randomly-distributed specimens are available for this genus. Measures are commonly based on one or few key specimens, so they are poor morphometric descriptors. As a result, a complex of different morphologies and morphometries might be hidden under the names *Mauritiidites* spp and *Mauritiidites franciscoi*. Two reasons for the lack of suitable statistical measurements are bad preservation and insufficient number of grains available in samples. However, this is not the case of *Mauritiidites* which is abundant and widely distributed, both in space and time, in the Tertiary of northern South America.

The present report is a part of a more general project aimed to record the morphometric patterns of *Mauritiidites* in different regions and time slices, in order to found statistical differences with possible taxonomic meaning, and help understanding their phylogenetic and evolutionary relationships (Rull 1998). This short note shows the morphometric characterisation of *Mauritiidites* from the Early Miocene of Venezuela using light microscopy. The establishment of formal taxa needs additional studies, as well as electron microscopy (SEM and TEM) research, and is beyond the scope of this study.

MATERIAL AND METHODS

The specimens for the present study were obtained from core samples of an oil well situated in the Maracaibo basin (Fig. 1). They proceed from the La Rosa and Lagunillas formations (1060 to 1150 m depth), settled in shallow marine and coastal environments, respectively (González de Juana et al. 1980). The age was deduced from the identification of the *Rugutricolporites* and *Psiladiporites-Echitricolporites* pollen zones, which correspond to the Early Miocene (Lorente 1986). Measurements are based on 30 well-preserved specimens, randomly distributed on 16 slides. The basic morphometric parameters considered are illustrated in Fig. 2. Other combinations of these parameters are in Tables I to III.
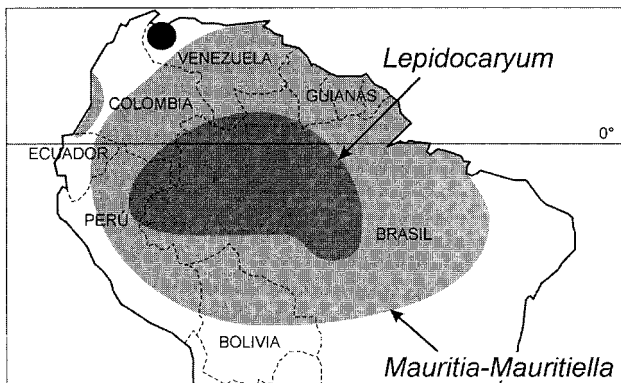

Fig. 1. Map of northern South America, indicating the sampling area (black area), and the geographical distribution of *Mauritia*, *Mauritiella* and *Lepidocaryum*, according to Henderson et al. (1995).

RESULTS

Description

Grains are ellipsoid and monosulcate monads. Apertures are variable in outline, ranging from long (as long as the long axis of the grain) and narrow sulci with sharp apices (Fig. 3 A–C) to slightly shorter and wider with more or less rounded apices (Fig. 3 E, F). A few grains ($<1\%$) show modified sulci, with lateral (equatorial) expansions, and ocassionally (less than 0.5% of the total grains observed) sulci with irregular outline (Fig. 3 G–I). One single grain has an imperfect trichotomosulcate aperture (Fig. 3 J). Porate or ulcerate grains were not observed. The aperture contours are more or less irregular, sometimes involuted, with no margins.
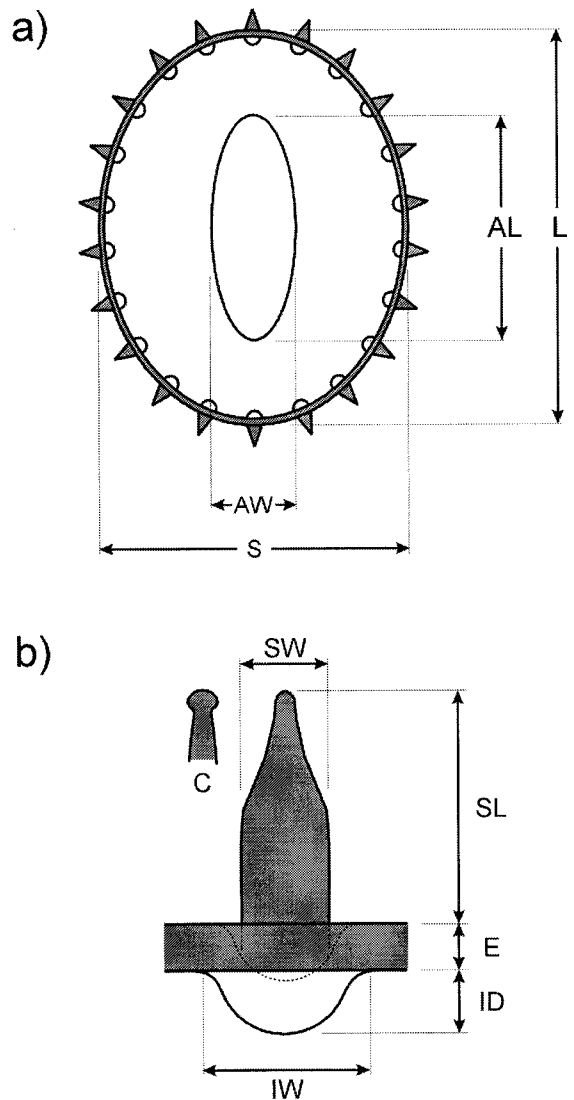

Fig. 2. Schematic representation of a) a pollen grain of *Mauritia*, and b) a magnified spine complex, with the measures considered in the present paper: L – long axis, S – short axis, AL – aperture length, AW – aperture width, SL – spine length, SW – spine width, E – exine thickness, ID -indentation depth (below the exine), IW – indentation width. C represents a capitate spine.
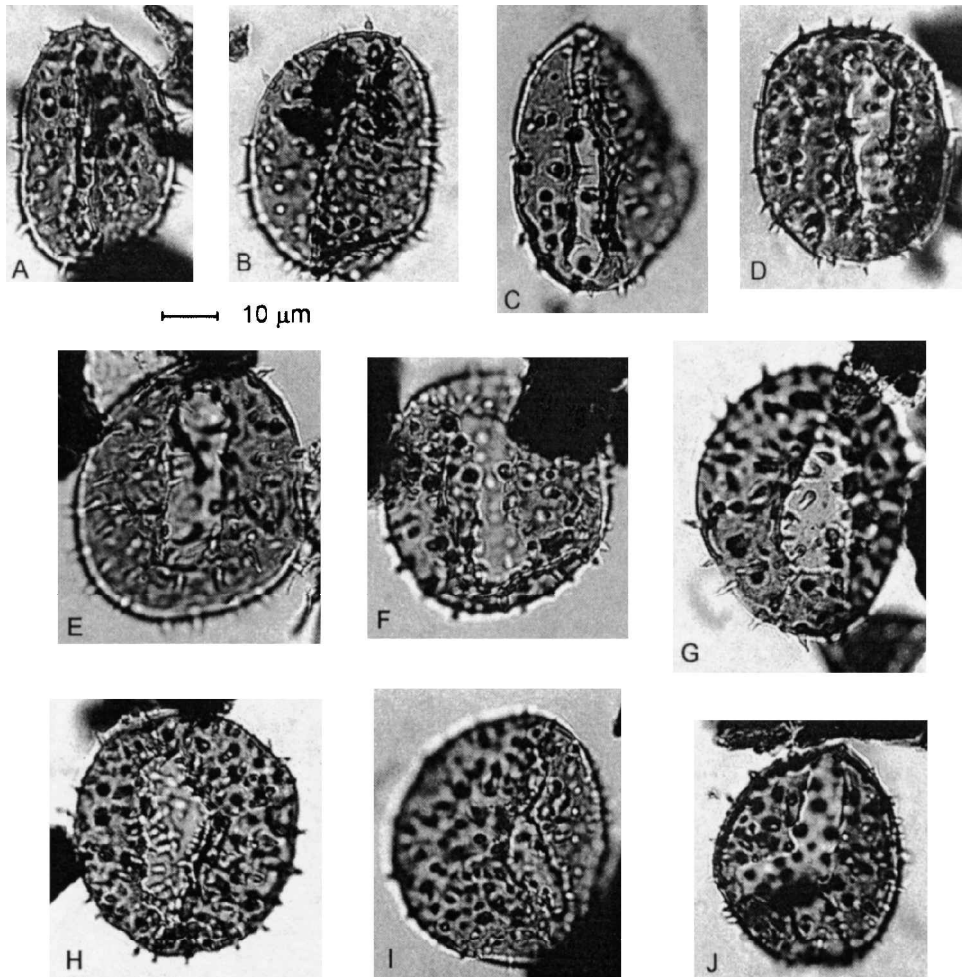
Fig. 3. Examples of morphological features in several *Mauritiidites* specimens from the samples analysed in the present note.

Table I. *Basic statistics for the parameters measured.*

L=long axis, S=short axis, AL=aperture length, AW=aperture width, SL=spine length, SW=spine width, SN=number of spines in perimeter, E=exine thickness, ID=indentation depth, IW=indentation width. Parameters with variation coefficient under 10% in bold.

Parameter	Mean±conf. int. (99%)	Standard deviation	Variation coefficient (%)
L	**44.54±1.36**	**2.71**	**6.08**
S	**34.14±1.68**	**3.35**	**9.80**
AL	31.54±2.58	5.13	16.27
AW	4.43±1.46	2.89	65.39
SL	2.53±0.21	0.41	16.39
SW	**1.59±0.07**	**0.14**	**8.73**
SN	18.27±2.21	4.39	24.01
E	0.88±0.13	0.25	28.85
ID	1.02±0.09	0.19	18.55
IW	2.38±0.13	0.27	11.19

Table II. *Basic statistics of several allometric coefficients, based on the parameters of Table I.*

SL%=relative spine length, as a percentage of the mean pollen grain size (the average of L and S), E%=relative exine thickness, AL%=relative aperture length. Parameters with variation coefficient under 10% in bold.

	Mean	Standard Deviation	Confidence interval (99%)	Variation coefficient (%)
L/S	**1.31±0.06**	**0.12**	**0.06**	**9.32**
AL/AW	12.34±6.24	12.39	6.24	100.48
SL/SW	1.60±0.12	0.25	0.12	15.44
IW/ID	2.41±0.22	0.43	0.22	17.93
SL%	6.46±0.58	1.15	0.58	17.86
E%	2.23±0.31	0.61	0.31	27.36
AL%	80.44±6.98	13.88	6.98	17.25
SL/E	3.13±0.53	1.05	0.53	33.44
SL/ID	2.56±0.28	0.55	0.28	21.68
SW/IW	1.51±0.10	0.21	0.10	13.64

The exine is very thin, usually less than 1 µm. Spines are more or less regularly distributed with variable density. They have swollen bases, and are solid and deeply rooted, determining an indentation of the exine under each of them (Fig. 3). Where spines have been detached, the indentation remains, and a hole is observed in the exine surface (Fig. 3). Spines usually have rounded ends, but some individual

Table III. *Linear correlation coefficients between the variables studied.*
Significant correlations at a level α<0.05 are in bold. See Table I for abbreviations.

	L	S	AL	AW	SL	SW	SN	E	ID
AL	−0.098	0.248							
AW	0.279	0.089	**−0.416**						
SL	−0.119	0.015	0.109	0.233					
SW	−0.109	−0.047	−0.045	0.215	0.361				
SN	0.320	0.252	−0.083	0.258	−0.027	−0.251			
E	0.300	0.188	−0.018	0.282	0.166	0.097	**0.429**		
ID	0.238	0.099	−0.0255	0.020	0.191	−0.143	−0.093	−0.005	
IW	0.148	0.224	−0.013	−0.086	0.283	0.188	0.005	0.215	0.332
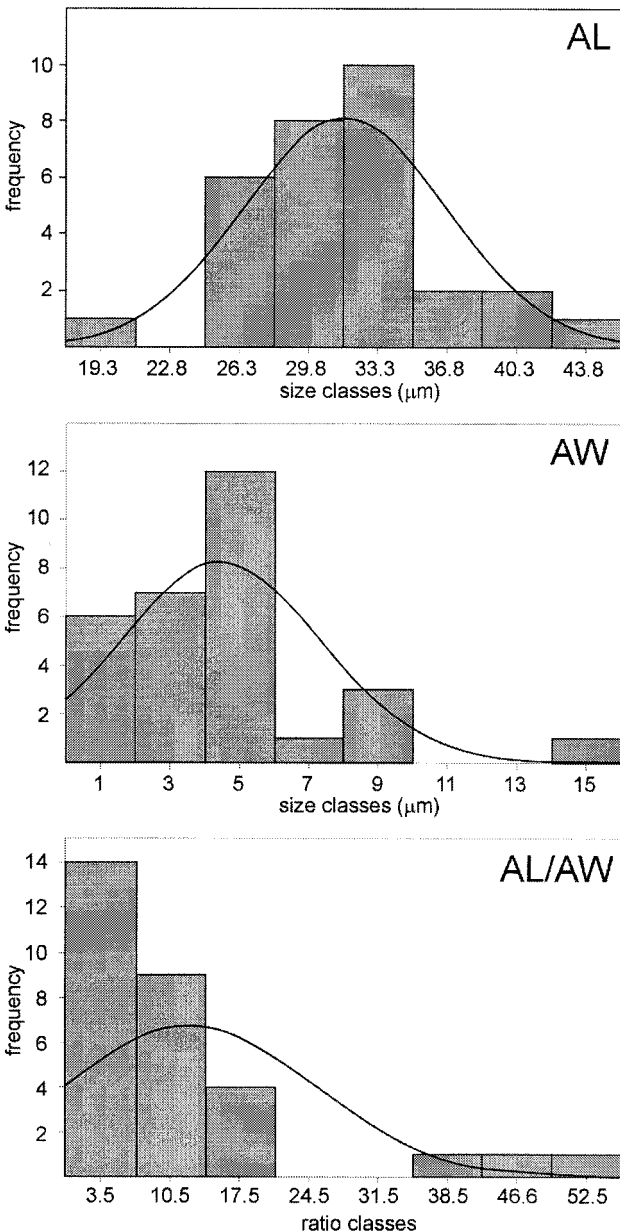
ones may be capitate. A small proportion can be oblique or curved, but they are generally straight (roughly perpendicular to the exine surface). The exine between spines appears more or less psilate.

Morphometry

The statistical descriptors for the parameters measured are shown in Tables I and II. The more constant characters (variation coefficient <10%) are the long grain axis, the short grain axis, and the spine width; whereas the aperture length, the spine length, and the indentation depth and width are below 20%. More variable (>20%) are the number of spines in the outline and the exine thickness. The highest variability is found in the aperture width (>65%), and is reflected in the wide range of aperture morphologies recorded. The aperture length remains fairly constant (var. coef. ∼16%). Concerning the allometric ratios, the more constant is the grain shape (L/S), whereas the more variable coefficient is the aperture shape (var. coef. ∼100%). The spine shape (SL/SW), relative spine length, relative exine width, relative aperture length, indentation shape (IW/ID), and spine/indentation ratio are intermediate. It is also interesting that the only significant correlations are, in the positive side, long grain axis-short grain axis, and exine thickness-number of spines; and, in the negative side, aperture length-aperture width (Table III). This indicates that, whereas grain shape tends to be stable (longer grains are also wider), aperture shape follows and inverse relationship (long colpi are narrower, and short colpi are wider). The positive correlation between exine thickness and number of spines, indicates that the more robust grains (with a thicker exine) have more spines in their perimeters. This is not apparently related to the perimeter length, since there is no significant correlation between exine thickness and long or short grain axis. There is no a clear correspondence between grain shape and aperture shape, as shown by the non-significant correlation (r=0.171); however, some grains with laterally expanded apertures can show concomitant alterations in shape (Fig. 3 H–J).

In the more variable characters, i. e. the aperture dimensions, the possibility of more than one morphometric type was checked through frequency histograms. However, none of them shows multi-modality, and the variation is due to the high dispersion and skewnes along the size classes (Fig. 4).

Fig. 4. Frequency histograms for the aperture length (AL) and width (AW), and the ratio (AL/AW).

DISCUSSION AND CONCLUSIONS

The basic morphological type of the grains described, and their measurements fit well with the holotype of *Mauritiidites franciscoi*, originally described by Van der Hammen (1956) as *Monocolpites franciscoi*, and later emended by Van der Hammen & Garća de Mutis (1966). There are minor variations in both shape and dimensions of apertures. The asymmetric lateral expansions of some sulci, together with the slight modification of the grain outline from ellipsoid to more triangular-like, suggest intermediate forms between monosulcate and trichotomosulcate grains. Although only one grain has been found to have near triangular shape and an imperfect trichotomosulcate aperture, the occurrence of trichotomosulci in *Mauritiidites* has been confirmed in further studies, in the same area (Rull 1999 *b*, 2000). However, in the present state of knowledge, there is no conclusive evidence, and alterations due to compression can not be disregarded.

Most morphological and morphometric parameters are fairly stable, as shown by their narrow confidence intervals (Tables I & II), and point towards the existence of a single basic pollen type. The aperture variations are tentatively interpreted as the consequence of natural variability within the same pollen type. Similar departures from the basic pollen morphology has been observed in several genera of modern palms such as *Cocos, Euterpe, Geonoma, Roscheria, Kentia, Pseudophoenix, Paralinospadix*, and others, in which monosulcate pollen grains coexist with others with laterally-expanded sulci and trichotomosulcate grains (Selling 1947, Nair & Sharma 1963, Sowunmi 1972, Harley 1990, Herrera & Urrego 1996).

In summary, the specimens studied here are considered to belong to a single pollen type, which characterised by the measures and allometric ratios shown in Tables I & II, except for those related with the apertures. Unfortunately, no morphometric studies based on parameters like those reported here and statistically-significant number of specimens of other *Mauritiidites* are available for comparison. Future research should consider this point, in order to help establish taxonomic, phylogenetic and evolutionary relationships.

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